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Bonamiosis status in natural *Ostrea puelchana* beds in San Matías Gulf (Patagonia, Argentina), 14 years after an epizootic

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ABSTRACT: Between 1995 and 1996, *Bonamia exitiosa* caused an epizootic in San Matías Gulf, Argentina, that spread from a commercial culture site of *Ostrea puelchana* to natural beds located at the northeastern coast of the gulf. A mortality rate of 95% was registered in cultured oysters, and oysters from natural beds were also affected. The aims of this study were to assess the parasite prevalence in oyster beds and the demographic structure 14 yr after the epizootic. Two different oyster beds were studied during 2009 and 2010. Parasite prevalence was studied related to oyster aggregation, density, sex, and oyster size. Prevalence reached 35.3% at Las Grutas and 18.9% at Banco Reparo and was proportionally associated with density. Prevalence was also associated with the type of aggregation in Banco Reparo, where carrier oysters were more infected. Infection was independent of sex category, and infected oysters were larger than the non-infected ones. Oyster density decreased markedly compared to previous studies in both beds and mean sizes were lower, while prevalence doubled. Because of the persistence of the beds in this period, disease seems to control the population structure.

KEY WORDS: *Ostrea puelchana* · *Bonamia exitiosa* · Epidemiological study · Survey of prevalence · Patagonia · Argentina

INTRODUCTION

Haplosporidians of the genus *Bonamia* are widespread obligate parasites that infect oysters (Carnegie & Cochennec-Laureau 2004). Species of this genus have caused significant disease and mortality in natural and cultured oyster populations around the world (e.g. Pichot et al. 1980, Hine et al. 2001, Burreson et al. 2004). Between 1995 and 1996, a *Bonamia* sp. caused an epizootic in cultured native flat oysters *Ostrea puelchana* that spread from a commercial culture site in San Antonio Bay (SAB), San Matías Gulf (SMG, 41° 0′ to 42° 0′ S, 63° 30′ to 65° 09′ W), Argentina, to the surrounding areas affecting natural beds (Kroeck & Montes 2005, Kroeck et al. 2008). When the first evidence of disease was detected, studies were conducted to determine the etiological agent and to evaluate its effect on natural beds. The results confirmed the presence of a *Bonamia* sp. pathogen in *O. puelchana* tissues, and described a spatial-temporal pattern of disease spread over the oyster beds (Kroeck et al. 2008). Phylogenetic results indicated that the parasite was *B. exitiosa* (Carnegie et al. 2014, Hill et al. 2010, 2014, this DAO Special). The

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most affected natural beds were Banco Reparo (BR), located at the mouth of SAB, 4 km away from the culture site, and the bed at Las Grutas (LG), located ~20 km from the culture site. The dispersal pattern of *B. exitiosa* suggested that the disease may have modified the density and population structure of *O. puelchana* through mortality in different beds close to the affected area. These dense natural beds have been only reported in the shallow subtidal of the northern coasts of the SMG, the southernmost limit of this oyster's distribution (Pascual et al. 2001). The microspatial organization of the individuals within the beds has been categorized by Morriconi & Calvo (1989) and Pascual (1993) as displaying 3 types of aggregation, reflecting the unusual reproductive strategy of *O. puelchana*. These were (1) free adult individuals, (2) clusters of adults, and (3) carrier oysters with dwarf males settled in the anterior border of the concave valve, which is a unique adaptation of this particular *Ostrea* species.

Epizootic events documented for marine invertebrates occur rapidly and can produce drastic consequences, such as the devastation of stocks of cultivated oysters (Cranfield et al. 1991, Jonsson & André 1992, Doonan et al. 1994, Cranfield et al. 2005, Kroeck & Montes 2005). Often the translocation of infected oyster stocks has greatly accelerated the spread of disease (Grizel 1985). Both density and population structure can be rapidly affected (Cranfield et al. 2005). Kroeck & Montes (2005) described a reduction in *B. exitiosa* prevalence in natural *Ostrea puelchana* beds, from more than 50% in 1996, to less than 10% in 2001, similar to a report by Cranfield et al. (2005) for *B. exitiosa* in *O. chilensis* in New Zealand. The prevalence reduction could likely be explained through the mortality of infected oysters, which are unable to eliminate the intracellular parasite and recover from infections. Even when it can be considered a slow process, we hypothesized that the population structure of *O. puelchana* may be modified due to differential mortality related to the types of aggregation of individuals at each natural bed. In order to assess the health condition of the population affected by *B. exitiosa*, we conducted a survey on the most affected natural bed of *O. puelchana*, 14 yr after the epizootic event.

