



Species associations and environmental factors influence activity of borers on *Ostrea puelchana* in northern Patagonia

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ABSTRACT

Seven borer species were identified affecting *Ostrea puelchana* in the southwestern Atlantic Ocean, including the sponges *Clionaopsis platei*, *Pione angelae* and *Cliona celata* (Clionidae), the borer bivalve *Lithophaga patagonica* (Mytilidae) and the polychaetes *Polydora rickettsi* (Spionidae), *Dodecaceria* cf. *choromytica* and *Caulleriella* cf. *bremecae* (Cirratulidae). Higher prevalences of borer sponges (55%) occurred in oysters from Puerto Lobos, Golfo San Matías (42°00'S, 65°3'W), while higher values of *L. patagonica* (80%) and borer polychaetes (93%) were recorded in oysters from Fracasso Beach, Golfo San José (42°25'S, 64°07'W). *Lithophaga patagonica* was the most harmful borer organism, lowering the condition index of the oyster. There was a positive association between the presence of *L. patagonica* and borer polychaetes, suggesting that the borer activity of *L. patagonica* favored the settlement of polychaetes.

INTRODUCTION

Borer organisms are a serious concern for bivalve farming and shellfisheries worldwide (Radashevsky & Pankova, 2013). The pathology caused by these organisms can be severe, depending on the degree of incidence and the species involved. The commonest borer organisms are sponges, bivalves and spionid polychaetes (Cremonte, 2011).

Interspecies interactions have traditionally been divided into 'interference', the negative effect of one species on another (e.g. Steele, 1998) and 'facilitation', the positive effect of one species on another (Callaway, Nadkarni & Mahal, 1991). Previous studies have reported an association between commensal polychaetes and boring sponges, where the latter provide 'advantageous' protective physiological or morphological characteristics (holes, chambers or channels) for the polychaetes (Bower, McGladdery & Price, 1994; Martín & Britayev, 1998). Martín (1996) reported a mutualistic association between the polychaete *Polydora rogeri* and the borer sponge *Cliona viridis*, suggesting that the feeding activity of the polychaete can be favoured by the inhalant flow generated by the filtering activity of the sponge, while the faeces discharged by the polychaete could be used as food by the sponge. Evans (1969) identified a positive relationship between borer bivalves (*Saxicava arctica*) and borer sponges, where the former nestle in empty holes previously excavated by *Cliona vastifica*.

In the Golfo San Matías (GSM) and Golfo San José (GSJ) of northern Patagonia (Argentina), the oyster *Ostrea puelchana* d'Orbigny, 1842 (Ostreidae) is commercially exploited (Orensanz *et al.*, 2006). The mytilid *Lithophaga patagonica* and the

polydorid *Polydora rickettsi* have already been reported boring on this oyster (Mauna *et al.*, 2005; Diez *et al.*, 2011). Here we provide further identification of borer species on *O. puelchana* and report their prevalence. We also investigate how the prevalence of these borer species is influenced by several variables (population origin, condition index, total weight, shell length, gonadal development stages of the oyster and presence of other borer species) using generalized linear model (GLM) analysis.

MATERIAL AND METHODS

Study area and sampling

The GSJ is a small, shallow, semi-enclosed waterbody (817 km²; mean depth 30 m) located on the northern coast of Argentinian Patagonia. It opens to the north into the much larger GSM (18,000 km²) through a narrow (6.9 km) mouth (Amoroso *et al.*, 2011). Oysters (40–117 mm maximum length) were collected monthly by scuba diving at Puerto Lobos, GSM (42°00'S, 65°3'W) from January to May 2006 ($n = 129$) and at Fracasso Beach, GSJ (42°25'S, 64°07'W) from January to December 2006 ($n = 295$).

Histological processing

The maximum valve length of each specimen was measured and valves and soft parts were inspected for the presence of borer organisms. Soft parts were removed from their valves and

separately weighed to calculate the condition index ((soft part weight/valve weight) \times 100) (Lucas & Benninger, 1985). Soft parts were fixed in Davidson's fixative (Howard *et al.*, 2004) and processed for histology (haematoxylin-eosin). Histological sections were examined under a light microscope, recording gonad development stages following Morriconi & Calvo (1979).

