



# Analysis of large-scale spatio-temporal trends of *Ostrea puelchana* beds in Northern Patagonian gulfs, Argentina



M.S. Doldan <sup>a, b, \*, 1</sup>, E.M. Morsan <sup>b, 1</sup>, P.C. Zaidman <sup>a, b</sup>, M.A. Kroeck <sup>b</sup>

<sup>a</sup> Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Rivadavia 1917, C1033AAJ Ciudad Autónoma de Buenos Aires, Argentina

<sup>b</sup> Instituto de Biología Marina y Pesquera “Almirante Storni”, Universidad Nacional del Comahue, Güemes 1030, 8520 San Antonio Oeste, Provincia de Río Negro, Argentina

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## ABSTRACT

Wild oyster populations have declined severely worldwide, however fluctuations of South Atlantic populations are poorly documented. We explored the changes in the abundance of *Ostrea puelchana* population of Northern Patagonia, Argentina, by linking data from paleontological, archaeological and informal sources, with time series data from fishing, ecological and studies of oyster pathology.

The present work is the first study which includes a South Atlantic time series concerning oyster beds. The focal area for this study is the San Matías Gulf (SMG, 40° 50′–42° 15′ S, 63° 5′–65° 10′ W). Populations of *O. puelchana* were inferred from sub-fossil deposits (>700 years ago) throughout the gulf, but were documented in surveys a century ago only in the NW coast.

The population has declined in the last decades. However, new populations have established recently in the NE and southern regions of the gulf.

A *Bonamia exitiosa* epizootic was coincident with the declining trend of the abundance provided by the time series, suggesting that beds declined as a consequence of parasite infections.

Dredging fisheries for scallops took place in the 1970s and 1980s on the NE coast of the gulf, in areas adjacent to the NE oyster beds. We proposed that fishing activities might have had a low impact on oyster beds, since NE beds expanded and increased during that period.

The southward expansion of oyster population at latitudes beyond the historical distribution range might reflect long-term adequate environmental conditions for larval survival on the NE and S of the SMG.

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## 1. Introduction

Wild oyster populations have declined severely worldwide because of overfishing, habitat destruction, or diseases (Beck et al., 2011). For instance, since 1884, commercial harvesting of *Crassostrea virginica* in Chesapeake Bay has declined (Rothschild et al., 1994) due to overfishing (Gouletquer et al., 1994). Overfishing has also caused the collapse of Sydney rock (*Saccostrea glomerata*) and flat oyster (*Ostrea angasi*) in Australia (Nell, 2001), *Ostrea edulis* in Wadden Sea (Wolff, 2005), and *Ostrea lurida* in Western North America (Kirby, 2004). Habitat degradation through fishing disturbance may exacerbate the impact of additional stresses from

anoxia, the outbreaks of parasitic diseases, and of other symptoms of environmental deterioration (Beck et al., 2011). In Foveaux Strait, New Zealand, dredge fishery for *Ostrea* (= *Tiostrea*) *chilensis* was maintained over 130 years (Cranfield et al., 1999). The continued exploitation of these oyster beds subsequently reduced oyster densities to low levels. An infection caused by the Haplosporidian parasite, *Bonamia exitiosa*, between 1986 and 1992, resulted in the closure of the fishery, until the population rebuilt in 1995 (Cranfield et al., 2005).

Fluctuations of native oyster populations from South Atlantic are poorly documented (Beck et al., 2011); however, there is a significant concern about this, since oysters along South American coasts are also showing signs of decline. Carranza et al. (2009) ranked 10 oyster species within 10 distinct ecoregions from the Caribbean Sea and the Atlantic Ocean according to their biological, ecological and socio-economic value to determine the conservation status of their populations. Among them, the native puelche oyster, *Ostrea puelchana* D'Orbigny 1842, in the North Patagonian Gulfs

\* Corresponding author. Instituto de Biología Marina y Pesquera “Almirante Storni”, Universidad Nacional del Comahue, Güemes 1030, 8520 San Antonio Oeste, Provincia de Río Negro, Argentina. Tel./fax: +54 2934 430 764.

E-mail address: [msdoldan@gmail.com](mailto:msdoldan@gmail.com) (M.S. Doldan).

<sup>1</sup> Doldan and Morsan contributed equally to this work.

ecoregion, received the highest priority for immediate conservation actions due to evidence of decline of the main beds. Scallop dredging operations, illegal fishing (vessels that operate in violation of the fishery laws, not declaring the catch) and diseases have been suggested as the main causes for bed contraction. However, recently *O. puelchana* was found outside the historic range, at the South coast of the San Matías Gulf (SMG) (Ciocco et al., 2001) and inside the San José Gulf (SJG; Cremonte et al., 2005).

In 1996, the oyster beds in the NW coast of the SMG were affected by *B. exitiosa*. Mortality in culture site inside the San Antonio Bay, SMG, was 95% (Kroeck and Montes, 2005), and the prevalence in wild beds reached a maximum of 57% (Kroeck et al., 2008). Its long-term effects on population density have not yet been evaluated.

The aims of this work were to explore the hypotheses that the *O. puelchana* populations of the NW of the SMG have declined as a consequence of epizootic infections by *B. exitiosa* while populations of the NE of the SMG have expanded and increased despite the impact of dredge activities. The possible underlying causes for the contraction-expansion population pattern were analyzed to recognize the temporal and spatial scales at which it occurred. These fluctuations of the oyster populations of the SMG were explored developing a timeline of distribution (and abundance since 1986) by linking the archival data collected from paleontological, archaeological and informal sources, with time series data collected during surveys and studies of oyster pathology.

## 2. Materials and methods

### 2.1. Biological background of the puelche oyster, *O. puelchana*

The native puelche oyster inhabits subtidal soft-bottoms (1–20 m depth) along the Atlantic coast of South America from Brazil to northern Patagonia, Argentina (Castellanos, 1957; Scarabino, 1977, Fig. 1). Relatively dense natural beds have been

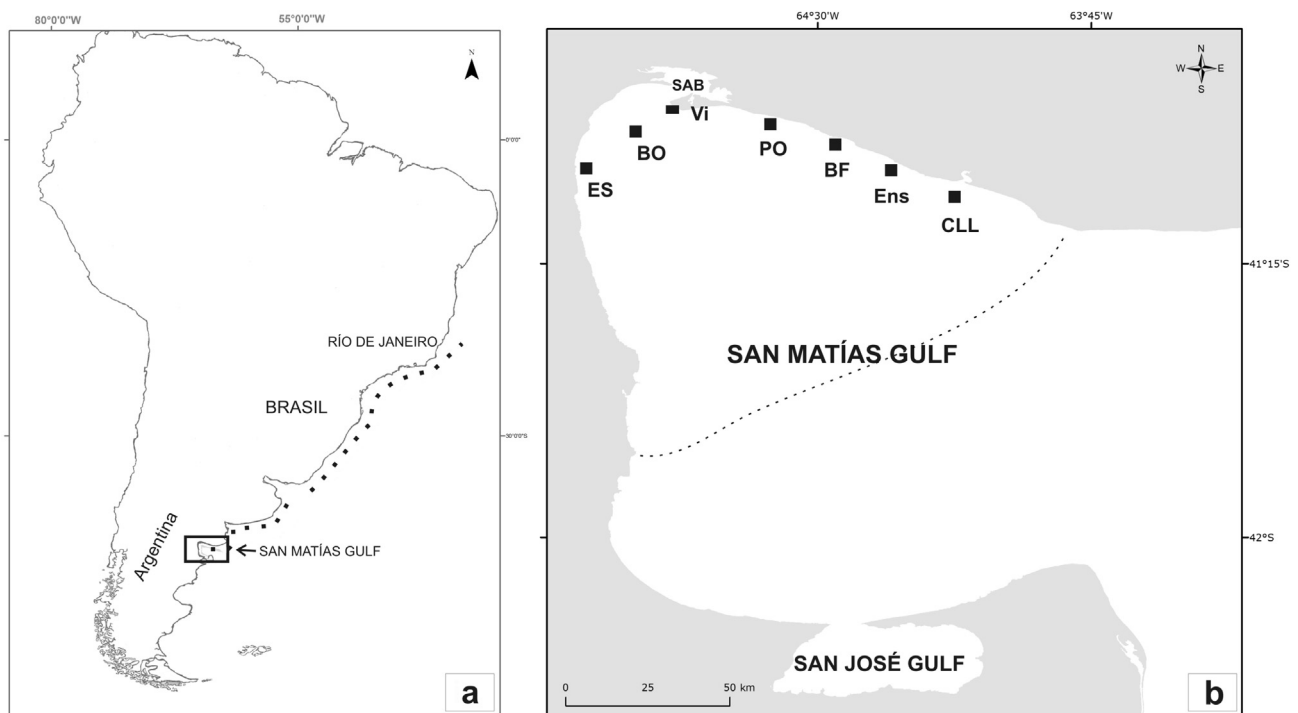
reported only in its southernmost geographical distribution, at the NW and NE of the SMG (41°–42° S, 63°30′–65°W, Fig. 1) (Pascual and Bocca, 1988), apparently isolated from populations outside the gulf. The puelche oyster lives isolated or in clusters. A cluster is formed when larvae settle and grow on the shells of a “founder” oyster (Pascual et al., 2001), generating a tridimensional architectural structure.