MATERIALS AND METHODS

Study area and sampling design

Sampling was performed at Las Grutas (LG) and Banco Reparo (BR) beds during April 2009 and April 2010, respectively. Based on previous information about location and extent of the beds (Pascual et al. 2001), 33 stations evenly distributed over a regular grid were sampled at each bed. At LG, sampling stations were located between 40° 49.07′ S and 40° 49.5′ S, and between 65° 05.0′ W and 65° 5.4′ W, whereas at BR, sampling stations were located between 40° 46.6′ S and 40° 47.5′ S, and between 64° 54.1′ W and 64° 55.0′ W (Fig. 1). Sampling stations were separated by 200 m. At each sampling station, live individuals of *Ostrea puelchana* as well as boxes, i.e. paired valves of dead oysters still attached by the umbo indicating recent *in situ* mortality (Cranfield et al. 2005), were collected by divers along a transect 1 m wide and 25 m long.

The collected oysters were measured, classified by type of aggregation as free, clustered, carrier females, dwarf epibiotic males, or recruits (<20 mm, Fig. 2), and counted. Live oyster and box densities (ind. per 10 m^2) were estimated for each sampling station. Individuals were measured, and based on the

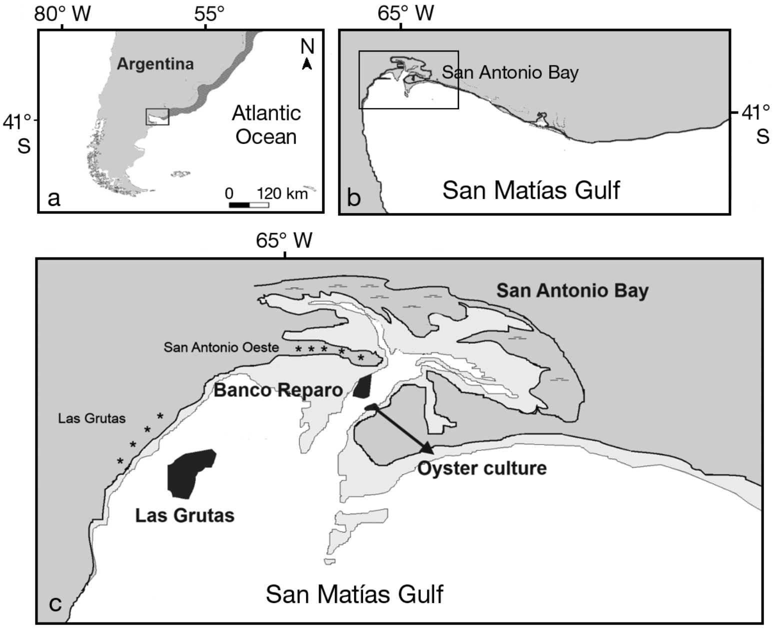

Fig. 1. Study area, oyster culture, and sampling sites. (a) Geographical distribution of *Ostrea puelchana* (dark grey) along the coast of South America. (b) Location of San Matías Gulf and San Antonio Bay. (c) Location of *O. puelchana* culture sites, showing the natural beds Las Grutas and Banco Reparo. (*) Tourist areas of Las Grutas and San Antonio Oeste city