Identification of borer organisms and description of their boring activity

Borer sponges and polychaetes were taxonomically identified using light and scanning electron microscopes. Spicule mounts for identification of sponges were obtained after freeing the skeleton from the cellular material by treatment with sodium hypochlorite (Rützler, 1974); length and width of sponge spicules were measured. Polychaete specimens were preserved in ethanol and identified on the basis of the morphology of chaetae. Voucher specimens were deposited in the Museo Argentino de Ciencias Naturales Bernardino Rivadavia (MACN-In 39178-39183). Oyster valves were X-rayed to describe the morphology and the extent of the chambers caused by borer organisms.

Data analysis

Prevalences for each of the three borer taxa (sponges, bivalve and polychaetes) were calculated as the percentage of oyster valves occupied. Intensities of *Lithophaga patagonica* specimens on oysters were calculated as the numbers of specimens or cavities per oyster valve. Three GLMs fitted with a binomial distribution with a logit link function (Crawley, 2000) were applied to assess the variables associated with the presence of each borer taxon (response variable). Different models were used to test these variables with regard to the following predictor variables: population site origin, oyster condition index, total weight, shell length, presence of borer sponges, presence of *L. patagonica* specimens, presence of borer polychaetes and the interactions among the borer organisms. The Akaike information criterion (AIC) was used to determine the best model for the analysed dataset. Model selection was performed with an IT approach using the AIC and model averaging (Grueber *et al.*, 2011). The AIC values and the AIC for small samples (AICc) were calculated for each model. Because the presence of borer sponges was overdispersed, we calculated an AIC modified by the principle of quasilikelihood (QAIC) and a version of QAIC for small sample sizes (QAICc). From the AICc differences (D_i), where $D_i = AICc_i - AICc_{min}$, Akaike weights (w_i) were obtained for all candidate models. For each dataset, the models were ranked by their w_i values. The model with the highest w_i was considered the one with the best supporting data. Model averaging was calculated using candidate models, which together account for the 95% confidence level. The top model set was averaged using a zero method (Symonds & Moussalli, 2011), where the best AIC model was not strongly weighted. The global model was performed in R (R Development Core Team, 2012) and the standardized function to input variables is available within the 'arm' (Data Analysis Using Regression and Multilevel/Hierarchical Models) package (Gelman *et al.*, 2009). Model selection and averaging were calculated with the MuMIn package (Barton, 2009). The predictor variables in the top models were reported with their relative importance weights, model-averaged parameter estimates, unconditional standard error and 95% confidence intervals. Results were expressed in terms of odds ratios. Odds were calculated as the exponential of the coefficient of each parameter corresponding to the averaging model.

To take into account some important information about these variables, a χ^2 test with $\alpha = 0.05$ and a Kruskal-Wallis test were

performed in punctual comparisons before applying GLMs. A χ^2 test was used to evaluate the significance of differences in frequencies of occupation of borers on left and right valves and to compare the frequencies of occupation of borer sponges and borer polychaetes with the gonadal development stages regrouped in four stages, to simplify the statistical analysis (maturation, total maturation, post-spawn masculinization and male predominant) of *O. puelchana*. The Kruskal-Wallis test was applied to compare intensity of *L. patagonica* specimens with different gonadal development stages (Siegel & Castellan, 1998).

RESULTS

Seven species of borer organisms were identified affecting *Ostrea puelchana*: three sponges, *Clionaopsis platei* (Thiele, 1905), *Pione angelae* Urteaga & Pastorino, 2007 and *Cliona celata* Grant, 1826 (Clionidae); the bivalve *Lithophaga patagonica* (d'Orbigny, 1842) (Mytilidae) and three polychaetes, *Polydora rickettsi* Woodwick, 1961 (Spionidae), *Dodecaceria* cf. *choromyticola* Carrasco, 1977 and *Caulleriella* cf. *bremecae* Elías & Rivero, 2009 (Cirratulidae).