*O. puelchana* is a protandric hermaphrodite, with consecutive sexuality. This species shows a unique breeding system: large oysters often carry small individuals attached to a flat platform originated from the anterior edge of the concave shell. “Carrier” oysters have a strong influence in the growth rate of small epibionts which are able to live in this “dwarf” condition for long periods (Pascual, 2000). Epibiotic individuals mature as males at about 3 mm of shell diameter (Morriconi and Calvo, 1989).

During the reproductive season oyster smaller than 55 mm in height are predominantly males. Spawning takes place from mid November to mid March (mid spring to late summer) (Morriconi and Calvo, 1979). Mean fertility ranges from 900,000 to 2,700,000 larvae. Brood size ranges from 447,500 to 3,790,000 larvae (mean = 1,868,212;  $s = 813,808$ ;  $n = 121$ ) (Castaños et al., 2005). Embryos are small (60–90  $\mu\text{m}$ ) and are incubated during a short breeding period (5–6 days; Zampatti and Pascual, 1989). Larvae have a long planktonic life (more than 10 days at 22 °C, Morriconi and Calvo, 1989). During the settlement season (December to March, Pascual and Bocca, 1988), oyster larvae settle on all available hard surfaces but preferentially on the shells of living oyster, probably mediated by chemical attraction (Pascual and Zampatti, 1995).

### 2.2. Study area

The San Matías Gulf (SMG) (40° 50′–42° 15′S, 63° 5′–65° 10′W, Fig. 1) is a semi-enclosed basin, partially communicated with the open sea through a shallow sill (60 m depth) (Rivas and Beier, 1990). Water circulation is driven by two eddies, one with cyclonic sense



**Fig. 1.** a: *Ostrea puelchana* geographic distribution. b. Natural beds of *O. puelchana* at North Patagonian Gulfs (ES: El Sótano; BO: Bajo Oliveira; Vi: Punta Villarino; PO: Playa Orengo; BF: Barranca Final; Ens: Ensenada; CLL: Caleta de los Loros). SAB: San Antonio Bay. San Matías Gulf showing thermohaline front.

located in the North and the other with anticyclonic sense in the South. An intense thermohaline front divides two water masses with different oceanographic conditions (Fig. 1): relatively cold-fresh waters –similar to the open shelf waters– are placed south of the front, while warm-salty waters are placed north of the front (Piola and Scasso, 1988). On the NW coast, waters from the NW and NE coasts are separated by the long sandy ridges around the mouth of San Antonio Bay and influenced by tidal currents (Lanfredi and Pousa, 1988). There, a coastal current rotates clockwise, predominantly driven by the tides, and it has restricted interchange with the offshore global circulation (Lanfredi and Pousa, 1988). Monthly average surface seawater temperature ranges between 6 °C in August (winter) and 22 °C in January (summer).

### 2.3. Reconstruction of the distribution of *O. puelchana* by the screening of archival data

The reconstruction of the distribution of *O. puelchana* in the SMG was performed based on four sources of information, each covering different periods. Non-quantitative records of oyster fossils from Holocene and archaeological records of *O. puelchana* were examined. Records of *O. puelchana* presence/absence from a historic baseline between 1884 and 1933 (predominantly 1925), and a current fishing baseline between 1970 and 2006 (including abundance data from 1986) were examined.

#### 2.3.1. Paleoecological and archaeological records

A thorough review of paleoecological and archaeological records drawing on scientific literature was conducted. The resulting data was discussed with scientific experts.

In addition, the paleoecological deposits of *O. puelchana* in Caleta de los Loros and Punta Villarino (Fig. 1) were visited in December 2011 to verify *in situ* that this species was a fossil constituent of the terraces. Furthermore, shell deposits from the N coast of the SMG were visited to confirm *in situ* that this species was a constituent of the fauna available to the first inhabitants of this area.

#### 2.3.2. Reconstruction of the distribution of *O. puelchana* from historical documents

A thorough review of historical records of species, fishery data, National Navy bulletins, navigational maps, and descriptions of naturalists was conducted to extract descriptions related to the distribution of oysters, location and characteristics of the natural beds.

#### 2.3.3. Ecological and fishery records

Several ecological and fishery surveys were conducted during the 1971–1985 period along the coasts of the SMG and SJG to evaluate the scallop population with qualitative records of other faunistic component of benthos. Information about the location of the oyster beds and the relatively density of *O. puelchana* were extracted from the original records collected on board, notes, charts and technical reports. In addition, researchers who participated in those surveys were interviewed. Resulting data was analyzed and digitalized.

During the 1986–2006 period, eight quantitative surveys were conducted off the N coast of the SMG (Table 1), to study spatial pattern distribution of the main epifaunal species. All sampling stations were distributed regularly over the fishing

**Table 1**  
Nature of the scientific and commercial surveys in northern Patagonian gulfs, between 1884 and 2006. SMG: San Matías Gulf; SJG: San José Gulf.