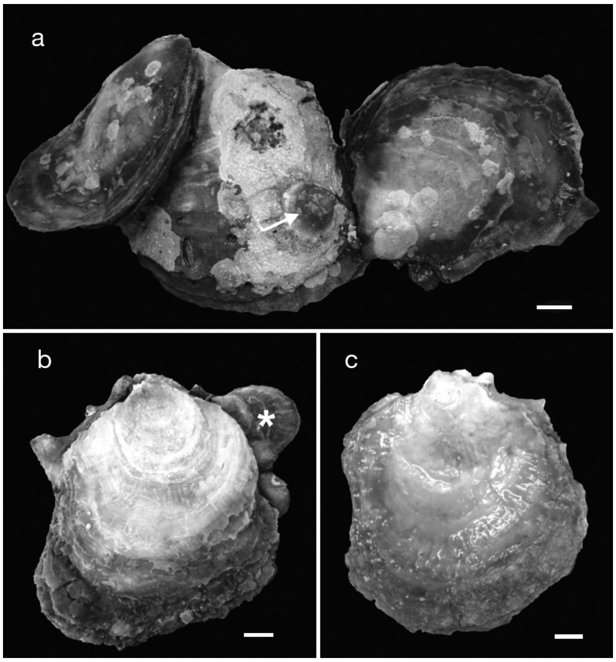

Fig. 2. *Ostrea puelchana*. Aggregation pattern. (a) Clusters of adult recruits (arrow) on oysters. (b) Carrier oysters with their epibiont males (★). (c) Free adult oyster. Scalebars = 1 cm

size frequency distribution, the demographic structure was analyzed. Differences in mean sizes between natural beds were analyzed with a Mann-Whitney *U*-test with InfoStat software (Balzarini et al. 2008).

Oyster tissues were removed from the shells, fixed in Davidson's solution (Howard & Smith 1983), and embedded in paraffin. Samples were sectioned (5 µm thick), stained with Harris hematoxylin and eosin, and examined under a light microscope. Based on the reproductive characteristics of *Ostrea puelchana*, each sample was histologically classified into 1 of 3 sexual categories, viz. hermaphrodite (H), female (F), or male (M), according to Morriconi & Calvo (1979, 1980, 1989) and Pascual (2000).

Disease diagnosis

Bonamia exitiosa prevalence was estimated for the entire population (P = number of infected oysters × 100 / number of observed oysters), and for each sampling station (relative prevalence, RP = number of infected oysters in each station × 100 / number of oysters collected in whole bed), with the aim to describe the spatial distribution of prevalence (see Figs. 3 & 4). For each station, the infection intensity was determined with a semi-quantitative table (Dunn et al. 2000). Prevalence was also determined for each type of aggregation and sex category. The relationships between the percentage of infection with sexual category, the type of aggregation, and the presence of hemocytic infiltrations were analyzed with contingency tables. Sizes of infected and non-infected individuals were compared in each bed with a Kolmogorov-Smirnov test. Finally, the health status of the beds was analyzed by comparing the current prevalence to that calculated 14 yr ago only for the size range 36–105 mm used to study the epizootic event in 1996 to 2001 (Kroeck et al. 2008).

RESULTS

Population structure, density, and spatial distribution

A total of 365 live individuals of *Ostrea puelchana* and 485 boxes were collected between both beds. At LG, most individuals were adults (63.1 %), followed by recruits (17.6 %) and epibiotic males (19.3 %), while at BR there was similar abundance of adults (44.7 %) and recruits (46.2 %), but epibiotic males were less represented (9 %).

The 3 types of aggregations were present at both beds (Table 1). At LG, most individuals were aggregated in clusters, while at BR most individuals were free oysters. Carrier oysters were found in both beds, but their sizes were different. The smallest carrier oysters at LG were 60 mm long, versus 50 mm at BR. In both beds, density was spatially heterogeneous, ranging from 0 to 4.8 ind. per 10 m^2 at LG (Fig. 3a), and from 0 to 5.2 ind. per 10 m^2 at BR (Fig. 4a).