The borer sponge *C. platei* was recorded only in the GSJ, *P. angelae* only in the GSM and *C. celata* in both gulfs. Their borer activity, revealed by X-rays, resulted in a tunnel network, consisting of short interconnected tubular galleries forming a polygonal network that occupies the entire valve thickness (Fig. 1A). Prevalence was higher in oysters from the GSM (55%) than in those from the GSJ (29%). Model analysis resulted in five top models with $\Delta QAIC < 2$ of the best model (Table 1). Population origin (gulf) emerged as the most robust predictor variable, with a relative importance weight of 1.00 and 95% confidence interval that did not include zero (Table 1). The probability of finding an oyster with borer sponges in the GSM was 3.32 ± 1.34 times higher than in the GSJ. Although both oyster total weight and presence of *L. patagonica* specimens had a relative importance weight of 1.00, the effects of these predictor variables were not significant, since their confidence intervals included zero (Table 1).

Specimens of *L. patagonica* were more frequent close to the umbo and in the so-called platform areas of the left valve, as well as in the insertion of the adductor muscle area of the inner surface of the oyster valve (Fig. 1B). When the cavities bored by the bivalve reached the inner surface of the valve, dark spots were visible (Fig. 2A). Prevalence of *L. patagonica* was higher in oysters from the GSJ (80%) than those from the GSM (64%). The model analysis resulted in five top models with $\Delta AIC < 2$ of the best model (Table 1), and all explanatory variables considered in the global model were included in at least one model in the top model set. Confidence intervals of oyster condition index, total weight and presence of polychaetes did not include zero (Table 1). A negative relationship was found between the presence of *L. patagonica* specimens and oyster condition index, indicating that the oysters affected by these borers had a poorer condition (Fig. 2B). In addition, the presence of *L. patagonica* was positively related to the presence of borer polychaetes. The model indicated that the probability of finding one oyster bored by *L. patagonica* increased 9.97 ± 0.44 times when polychaetes were present. Images by X-ray showed that the burrows made by the borer polychaetes began around the cavities made by *L. patagonica* (Fig. 1C).

Three polychaete species were found in oysters from both the GSM and the GSJ. Borer activity was mostly present in the ventral region of the oyster valve (Fig. 1C). Prevalence was higher in oysters from the GSJ (93%) than in those from the larger and more open GSM (55%). The model analysis resulted in three top models with $\Delta AIC < 2$ of the best model (Table 1), where the confidence intervals of population origin, oyster condition index and presence of *L. patagonica* did not include zero.