Year	Survey name	Gear	Sampling stations	Surveyed coasts			Depth range (m)	References
				SMG		SJG		
				NW	NE			
1884	Vigilante	Unknown		x			Eyroa, 1884	
1899	Azopardo	Trawl net		x	x		Lahille, 1900	
1925	Tehuelche	Unknown	44	x		9–30	Valette, 1929	
1933	Gob. Valentín Vergara	Unknown		x			Carcelles and Pozzi, 1933	
1970	Scallop surveys	Diving		x		18	Olivier et al., 1970	
1970–1977	Scallop surveys	Diving					Orensanz, 1986; Ciocco, 1995	
1971	SAO I – María Casanelas	Posgay dredge (1.3 m)	33	x	x	12–41	Olivier et al., 1971; Scarabino, 1977	
1971	SAO II – Cruz del Sur	Dredge	35	x	x	13–160	Scarabino, 1977	
1971–1977	Mussel surveys	Diving					Picallo, 1980; Ciocco, 1995	
1972	SAO III	Dredge	48	x	x		Scarabino, 1977	
1973	SAO IV - SAO V – Supremacía	Picard dredge	45	x		5–43	Olivier et al., 1973	
1974	Ría de Vigo	Picard dredge – quadrats	14			2–12	Olivier et al., 1974	
1975	Neptunia I – Nueva Neptunia	Dredge (2.5 m)	40	x		9–42	Marziale et al., 1975	
1977	Desolación	Dredge			x		Escofet et al., 1977	
1980	Santa Ana	dredge	39	x		13–35	Boardbooks records	
1980–1989	Scallop surveys	Diving					Ciocco, 1991; Ciocco, 1995	
1984	Austral	Van Veen dredge	120			0–185	Zaixso et al., 1998	
1985	IBMP	Diving	25	x		0.5–3	Pascual et al., 2001	
1986	Capitán Cánepa I	Dredge (2.5 m)	136	x	x	8–70	Pascual et al., 2001	
1987	Capitán Cánepa II	dredge (2.5 m)	214	x	x	5–20	Pascual et al., 2001	
1990	Capitán Cánepa V	Dredge (2.5 m)	146	x	x	12–95	Boardbooks records	
1991	Austral	Picard dredge	135	x	x	10–50	Vacas, 1991	
1996	Capitán Cánepa VI	dredge (2.5 m)	167	x	x	10–87	Morsan, 2008	
1997	Capitán Cánepa VII	Dredge (2.5 m)	145	x	x	10–65	Morsan, 2008	
1998	Cota Cero	Diving	48	x		2–23	Morsan, 2008	
2000	Virginia	dredge	90	x		4–60	Morsan, 2008	
2001	Antonella	Diving	414				Ciocco et al., 2001	
2002	CENPAT II	Diving	1				Cremonte et al., 2005	
2002	Holberg	Trawl net	136	x	x	5–160	Boardbooks records	
2006	Nadia Belén	Dredge (1.8 m)	255	x	x	14–30	Narvarte et al., 2012; Boardbooks records	
2006	CENPAT II	Diving	148				Ciocco, 2006	

ground, between 10 and 25 m depth on the NW coast, and between 10 and 40 m depth on the NE coast; one haul (sampling unit) was made at each station. Haul duration was 5–10 min of dredging. The tow speed was 3.15 knots, and the mean sweep area per haul varied from 365.2 m<sup>2</sup> to 2343.2 m<sup>2</sup>. Catch was spilled on the deck and quantified by taking a subsample of four bags and recording the total number of bags per haul. Oysters were counted and weighed. Its density was estimated using catch and swept area data:

$$D_h = (N_h/a_h)1000$$

where  $D_h$  is the oyster density in the sampling station,  $h$ ,  $N_h$  is the number of oysters, and  $a_h$  is the swept area in m<sup>2</sup>, estimated from dredging time, dredge width, and vessel speed. Also, numbers of “cluckers” (empty shells which are still joined together by the ligament as evidence of mortality *in situ*, Cranfield et al., 2005) were quantified in each sampling station.

The occurrence of *O. puelchana* on the SW coast of the SMG and in the SJG was extracted from the records collected on technical reports from the scallop and mussel surveys.

#### 2.4. Data extracted from studies of oyster pathology

In 1996, 95% of cultured commercial-sized native oysters died inside San Antonio Bay. The protozoan parasite *B. exitiosa* (Phylum Haplosporidia) was identified as the cause of mass mortality (Kroeck and Montes, 2005; Kroeck, 2010). As it infected several oyster beds located close to San Antonio Bay (Kroeck et al., 2008), it was defined as an epizootic (disease affecting many animals within a given area at the same time; widely diffused and rapidly spreading) (FAO) <http://www.fao.org/fi/glossary/aquaculture/>.

In order to explore possible causes of population contraction of the oyster beds in the NW of the SMG, the prevalence of *B. exitiosa* data collected between 1996 and 2001 from the samples of five natural beds (Banco Reparo, BR; Las Grutas, LG; Bajo Oliveira, BO; El Sótano, ES, and Playa Orenge, PO, Fig. 1) was revised. The analysis about evolution of the *Bonamia* prevalence in different beds during the study period was performed again. Samples of 30 wild oysters had been randomly collected by diving from each of the five oyster beds half-yearly (spring and late summer samplings). Samples from BO, ES and PO were collected between 1998 and 2001 (for detailed methodologies see Kroeck et al., 2008).

#### 2.5. Fishing activities

Dredging operations for scallops (*Aequipecten tehuelcha*) and mussels (*Mytilus edulis platensis*) took place on several fishing grounds on the NE and NW coast of the SMG. Dredging intensity varied over time (from 1969 to 2010) establishing a pulse-type fishery (Morsan, 2008). In order to explore possible effects of fishing activities on oyster beds, the intensity and frequency of the dredging activity were analyzed, considering fishing gear, fishing effort, fishing periods and areas extracted from fishermen reports to the fisheries authorities.

Fishing effort was measured as time over the ground. This unit has two components: dredging time (time duration of a haul × number of hauls), and handling time (time spent to process the catch on the deck). Data was recorded by on-board observers from 1984. Annual fishing effort of the fleet was calculated as total fishing time (hours) on each ground during the last three decades.

### 3. Results

#### 3.1. Reconstructing the occurrence of *O. puelchana* by archival data screening

##### 3.1.1. Paleocological records of *O. puelchana*

Pleistocene deposits found in SMG are typically a conglomerate with shells in a muddy matrix. *O. puelchana* oyster was recorded in the Pleistocene deposits from the north coast of SMG. These Pleistocene deposits stand in the region of embayments (San Antonio Bay and Caleta de los Loros, Fig. 1) which were flooded during marine transgressions, when sea level raised and the shoreline moved toward higher ground. The marine transgressions constructed beach ridges while wind and wave-induced currents formed littoral barriers. The Holocene drop in sea level left emergent tidal flats, marshes and large sand banks flanking a main ebb channel (Rutter et al., 1990). Radiocarbon age of Pleistocene formation containing a mixture of mollusks shell (oyster, among others) was established in more than 40,000 <sup>14</sup>C yr BP (Fidalgo et al., 1980). There were no outcrops of mollusk fossils on the west coast, with the exception of Puerto Lobos where six ridges stand parallel to the coastline. Two of the coastal ridges contain shell of *O. puelchana* (Pastorino, 1989). Ridges were aged by Bayarsky and Codignotto (1982) between 3300 and 750 yr BP.

##### 3.1.2. Archaeological records

Human occupations on the coast of the SMG are recorded from Mid-Holocene 5000 yr BP. These documented human exploitation of coastal resources for food and materials by past populations were restricted to small-scale nomadic aboriginal societies.

Archaeological studies on the SMG coasts described a large number of prehistoric shell deposits (shell middens) along the coast, mixture of elements from different timelines and modification of the middens by wind erosion (Bormida, 1968). Archaeological studies on the northern coast of the SMG found more than 50 archaeological loci along 350 km in the N and W coast of the gulf. An intense use of shellfish resources in shallow waters, especially mussels (*M. edulis platensis* and *Aulacomya atra*) and clams (*Amiantis purpurata*) was evidenced by numerous shell middens and by the rest of carbon on the shell surfaces. Isotopes led to establish the age of shell deposits between 3300 yr BP and 1700 yr BP (Favier-Dubois and Kokot, 2011). However, records did not refer to *O. puelchana* as food for aborigines (Favier-Dubois, pers. comm.).

The occurrence of *O. puelchana* shells in areas with the same age of the shell middens was verified *in situ* albeit this species was not found in the middens. Archaeological studies in the SJG came to the same result: *O. puelchana* was not used as a resource (Gomez Otero, pers. comm.).