At LG, the size structure presented 3 weak modes, with all sizes homogeneously represented. On the other hand, size structure at BR was bimodal (Fig. 5). The size class histogram showed a peak frequency corresponding mostly to recruits (≤40 mm) and a smaller mode of larger individuals (>40 mm). Size range was wider at LG (0.02–99.97 mm) than at BR

Table 1. *Ostrea puelchana*. Aggregation pattern variation in the prevalence (P) of *Bonamia exitiosa* infection at Las Grutas and Banco Reparo beds

Aggregation pattern	Las Grutas n (%)	Las Grutas P (%)	Banco Reparo n (%)	Banco Reparo P (%)
Clustered	34 (47.2)	35.3	17 (28.1)	35.6
Free	27 (37.5)	29.6	36 (59.3)	28.6
Carrier	11 (15.3)	63.6	7 (11.7)	85.7

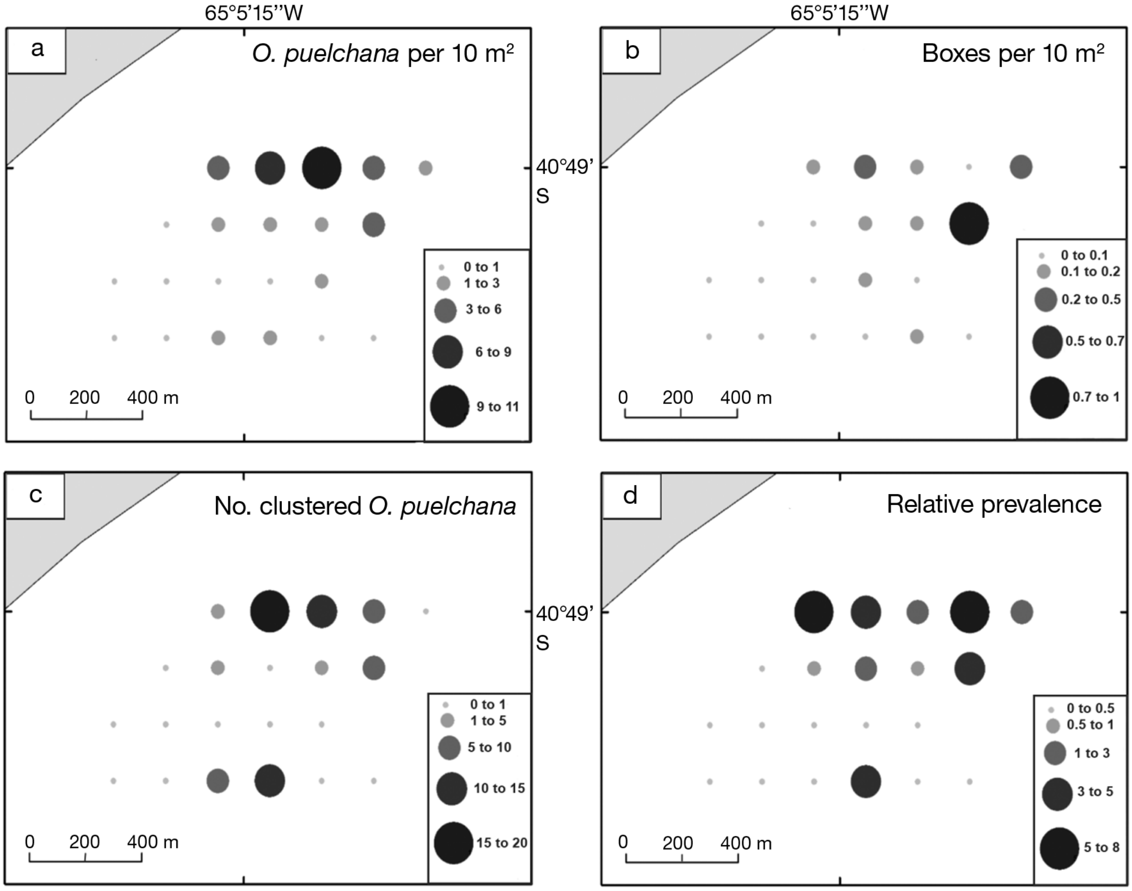

Fig. 3. *Ostrea puelchana*. Spatial distribution of living and dead oysters (boxes), clustered oysters, and prevalence of infection, estimated from the survey of Las Grutas bed. (a) Density per 10 m^2. (b) Density of boxes per 10 m^2. (c) Number of clustered oysters per sampling station. (d) Distribution of relative prevalence of infection

(2.23–80.29 mm), and mean size was larger at LG than at BR (U = 9719, p = 0.01). Sex category was determined for 116 oysters. All 3 sex categories were observed, with a large proportion of males in both beds (Table 2).