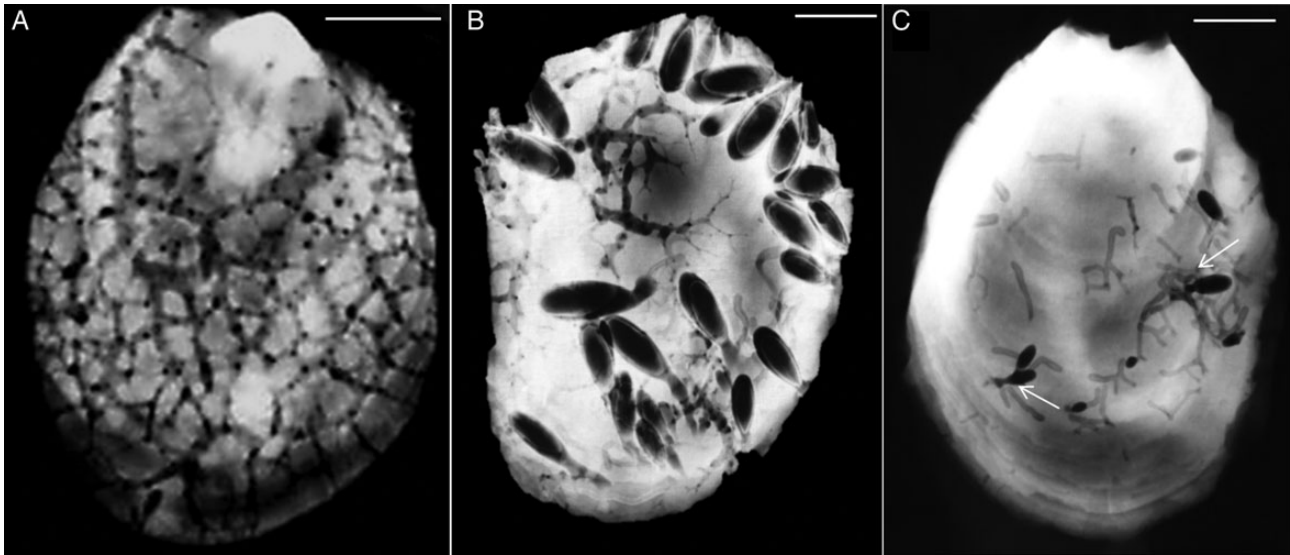


Figure 1. X-ray images showing the activity of borer organisms in valves of *Ostrea puelchana* from northern Patagonia. **A.** Tunnel network of shell burrows made by sponges. **B.** Cavities made by *Lithophaga patagonica*. **C.** Burrows (arrows) made by boring polychaetes begin around the cavities made by *L. patagonica*. Scale bars: **A** = 20 mm; **B** = 10 mm; **C** = 25 mm.

The probability of finding one oyster bored by *L. patagonica* specimens in the GSM was 17.99 ± 1.53 times lower than in the GSJ. In addition, a positive relationship between the presence of *L. patagonica* and polychaetes was observed, indicating that the probability of finding polychaetes in one oyster bored by *L. patagonica* was 9.11 ± 1.48 times higher than in an oyster without *L. patagonica* (Table 1).

The frequency of boring by each of the three taxa studied (sponges, bivalve and polychaetes) was significantly higher on

the left than on the right valve ($\chi^2 = 42.2$, $\chi^2 = 84.6$, $\chi^2 = 30.1$, $P < 0.001$, respectively). No associations between the frequencies of borer sponges and polychaetes and the gonadal development stages of *O. puelchana* were observed ($\chi^2 = 3.5$, $P = 0.278$; $\chi^2 = 2.2$, $P = 0.52$, respectively) or between the intensity of *L. patagonica* and the gonadal development stages (Kruskal-Wallis, $P = 0.55$). Nevertheless, the highest prevalences of the three boring taxa were observed during the post-spawning stage of the oysters (23, 36 and 30%, respectively).

Table 1. Predictor variables from top models for each response variable in *Ostrea puelchana* from two northern Patagonian gulfs.

| Response | Predictor variable | Estimate | SE | 95% CI | | wi |
|----------------------------------|---|----------|------|--------|-------|-------------|
| Presence of borer sponges | Intercept | -0.61 | 0.13 | -0.87 | -0.36 | |
| | Population origin (GSM)* | 1.20 | 0.29 | 0.61 | 1.78 | 1.00 |
| | Condition index | -0.02 | 0.11 | -0.25 | 0.20 | 0.15 |
| | Total weight | 0.75 | 0.26 | -0.22 | 1.28 | 1.00 |
| | Shell length | 0.00 | 0.11 | -0.22 | 0.23 | 0.13 |
| | Presence of <i>L. patagonica</i> | 0.62 | 0.34 | -0.05 | 1.31 | 1.00 |
| | Presence of polychaetes | 0.02 | 0.26 | -0.48 | 0.54 | 0.37 |
| | <i>L. patagonica</i> : polychaete | -0.26 | 0.60 | -1.46 | 0.92 | 0.22 |
| Presence of <i>L. patagonica</i> | Intercept | 1.41 | 0.15 | 1.10 | 1.72 | |
| | Condition index | -0.67 | 0.29 | -1.24 | -0.09 | 1.00 |
| | Total weight | 1.17 | 0.46 | 0.25 | 2.08 | 1.00 |
| | Shell length | 0.58 | 0.49 | -0.38 | 1.55 | 0.72 |
| | Presence of boring sponges | 0.27 | 0.34 | -0.39 | 0.93 | 0.58 |
| | Presence of polychaetes | 2.32 | 0.36 | 1.60 | 3.03 | 1.00 |
| | Boring sponges: polychaetes | -0.06 | 0.32 | -0.70 | 0.56 | 0.14 |
| | | | | | | |
| Presence of borer polychaetes | Intercept | 2.34 | 0.23 | 1.87 | 2.80 | |
| | Population origin (GSM)* | -2.89 | 0.43 | -3.74 | -2.05 | 1.00 |
| | Condition index | 1.26 | 0.43 | 0.40 | 2.11 | 1.00 |
| | Total weight | 0.11 | 0.26 | -0.40 | 0.62 | 0.3 |
| | Presence of boring sponges | 0.03 | 0.19 | -0.34 | 0.41 | 0.2 |
| | Presence of <i>L. patagonica</i> | 2.21 | 0.39 | 1.43 | 2.98 | 1.00 |