##### 3.1.3. Reconstruction of the distribution of *O. puelchana* from historical documents

Historical documents and maps of the explorers who arrived at the SMG during the late 19th century and the first half of the 20th century described -among other geographic aspects- the environment and the faunistic composition of the area. Descriptions about the location of natural oyster beds were extracted and gathered together in a historic baseline (Table 1).

The interest to explore the Patagonian coast started in the last quarter of the 19th century, with the incorporation of Patagonia to the Argentine National Territory. Until then, it was considered uninhabitable with sterile soil (García, 2009). Eyroa (1884) recorded living oysters around the San Antonio Bay, and in other sites situated further North:

*“The diversity and quantity of molluscs and shells that have this port (natural port inside San Antonio Bay), could be immense. This is demonstrated by the numerous middens of empty shells that are crowded inside the bay. We have found living oysters and snails, both abundant in beds placed in the central area of the port”*

The occurrence of oysters near San Antonio Bay was also confirmed by explorations conducted by Lahille (1900). He suggested this place to promote oyster culture based on native oysters, but he did not provide the precise localization of natural oyster beds.

The first distribution map of *O. puelchana* was produced in 1925, as a result of a survey to assess the natural oyster population in the SMG. Oysters were recorded in 26 hauls from a total of 44, mainly at Bajo Oliveira (BO) (Fig. 2a). Further studies confirmed the occurrence of this bed and recorded other concentrations around San Antonio Bay (Carcelles and Pozzi, 1933).

### 3.1.4. Ecological and fishery records

*O. puechana* was recorded in the scallop surveys conducted between 1970 and 1980 in SMG (Table 1), predominantly 1971–1975 (Fig. 2b). It was found mainly between 9 and 20 m depth, with a spatial distribution similar to the one described previously. The distribution area was partially overlapped with an area disturbed by dredging in BO and ES (Fig. 2b) during scallop fishery.

Results of the quantitative surveys conducted between 1986 and 2006 showed an intriguing spatial pattern of oyster densities distribution with differences between the NW and NE coast of the SMG. On the NW coast, BO and ES beds showed the same location observed in prior historical information. Density decreased in the 1997–2000 period showing no recovery by 2006 (Figs. 3 and 5). In addition, the number of cluckers collected in 2006 on the NW coast was 1.28 m<sup>-2</sup>, and the ratio cluckers: living oysters was 2.2:1; therefore BO oyster bed had virtually disappeared.

Oyster beds on the NE coast showed an inverse pattern. In 1987, the occurrence of oysters was occasional (max. density <0.05 ind. m<sup>-2</sup>). Density gradually increased during the analyzed period and by 2006 mean density was 0.1 ind. m<sup>-2</sup>. In addition, areal

extent increased covering the entire NE coast reaching CLL (eastern limit of the SMG) (Figs. 4 and 5). Number of cluckers per station was 0.77, and the relationship cluckers: living oyster was 0.3:1.

On the SW coast, however, the occurrence of oysters was not reported before 2000 even though surveys in the area started in 1970 (Table 1). Ciocco et al. (2001) cited the occurrence of oysters at Puerto Lobos as the first report of this species south of parallel 42° S and in the SJG (Ciocco, 2006). This place is located about 170 km south of the beds of the NW of SMG, outside the historical distribution range. Inside the SJG, this species had never been reported as a component of the benthic community in the ecological surveys carried out during the 1970s and 1980s (Ciocco, 1991, 1995; Olivier et al., 1974; Orensanz, 1986; Picallo, 1980; Zaixso et al., 1998, Table 1). Its occurrence consisted in isolated records during the 90s, but according to the density estimated in 2000, they were considered established populations (Ciocco, 2006, Fig. 6).

### 3.2. Studies of oyster pathology

The chronological sequence of *B. exitiosa* prevalence at the SMG oyster beds showed a fluctuating pattern. The infection peaked to more than 50% in 1997, followed by a declining trend until 2000 (8.7%), and rose up to 15.3% in 2001 (Fig. 7). However, statistical analysis indicated that the infection probabilities depended on the bed sampled ( $\chi^2 = 24.55$ ;  $df = 5$ ;  $P < 0.05$ ). Maximum *B. exitiosa* prevalence (63.3%) was registered at a commercial culture during 1997 at San Antonio Bay, one year after mass mortality. Maximum values of prevalence in natural beds were found at BR and LG, two small beds near the bay (Fig. 8). A similar pattern was followed by the beds of the NW coast (BO and ES) sampled since 1998. On the other hand, the lowest prevalence was registered at PO bed, on the NE coast of the gulf (Fig. 1) far from the cultivation area and separated from the influence of water flow of the bay by wide sand banks uncovered during low tide period (Fig. 8).

The spatial pattern of prevalence showed that the evolution of infection followed nearly the same pattern in all natural beds, but there were highly significant differences ( $P < 0.01$ ) in the prevalence values between NW (BR, LG, BO, ES) and NE (PO) natural beds (Fig. 7).