Bonamiosis in natural *Ostrea puelchana* beds

Infected oysters were found in both beds. Prevalence of *Bonamia exitiosa* was 35.3% for LG and 18.9% for BR. Spatial distributions of live oysters, boxes, clustered oysters, and relative prevalence (RP) for LG and BR are shown in Figs. 3 & 4.

Relative prevalence varied spatially, ranging from 1.1 to 8.1%, and infection intensity was generally low (stage 1 to 2, according to the scale of Dunn et al. 2000). Higher relative prevalence was observed at stations where oysters were denser. Only 3 stations were found without infected oysters (stage 0, according to Dunn et al. 2000). Moreover, the low abundance of boxes (n = 30) found at LG did not show a spatial relationship with infected oysters (Fig. 3b,d).

At BR, relative prevalence ranged from 0.7 to 1.5%, with highest relative prevalence at stations with moderate to high oyster densities (see Fig. 4d). In this bed, *Bonamia exitiosa* was found at 17 of the stations. The intensity was low (stage 1 to 2) at most stations, except for 6 stations where infection in-

Table 2. *Ostrea puelchana*. Sex-related variation in the prevalence (P) of *Bonamia exitiosa* infection at Las Grutas and Banco Reparo beds

Sex	Las Grutas		Banco Reparo	
	n (%)	P (%)	n (%)	P (%)
Hermaphrodite	15 (22.3)	46.6	13 (30.6)	40
Female	14 (20.8)	35.7	11 (14.3)	42.8
Male	54 (56.7)	42.1	31 (55.1)	14.8