Coefficient estimates, their unconditional standard error (SE), 95% confidence interval (CI) and relative importance weights (wi) after model averaging are shown. Variables in bold have a 95% confidence interval that does not include zero (significant results).

*The GSJ was the reference sampling site.

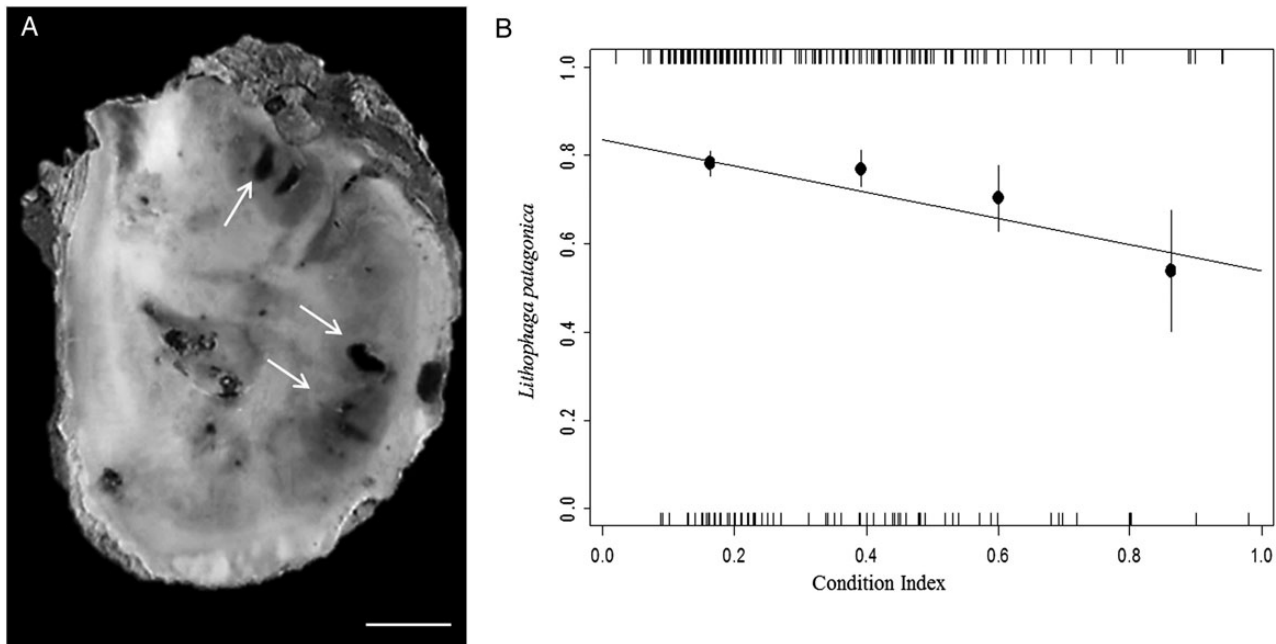


Figure 2. **A.** Dark spots in the inner surface of the valve of *Ostrea puelchana* caused by boring by *Lithophaga patagonica*. Scale bar 20 mm. **B.** Relationship between the absence (0) or presence (1) of *L. patagonica* specimens and oyster condition index.