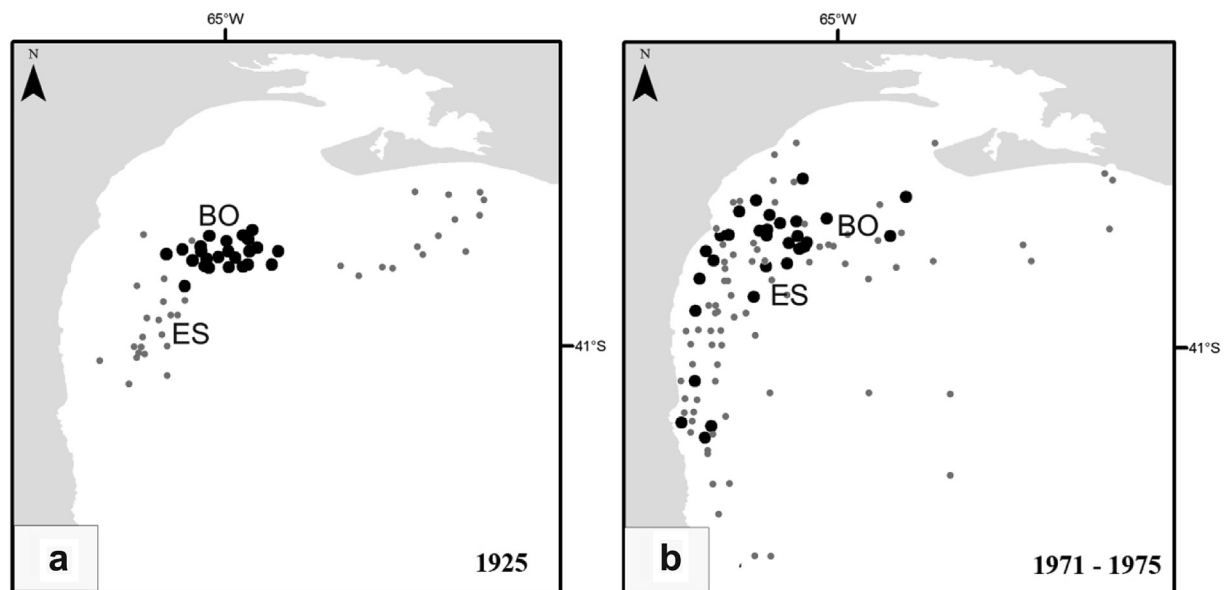
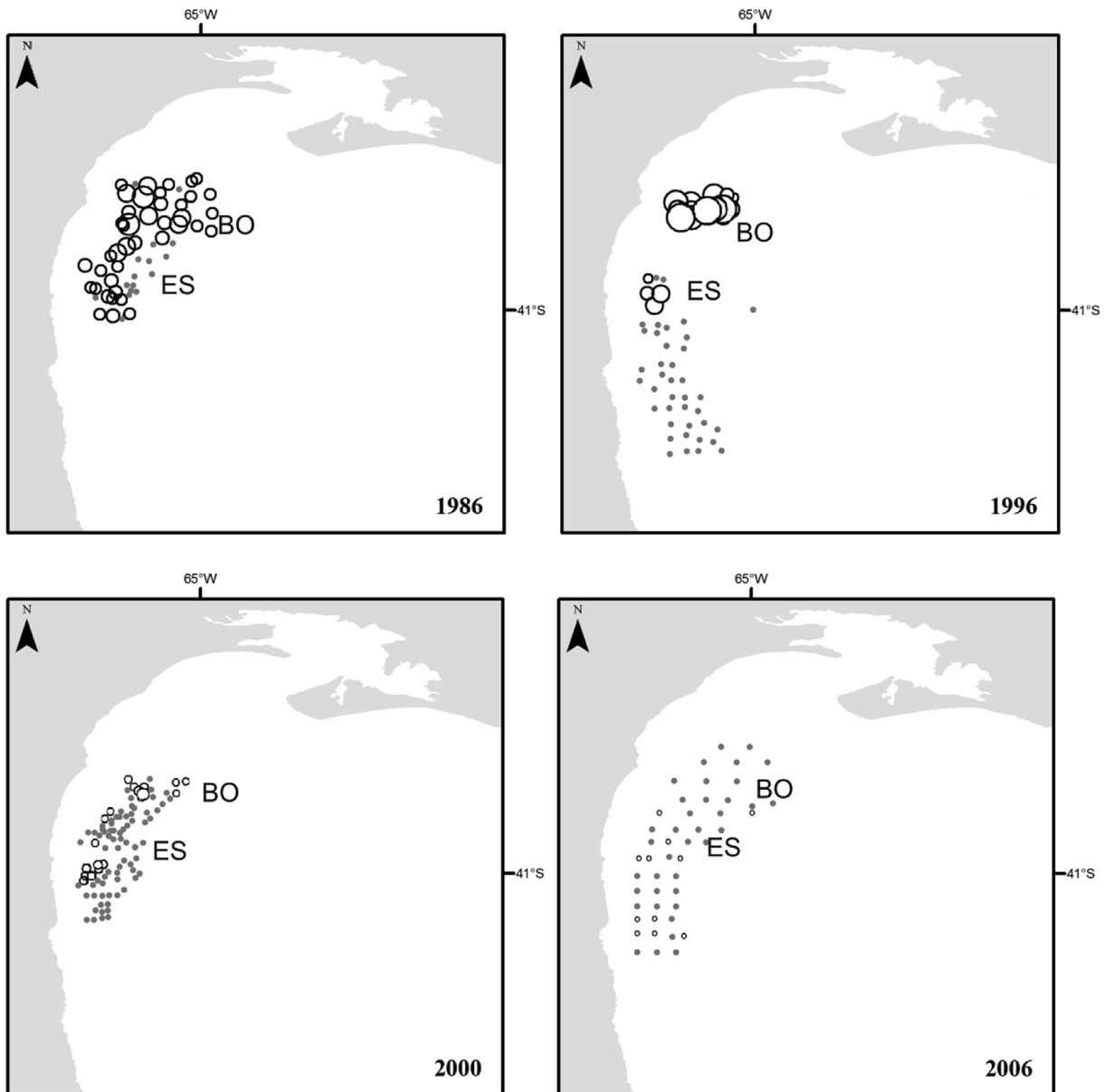


Fig. 2. Digitalized position of hauls with records of oyster in the surveys “Tehuelche” in 1925 and in the ecological and fishery studies in the period 1971–1975. Small gray circles shows the total extend of the survey; hauls at which oysters were caught are shown as black circles. ES: El Sótano bed; BO: Bajo Oliveira bed.



**Fig. 3.** Density of *Ostrea puelchana* in quantitative surveys on the NW coast of the SMG, in the period 1986–2006. Small filled circles show the total extent of the survey; hauls at which oysters were caught are shown as bubbles. Maximum size of bubble represent maximum density = 3 oysters/m<sup>2</sup>. ES: El Sótano bed; BO: Bajo Oliveira bed.

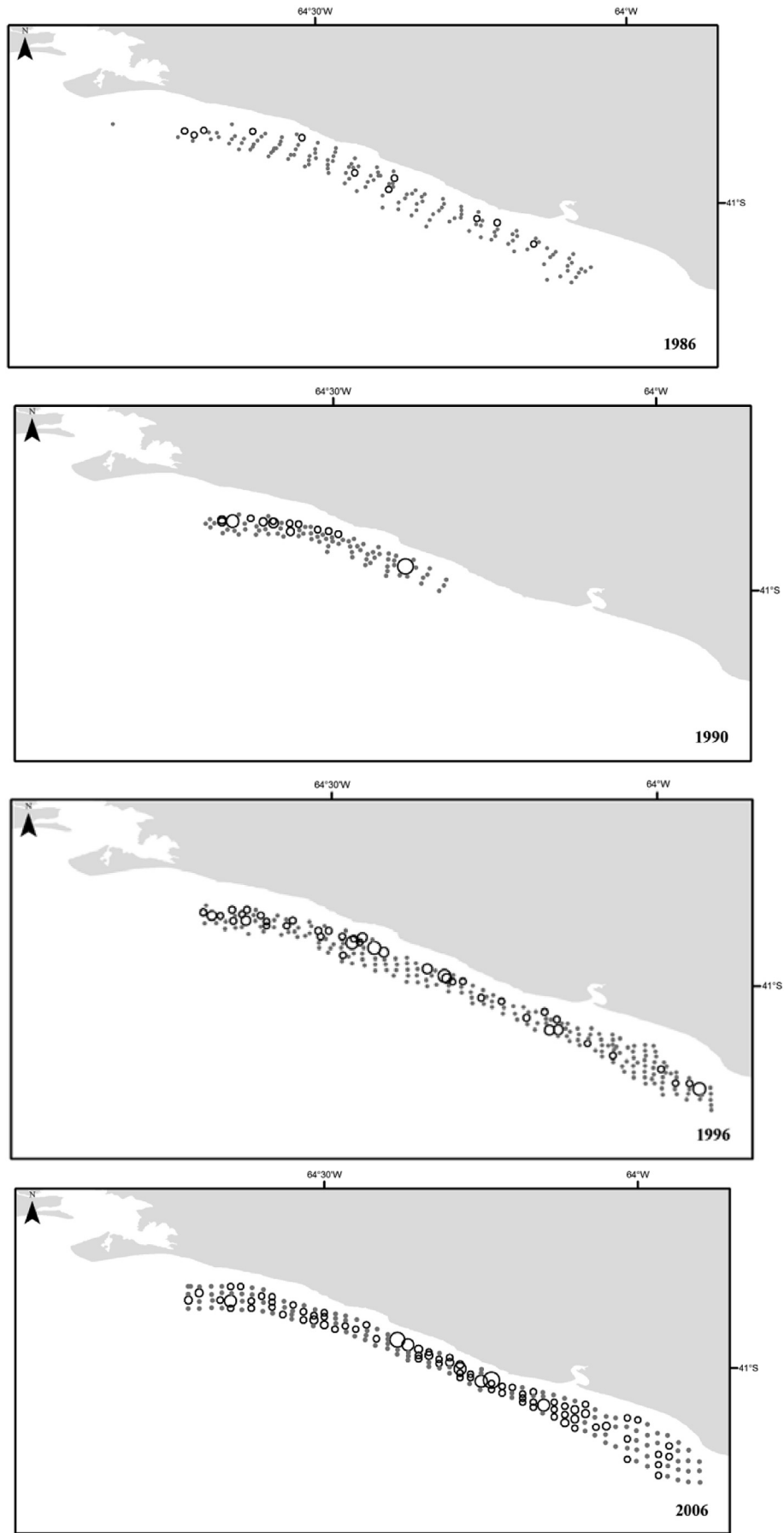
The prevalence of infection by *Bonamia exitiosa* in 1996–2001 was defined by Kroeck et al. (2008) as a focus of infection placed in cultured areas from which the parasite spread radiating through the oyster beds located around the bay (Fig. 8).