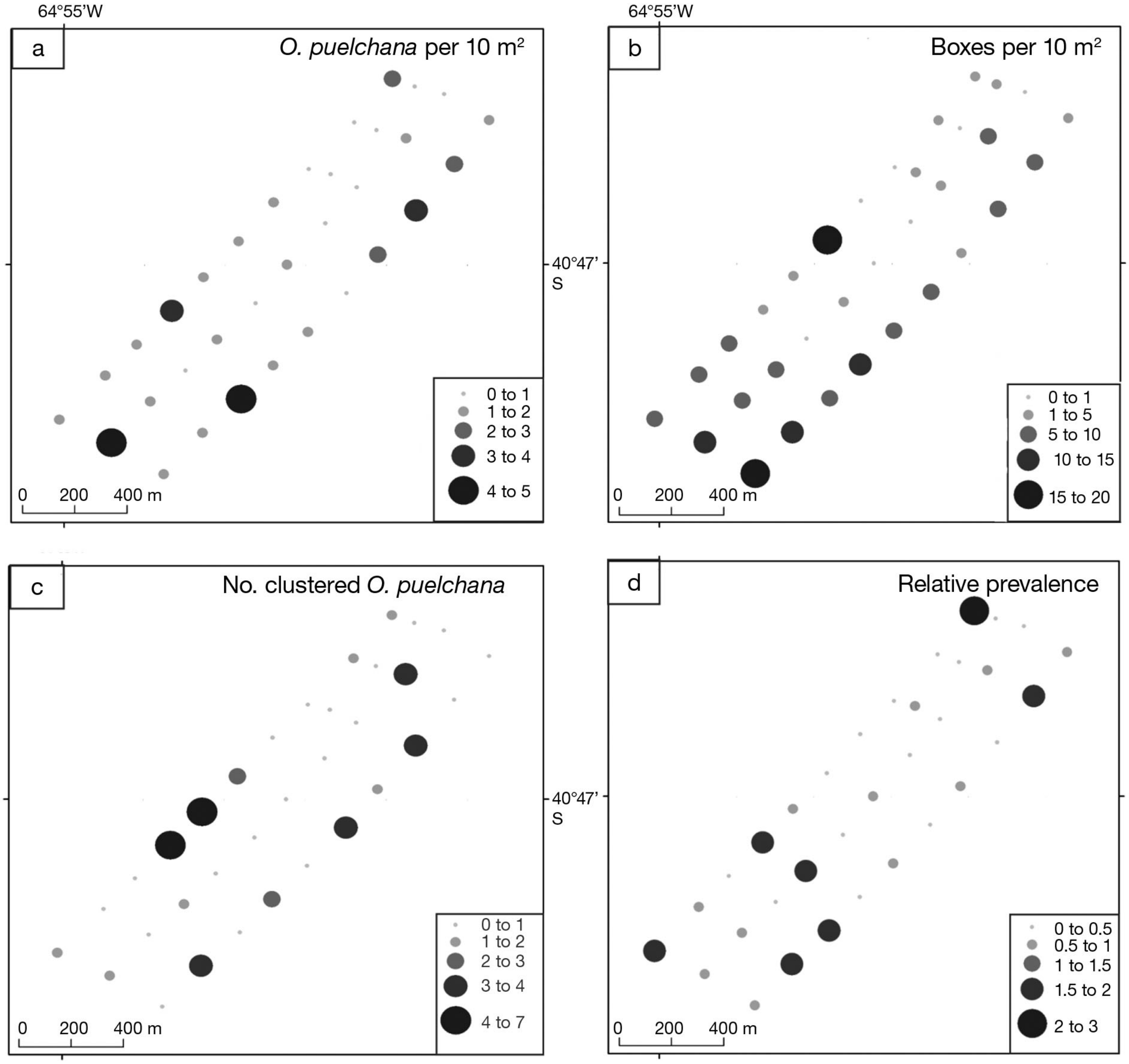

Fig. 4. *Ostrea puelchana*. Spatial distribution of living and dead oysters (boxes), clustered oysters, and prevalence of infection, estimated from the survey of the Banco Reparo bed. (a) Density per 10 m^2. (b) Density of boxes per 10 m^2. (c) Number of clustered oysters per sampling station. (d) Distribution of relative prevalence of infection

tensity was significantly high (stage 3 to 5). Unlike LG, the number of boxes was high (n = 455), homogenously scattered over 70% of the total bed area (Fig. 4b). Analyzing the relationship between infection and the type of aggregation revealed differences between beds. At LG, the probability of infection was independent of the type of aggregation ($\chi^2 = 3.99$, df = 2, p = 0.13), while at BR infection was not independent, and carrier oysters were more infected ($\chi^2 = 8.97$, df = 2, p = 0.01; Table 1). Regarding the sex category, infection was independent of the sex category for both beds (LG: $\chi^2 = 0.91$, df = 2, p = 0.63; BR: $\chi^2 = 1.96$, df = 2, p = 0.37; Table 2).

Hemocytic infiltration was observed in 33.3% of oysters. The presence of such infiltration in connective tissue around the intestine, digestive gland, and mantle is one of the main microscopic signs of *Bonamia exitiosa* infection in *Ostrea puelchana* (BR: $\chi^2 = 58.04$, df = 1, p < 0.001; LG: $\chi^2 = 26.64$, df = 1, p < 0.001; Kroeck 2010).

The size structure of infected and non-infected oysters was different in both beds (LG: KS = 0.28, p = 0.05; BR: KS = 0.65, p < 0.001). Infected oysters were larger than non-infected ones. Infected oysters of all size classes were found, and at LG the highest prevalence (66.7%) was found for the 66–75 mm class,