DISCUSSION

A total of seven species (three sponges, one bivalve and three polychaetes) were identified as shell-boring species on *Ostrea puelchana* in the two contiguous northern Patagonian gulfs. Among the species identified, the borer sponge *Clionaopsis platei* constitutes the first record in the southwestern Atlantic Ocean. *Pione angelae* is recorded for the first time in the GSM (42°S), extending its known distribution southwards from Mar del Plata (38°S) (Urteaga & Pastorino, 2007). The polychaetes *Dodecaceria* cf. *choromyticola* and *Caulleliella* cf. *bremecae* (Cirratulidae) are the first records on *O. puelchana* and for both Patagonian gulfs.

The presence of borer sponges on *O. puelchana* valves was mainly influenced by the host population origin (i.e. gulf), since neither oyster total weight, nor the presence of *Lithophaga patagonica* had a significant influence on the presence of borer sponges.

The most harmful borer was the mytilid bivalve *L. patagonica*. Boring by *L. patagonica* had a significantly detrimental effect on oyster condition. This could perhaps be associated with additional metabolic energy costs for the host, since the oyster mantle tissue produces organic matter (conchiolin) (Lauckner, 1983) to seal off the holes. In addition, a positive relationship between the presences of *L. patagonica* and boring polychaetes was found. It is known that the settlement of a given species may be affected by previously settled species, which inhibit or promote rates of subsequent occupation. In our study, the feeding activity of *L. patagonica* specimens may favour the later settlement of borer polychaetes, since the latter could take advantage of the current flows generated by ciliary action of the gills of the mytilid bivalve to capture food particles more easily. Moreover, the cavities bored by *L. patagonica* may also provide shelters favouring the settlement of larvae of the polychaete. This is very likely for *D. cf. choromyticola* and *C. cf. bremecae*, since these cirratulid polychaetes are considered to be secondary borers because they occupy and adapt to vacant diggings carried out by primary borers (Rozbaczylo *et al.*, 2007). Nevertheless, further experimental studies are necessary to assess this relationship.

The higher prevalences of *L. patagonica* and boring polychaetes recorded for oysters from Fracasso Beach (GSJ) may be related to the particular characteristics of this environment. Amoroso & Gagliardini (2010) suggested that a combination of circulation, tidal currents, coastal topography and bathymetry creates particular conditions for high primary productivity and larval retention. The GSJ is divided into two oceanographic domains (West and East) with distinct hydrographic regimes. The West domain is connected with the GSM and is highly turbulent due to the formation of vortices and dipoles during the tidal cycle, while the East domain is less turbulent and more homogeneous, where the nutrients from the continental shelf are ‘trapped in’ and larvae are retained (Amoroso & Gagliardini, 2010; Amoroso *et al.*, 2011). Fracasso Beach is located in the East domain, where the oceanographic characteristics would favour the retention of larvae of *L. patagonica* and polychaetes.

Furthermore, the prevalence of borer organisms seems to be influenced by the life position of the oyster. Prevalence was significantly higher on the left valve (uppermost in life position) with respect to the right valve (lowermost), probably representing differential larval settlement advantage/preference.

Our study is the first to consider the relationship between the borer organisms and the gonadal development stages of the oyster. We did not find a direct relationship between the gonadal development stages of *O. puelchana* and prevalence of any of the borer taxa; however the oysters in the post-spawning stage were more frequently bored. During this stage, the oysters store energy for the next gametogenesis cycle, which might reduce the investment of energy required to seal off bored holes, making the oyster weaker and thereby increasing the probability of further occupation by borers.

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