### 3.3. Fishing activities

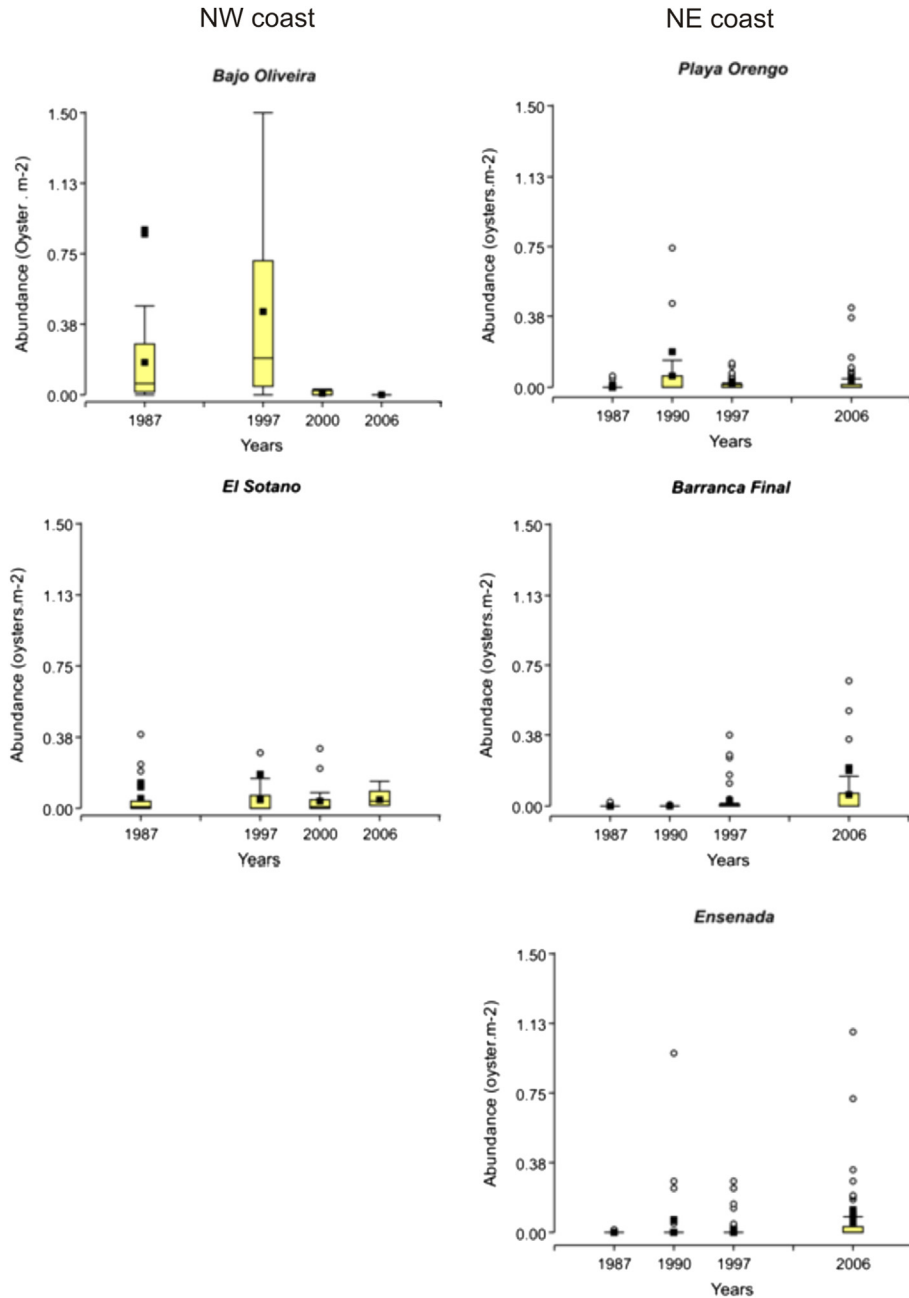
*O. puelchana* has never been a target species for fishing. There exist no records of oyster landings, except by the 1940s, when 71 tons were fished in the San Antonio port (Carcelles, 1946). In order to promote the oyster culture industry, natural stocks were protected closing the fishing in 1975. However, fishing of scallops (*A. tehuelcha*) and mussels (*M. edulis platensis*) took place in areas near the oyster beds of the NW coast. Harvesting for these species in the SMG was performed with two fishing gears: dredging and SCUBA diving. The former was used from the beginning of the fishing activities, while diving started in 1988 and continued

increasing until 2010. The shellfish fisheries changed throughout the decades in relation to the target species, gear preference, type of dredges and regional allocation of fishing effort in response to market preferences or management regulations.

Before 1993, dredge fishing in the SMG was conducted with dredges which had a heavy design, built of iron pipe, 3-cm mesh chicken wire, and stripes of spare tires; the seafloor was scraped by the tense tickler chain. Dredges were up to 2.5 m wide, and weighted up to 300 kg (Table 1). The landed catch was composed of scallops (normally 30–40% of gross yield), other benthic invertebrates, and shell hash. Efficiency of the dredge (percent relationship between individuals caught and individuals present in the path of the dredge) was estimated to be between 11–16% and 15–21% (Iribarne et al., 1991); it is completely non-selective due to the clogging of the bag. After the year 2000, when a mandatory resolution modified the dredge design to a light and short gear (1.8 m width), the fleet became artisanal and the number of vessels increased.



**Fig. 4.** Density of *Ostrea puelchana* in quantitative surveys on the NE coast of the SMG, in the period 1986–2006. Small filled circles show the total extent of the survey; hauls at which oysters were caught are shown as bubbles. Maximum size of bubble represent maximum density = 1.08 oysters/m<sup>2</sup>.



**Fig. 5.** Box plots representing density trend over the years. Quantitative data from surveys during the period 1986–2006 at the NW coast beds (Bajo Oliveira and El Sótano) and at the NE coast beds (Playa Orengo, Ensenada and Barranca Final).

The removal of substrate by dredges may have impacted on the benthic ecosystem and on the substrate available for bivalve settling (Morsan, 2008). The removal of thousands of tons of shell hash from the seafloor has been the reason for the low or no scallop recruitment on the SMG for several years, and it could have had a similar effect on other bivalve populations, such as oysters (Morsan, 2008).

Dredging operations took place on several fishing grounds on the NE and NW coast of the SMG with variable dredging intensity over time (from 1969 to 2010) establishing a pulse-type fishery (Morsan, 2008). Grounds of the NW (ES and BO) were intensively dredged during the first pulse of scallop fishing (1969–1972). Even when fishing effort data was not available for this period, it was estimated that a bulk catch of 27,270 tons was landed (including

sediment, shell hash, and benthic organisms), but only 7300 tons corresponded to scallops. During the second pulse (1983–1985), the bulk catch was estimated to be 4714 tons and landings of scallop and mussel in that period were 2664 tons (56.5%). In 2000, scallop fishery was re-opened seasonally for four years (two months *per year*) and under an artisanal scheme: only vessels shorter than 9 m with external engines and small dredges were allowed. On-board discards were mandatory.