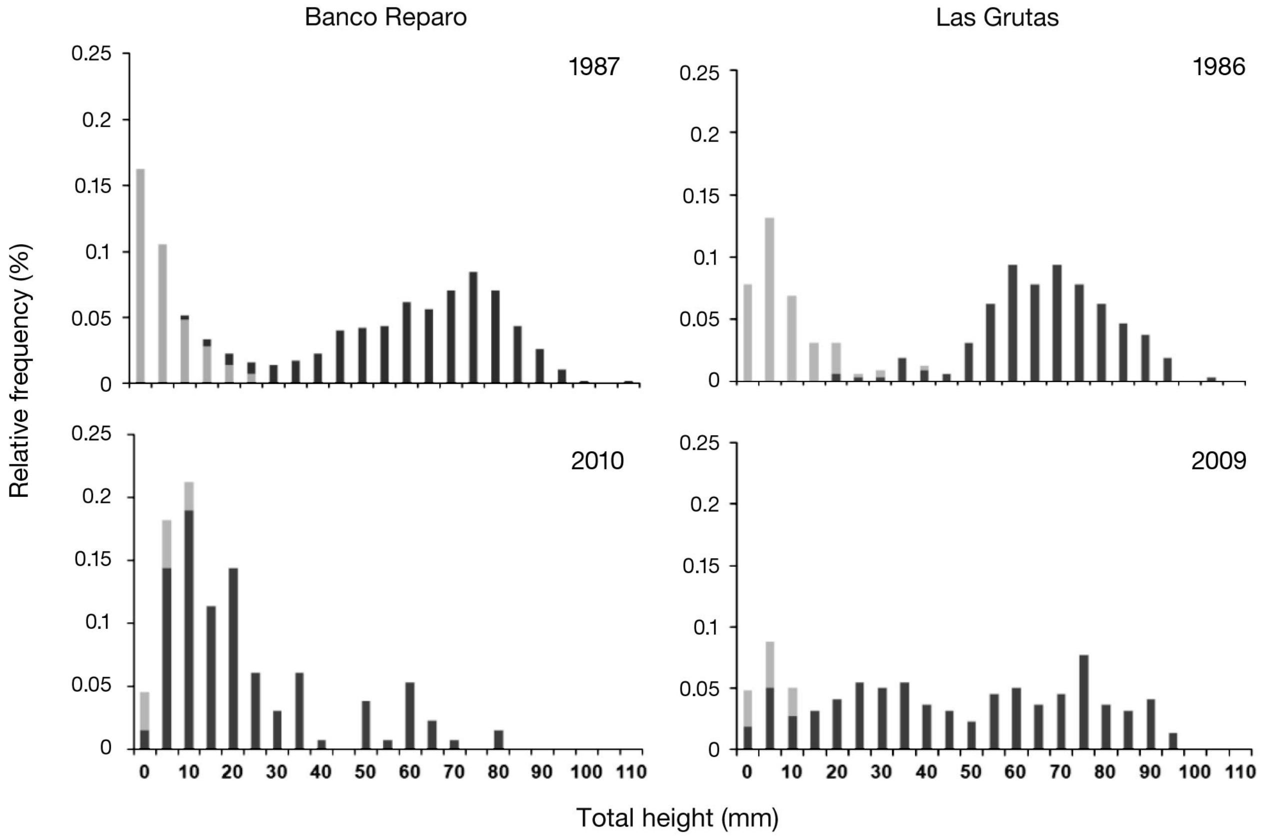

Fig. 5. *Ostrea puelchana*. Size frequency distribution at Banco Reparo and Las Grutas beds in 1986–1987 (top) and 2009–2010 (bottom). Light grey: epibiontic males; dark grey: free oysters

while at BR the highest prevalence (95%) was for the 46–55 mm size class.

Prevalence for the size range reported in 1996 to 2001 (36–105 mm) was 45.8% for oysters larger than 53 mm (n = 48) at LG and 66.7% at BR (in sizes >36 mm, n = 27).

DISCUSSION

In this study, we re-visited 2 natural beds severely affected by *Bonamia exitiosa* epizootics during 1997 to 2001 to perform a population and epidemiological analysis of the current state of the beds. We found modifications to the extent of the beds, size structure, total abundance of oysters, and number of oysters affected by *B. exitiosa*.

The parasite seems to respond positively to *Ostrea puelchana* density, as would be expected for a directly transmissible parasite. Oyster densities were low at both beds. At LG, current density (maximum density: 4.8 ind. per 10 m^2) decreased markedly compared with the 1987 density (maximum density: 22 ind. per 10 m^2, Pascual et al. 2001). At BR, the bed extension remained invariant with respect to that reported by Pascual (1993), but the maximum density decreased considerably (from 32 ind. per 10 m^2 in 1993 to 5.2 ind. per 10 m^2 in 2010). The densities of the boxes differed between beds (Table 3); however, this difference cannot be explained simply by oyster mortality. The differences could be due to differences in oceanographic conditions along the coast and differences of time during which the valves are held together as boxes. These uncertainties invalidate the use of boxes to infer pulses of mortality from a simple

Table 3. *Ostrea puelchana*. Comparison of the number of live oysters and boxes found between 1986/1987 and 2010 on the beds of Las Grutas and Banco Reparo. nd: no data

Year	No. live oysters	No. boxes	Size (mm) Max.	Min.	Mean	SD
Banco Reparo						
1986	1327	nd	120	10	68.69	17.34
2010	132	455	80.29	2.23	23.52	14.78
Las Grutas						
1987	722	nd	115	15	66.67	18.67
2010	233	30	99.97	0.02	41.31	29.20

survey. To detect a pulse of mortality, a time series of density with records of the number of boxes is needed.