Conversely, during the period 1984–1994 the fishing effort concentrated on NE grounds, switching between mussel and scallop as target species. The temporal pattern of the fishing effort of the fleet on both coasts is shown in Fig. 9.

Since 1983, catch composition was quantified. Occasionally, oysters were caught as by-catch, but no landings of oysters



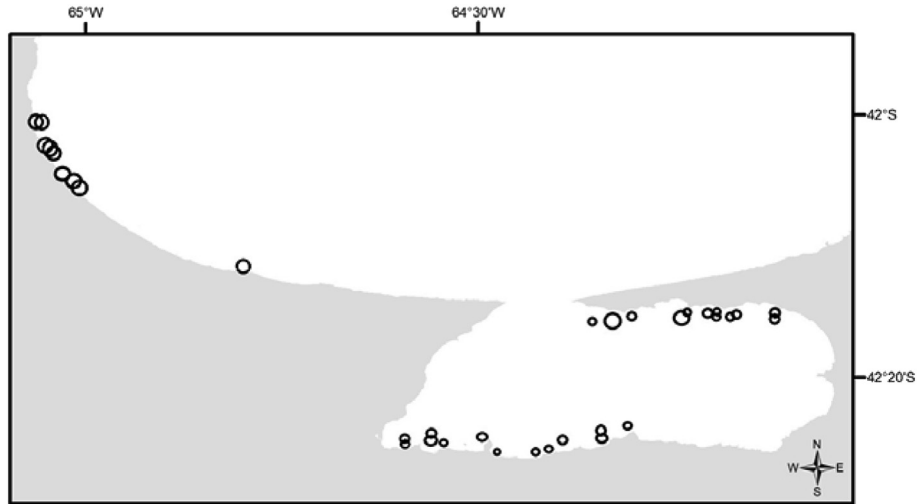


Fig. 6. Density of *Ostrea puelchana* in quantitative surveys on the SW coast of the SMG and at the San José Gulf, in the period 2001–2006. Maximum size of bubble represent maximum density = 1 oysters/m<sup>2</sup>. Data from Ciocco et al., 2001 and Ciocco 2006.

were recorded. The spatial distributions of oysters and other species targeted by the fishery did not overlap because scallop and mussels beds occurred deeper than oyster aggregations.

4. Discussion

For many years some statements about *O. puelchana* have been accepted as true: i) North of SMG is the southern limit of

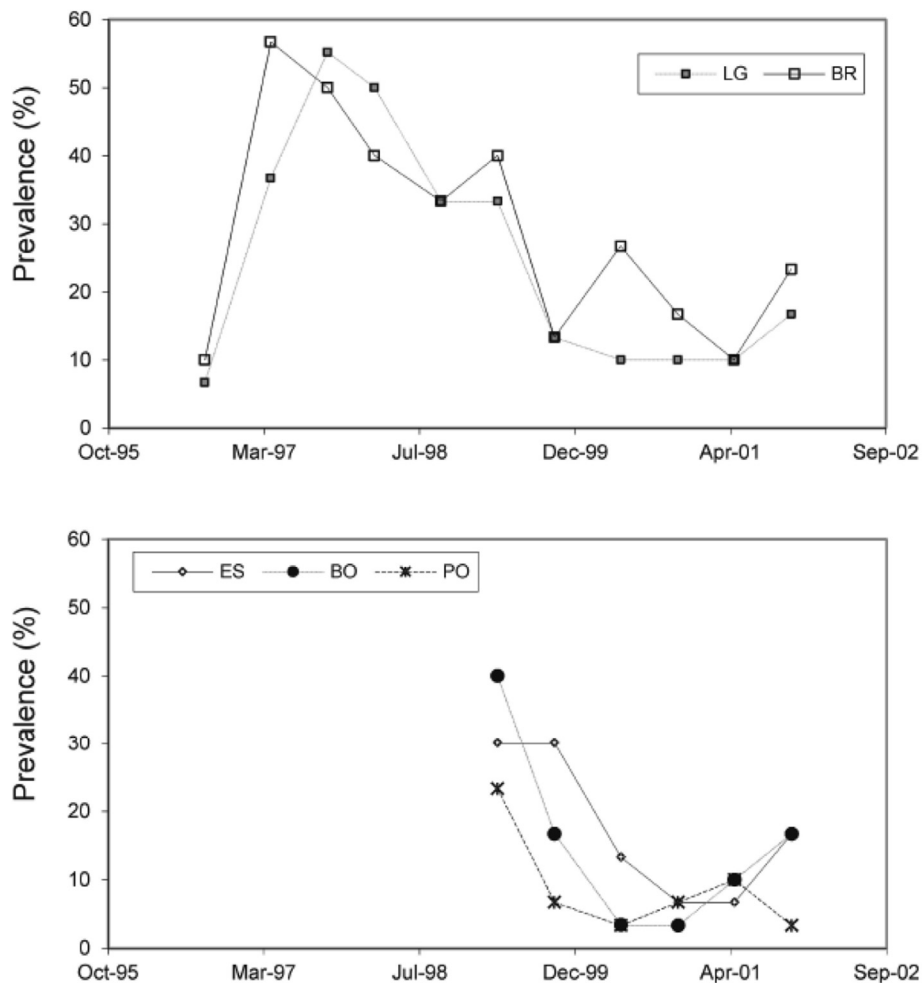
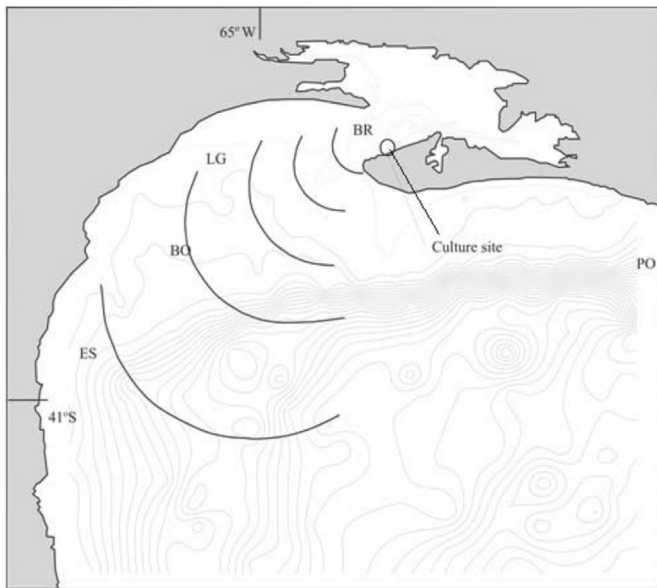


Fig. 7. Trend of prevalence of *Bonamia exitiosa* in *Ostrea puelchana*, in the beds located around the San Antonio Bay. Las Gutas (LG) and Banco Reparo (BR) beds were studied from September 1996 to November 2001, and El Sótano (ES), Bajo Oliveira (BO) and Playa Orengo (PO) were studied from April 1999 to November 2001.



**Fig. 8.** Theoretical expansion of the *Bonamia exitiosa* infection from the culture site to the surrounding areas, affecting sequentially Banco Reparó (BR), Las Grutas (LG), Bajo Oliveira (BO) and El Sótano (ES) oyster beds. Playa Orenge bed (PO), located on the NE coast, showed lower prevalence values.

distribution of this species, and the thermohaline front of SMG operates as a barrier to Southern distribution; ii) the NW coast of SMG is the only place where this species forms beds, due to the special oceanographic conditions; iii) these beds, closed to fishing, have a long term spatial persistence; iv) this species have a low paced dynamic which balances the high post-settlement mortality with unique breeding pattern.

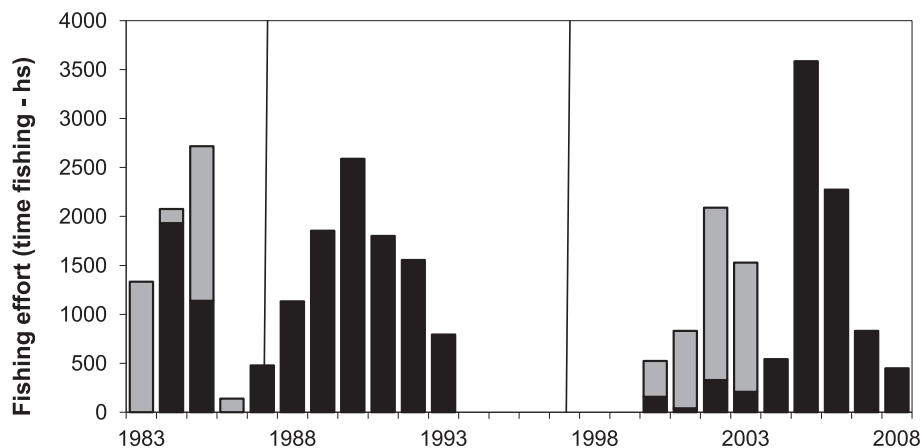
Recently, such statements were challenged with new information. Ciocco et al. (2001) recorded the occurrence of living oysters in the south of the SMG and at the SJG, confirming anecdotic records (Scarabino, 1977; Ciocco, 1995; Orensanz, pers. comm.). These aggregations can be considered as beds according to their current density (1 oyster per square meter, Ciocco, 2006). This record indicates a southward expansion of *O. puelchana* populations, beyond the thermohaline front. However, the occurrence of sub-fossil oysters in Holocene ridges of Puerto Lobos (Pastorino, 1989) indicates that the geographical range of distribution in the past could have been similar to the current one. The global mid-Holocene

climatic change -period known as *hypsihermal* and characterized by high temperature and humidity- was responsible of the faunistic migrations and southward displacement of the limit between Argentinean (warm temperate) and Magellanic (cold temperate) malacological provinces (Pastorino, 2000). The occurrence of *O. puelchana* on the south coasts of the SMG during the Holocene could be explained as a response to this warm period, and the geographic limit might have moved in response to subtle climatic fluctuations. The occurrence of *O. puelchana* on the NE coast of the SMG is evidenced by the outcrops of shells in Pleistocene and Holocene terraces that were corroborated *in situ* at several places along the coast.

The newly-discovered oyster populations beyond the historical southern limit (Fig. 6) are potential indicators of climate change. There has been demonstrated that climate regulates the abundance of species, and its geographic range of distribution (Lutaenko, 1993; Strom, 2003; Harley et al., 2006). The current oyster distribution, due to a lack of suitable temperature records, suggests a potential warming in the SMG and as a result the species may have found dispersal opportunities to southern areas. However, this hypothesis needs further exploration.

The occurrence of *O. puelchana* on the NE coast was limited to isolated individuals at shallow waters in the 1980s. During the subsequent 20 years, beds were consolidated throughout the NE coast. This expansion process was temporally coincident with an intense dredging activity for mussels and scallops (up to 3500 fishing h. year<sup>-1</sup>, Fig. 9). Disturbance by dredging produces habitat disruption, re-suspension of sediment, removal of substrates (inhibiting bivalve settlement) and changes in faunistic composition (Morsan, 2008). However, the evidence suggests that dredging in adjacent deeper areas for over 20 years did not affect negatively the bed expansion.

The dynamics of a spatially structured population depends on two separated processes: i) connectivity between subpopulations and, ii) demographic processes within subpopulations (Gilbert, 2011). In marine bivalves, connectivity between beds (and colonization of new areas) is mediated by larval dispersion. Unlike other bivalve populations which show sudden and irregular pulses of high abundance, the puelche oyster show a high post-settlement mortality (Pascual, 1997) and a particular substrate requirement of larvae (Pascual et al., 2001). There has been demonstrated that post-settlement mortality is very high in this species (89%) mainly due to grazing by chitons (Pascual, 1997). Other causes, such as predation, intraspecific competition and smothering by sediment, or a combined effect of them, may also explain this high mortality



**Fig. 9.** Yearly records of fishing effort with dredge on the NW (gray) and NE (black) coast of the SMG between 1984 and 2008. Vertical lines denote years on which the quantitative surveys were conducted in both zones.

(Pascual, 1997). Pascual and Zampatti (1995) stated that the larvae of *O. puelchana* settle on hard substrates, but preferentially on the shells of living oysters, and a chemically mediated adult-larval interaction could trigger the settlement. Therefore, the *O. puelchana* population of Northern Patagonian gulfs is spatially structured. The geographic expansion of NE beds of SMG may reflect long-term suitable general conditions for larval. In contrast, beds on the NW coast of the gulf showed a pattern of contraction at smaller temporal and spatial scale.

The NW beds of SMG were first documented by explorers during the end of the 19th century. During the following century, they were recurrently documented, by the “Tehuelche” survey in 1925, the exploratory post scallop’s fishery surveys (1971–1975), and by quantitative surveys that were carried out during the 1987–1996 period. The long-term spatial persistence of the NW beds may reflect that scallop dredging that took place in adjacent deeper areas had a low impact on them. The dramatic contraction of these beds between 1996 and 2000 occurred 12 years after the closure of the fishing operations along this coast. Even when the scallop fishery re-opened in 2000, it operated only three months *per year* by an artisanal fleet. Landings were intensely monitored by authorities, and oysters were not caught as by catch nor re-released to the sea (Morsan, 2008).

The epizootic of *B. exitiosa* in the oyster culture and the temporal and spatial dispersion pattern of the parasite in natural beds can be interpreted as the key factor that explains the contraction of the NW beds of SMG. The reduction on the prevalence of the parasite in natural beds may be explained only by the mortality of the infected oysters (Kroeck et al. 2008), because they are unable to eliminate the intracellular parasite (Hine, 1991). The water circulation system around San Antonio Bay is dominated by the tidal regime. The bay is filled and emptied twice a day, producing a strong current in the site where the culture was situated. Sandy ridges around the mouth of the bay act as a barrier, directing the flow to the SW of the SMG. Based on the *Bonamia* prevalence trend, we hypothesized that the infection behaved as a wave, starting at the culture site and expanding following the tidal flow (Fig. 8). NW beds were sequentially affected: initially BR, followed by LG, BO and ES. The NW beds (namely PO, Fig. 1) were less influenced by the wave of infection due to geomorphology of the San Antonio Bay and the water circularion.

Two pieces of evidence strengthens the hypothesis of contraction of the oyster beds as a consequence of *Bonamia* epizootic: i) within the temporal window in which the population was analyzed, *Bonamia* prevalence was coincident with the declining trend of the abundance provided by the time series; and ii) the number of cluckers and the ratio cluckers: living oysters in BO and ES was higher than in the NE beds, revealing that a great number of oysters died *in situ*. By 2006, beds did not show signs of recovery. Only small concentrations were found and mean density of BO and ES were the lowest recorded for a survey (0.1 oysters *per square meter*). This highlights the long-term effects of the epizootic, a fact which implies a trade-off between a stable level of *Bonamia* prevalence as a regulatory mechanism and, the natural low-paced process of recovery.

## 5. Conclusions

The present work is the first study which includes a South Atlantic time series concerning oyster beds. Critical points related to the development of the region will need to be harmonized with conservation actions which will require not only maintaining the banning of the oyster harvesting, but also making a series of planned and coordinated decisions in relation to the new location of new oyster culture sites, and the fishing activities for shellfish in this area.

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