Mean oyster sizes at both beds were different and significantly lower than those reported for the 1986 to 1987 period (Table 3, Fig. 5). At LG, the size frequency distribution was modified, but the size range remained unchanged. On the other hand, the bimodal pattern at BR was similar to that reported in previous studies, but the size distribution was mainly dominated by smaller oysters (Fig. 5). This difference may be considered as evidence of recovery. However, in the previous studies at BR, no recruitment was detected, and the demographic composition was represented only by adult oysters (Pascual 1993). The reduction in oyster densities and the modification of the size patterns may be due to the combination of different factors. However, the epizootic disease that occurred 14 yr ago was probably the factor with the greatest impact in reducing the number and density of oysters.

Total prevalence of *Bonamia exitiosa* differed between beds. At LG, prevalence was 35.3%, which suggested that even when density decreased, the size range remained the same and the abundance of infected oysters increased proportionally. Prevalence was lower at BR than at LG. This difference may be attributed to the fact that most sampled oysters at BR were recruits (85.6%), which are not the most infected. Total prevalence based on the size range analyzed by Kroeck et al. (2008) showed a proportional increase in the abundance of infected oysters to approximately double for both beds compared to 1996 to 2001 results.

In 1978 to 1979, Morriconi & Calvo (1989) noted that at LG all 3 types of aggregation were present, while at BR free oysters and carrier oysters were predominant. In our study, the same pattern of aggregation was observed in both beds. The 3 types of aggregations were found in similar proportions in infected oysters at LG, whereas at BR, a higher prevalence of carrier oysters was observed.

We found infected oysters of all sizes and noted differences between the sizes of infected and noninfected oysters, with the mean size of infected oysters being larger than that of non-infected oysters. When describing the evolution of the infection, some authors have argued that there is a 'critical age' of infection. In the case of *Bonamia ostreae* infecting *Ostrea edulis* (Culloty & Mulcahy 2001), infection was observed for all age classes, but parasite levels became significant only after the first spawning event (approximately 2 yr old). On the other hand, Cáceres-Martínez et al. (1995) argued that the presence of *Bonamia* is related to size more than to age. In our survey, the highest values were found in oysters larger than may represent individuals older than 2 yr (M. del Socorro Doldan unpubl. data). This work confirms studies by Burreson et al. (2004) and Bishop et al. (2006). Large oysters filter more water because of their size, while older oysters, having been exposed to *B. exitiosa* for a longer time, have higher levels of parasitism. Infected oysters basically accumulate the parasite throughout their lifespan. In this sense, bonamiosis in *O. puelchana* in Argentina looks more like a chronic parasitosis than an acute disease. The beginning of the infection might coincide with the beginning of the functionality of the feminine phase, which occurs when oysters reach a shell size of 50 to 55 mm (Pascual et al. 2001). This hypothesis was partially supported by the results found at BR, where prevalence was higher for carrier oysters. However, the probability of infection was independent of the sex category, as found for *O. edulis* infected by *B. ostreae* (Cáceres-Martínez et al. 1995, Culloty & Mulcahy 1996) and earlier for *O. puelchana* infected by *B. exitiosa* (Kroeck & Montes 2005).

After 14 yr of epizootic disease, natural *Ostrea puelchana* beds have decreased in oyster densities and in extent, while size structure has also been modified. Regarding *Bonamia exitiosa*, we have observed a persistent infection over time and an increase in prevalence. However, oyster beds continue to remain viable and recruitment occurs despite the infections. Future studies will provide evidence of whether beds have recovered their pre-epizootic density and extent or whether they continue to decline.

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