

Differential Settlement of Associated Species on *Ostrea puelchana* d'Orbigny, 1842 (Ostreidae) in Patagonia (Argentina)

Author(s): M. V. Romero , S. S. Brezina , D. Hernández , S. Casadío and C. Bremec

Source: American Malacological Bulletin, 31(2):311-320. 2013.

Published By: American Malacological Society

DOI: <http://dx.doi.org/10.4003/006.031.0210>

URL: <http://www.bioone.org/doi/full/10.4003/006.031.0210>

BioOne (www.bioone.org) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/page/terms_of_use.

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

Differential settlement of associated species on *Ostrea puelchana* d'Orbigny, 1842 (Ostreidae) in Patagonia (Argentina)

M. V. Romero^{1,2}, S. S. Brezina³, D. Hernández², S. Casadío^{1,3} and C. Bremec^{1,2}

¹ Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Rivadavia 1917, 1033AAJ, Buenos Aires, Argentina

² Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), Paseo Victoria Ocampo 1, B7602HSA, Mar del Plata, Argentina

³ Instituto de Investigación en Paleobiología y Geología, Universidad Nacional de Río Negro (UNRN), Isidro Lobo y Belgrano, (8332) Gral. Roca, Argentina

Correspondence, M.V. Romero: mvromero@inidep.edu.ar

Abstract: *Ostrea puelchana* d'Orbigny, 1842 is a common species of commercial interest in Patagonia and is distributed from Rio Grande do Sul (Brazil) to San Matías Gulf (SMG, Argentina). In SMG, the species develops natural banks that provide irregular surfaces suitable for colonization of organisms. We studied the composition and frequency of encrusting and associated species on *O. puelchana* shells as well as the preferential settlement of epibionts on different areas within left and right valves. A total of 55 taxa were identified. The dominant groups were Annelida, Foraminifera, Bryozoa and Mollusca in two different oyster banks. The lifestyle of the oyster favors a preferential settlement of epibionts on different valves and areas within the valves. Substratum heterogeneity, reproductive cues, gregarious behavior, protection against predation and/or brooding care could be responsible for this differential settlement. The left valve was more encrusted than the right one. Spirorbinae, Cirratulidae, Foraminifera, juvenile *O. puelchana*, Bryozoa and Hydrozoa showed preferential settlement in different areas on the external left valves. On the external right valves, the same taxa except for Hydrozoa showed a nonrandom distribution between areas.

Key words: Epibiosis, oyster, preferential colonization, SW Atlantic Ocean

Colonization of hard substrates is a well-known phenomenon in marine environments since the Archaean (Taylor and Wilson 2003). In such environments, availability of stable substrate for the settlement of sessile organisms is a main resource in the colonization process (Wahl 1989). However, in soft bottoms, a wide variety of biogenic, abiogenic and even anthropogenic surfaces are often occupied and provide available substrate for settlement and shelter of benthic invertebrates (Taylor and Wilson 2003).

Epibiosis is defined as a spatial and non-symbiotic association in which a living organism is used as substrate (basibiont) by a sessile organism (epibiont). Trophic exchange with the substrate organism, if present, is facultative (Wahl 1989). Usually, this interaction is not specific (Barnes and Clarke 1995, Cook *et al.* 1998, Wahl and Mark 1999, Williams and McDermott 2004) and both organisms may experience advantages and disadvantages depending on the species involved in the association and on the environmental variables (Wahl 2009). In consequence, the nature of the effects of epibionts on basibionts is often context-specific (Hay *et al.* 2004, Wahl 2008).

Oysters are ubiquitous and provide stable substrates for settlement and development of benthic communities (Dauer *et al.* 1982, Zimmerman *et al.* 1989, Rosell *et al.* 1999). In soft bottoms, oyster larvae or spat settle on adult oysters, shell fragments, rhizomes and stems of *Spartina* Schreb or consolidated sediment (M.V. Romero pers. obs., Escapa *et al.* 2004,

Borges 2006, Kochmann *et al.* 2008). Thus, they generate aggregates or clusters on adult oysters resulting in large accumulations that can modify the environment with their own physical structure and create different habitats available for colonization (Gristina *et al.* 1996, Barnes 2001, Zuschin and Baal 2007).

Oyster reefs and associated fauna also play an important role in carbon, nitrogen and phosphorus cycles, allowing the mineralization of organic carbon and the release of nitrogen and phosphorus available to primary producers (Parras and Casadío 2006). They can modify the speed and turbulence of water flow as a consequence of growth in aggregates, causing changes in the availability of resources that affect other organisms (Lenihan 1999). Finally, reefs may offer protection against predation and physical stress generated by wave action (Kochmann *et al.* 2008). These changes in structure and performance of an ecosystem caused by certain species have been included in the conceptual framework of ecosystem engineering (see Jones *et al.* 1994, 1997).

Numerous recent papers have focused on key issues such as distribution, diversity, management, conservation and restoration of oyster reefs and coastal marine estuarine systems throughout the world (7th International Conference on Shellfish Restoration 2005, Carranza *et al.* 2009). Most knowledge available about changes in diversity of benthic communities associated with oysters compare the macrofauna composition

between exploited and unexploited reefs or between reefs and surrounding habitats or substrates (de Grave *et al.* 1998, Escapa *et al.* 2004, Hosack *et al.* 2006, Rodney and Paynter 2006, Markert *et al.* 2010, Lejart and Hily 2011). However, few studies have examined the shell surfaces of oysters and associated epifauna collected from natural reefs, banks or beds.

Ostrea puelchana d'Orbigny, 1842, often known as "puelche" or "Patagonian oyster", is a common species in Patagonia that belongs to the family Ostreidae, subfamily Ostreinae (Stenzel, 1971). The shell is inequivalve; right valve tends to be flat and smooth whereas the left valve is convex and rough with pronounced ribs and scarce lamellae. The right valve is covered by many conchiolinous growth squamae (*i.e.*, lamellae) that develop from the center of valve toward the labrum, reaching thicknesses greater than 1.5 cm.

Ostrea puelchana is an endemic/native species (Sacco, 1897) widely distributed from Rio Grande do Sul (27°–35°S, Brazil) to San Matías Gulf (SMG) (40°–42°S, Argentina), where major banks with commercial interest are reported (Castellanos 1957, Rios 1970). Recently, Oehrens Kissner *et al.* (2011) recognized the development of small banks in San José Gulf (42°20'S, 64°20'W). *Ostrea puelchana* can reach a commercial height of 120 mm, although fishery is not established in the market (Borges 2006). The species develops natural extensive banks that provide highly irregular surfaces suitable for colonization of other organisms. However, information about the biota associated with its shells is scarce and refers to particular infestations (Mauna 2003, Cremonte *et al.* 2005, Rodríguez 2007, Diez *et al.* 2011). We studied the composition, frequency and distribution of encrusting and associated species on the shells of *O. puelchana* in SMG. The preferential settlement of epibionts on different areas within left and right valves was evaluated.

MATERIALS AND METHODS

Study area

SMG is located between 40°42'–42°41'S and 63°45'–65°09'W and presents important biological and fishery production (Morsan 2002, Narvarte *et al.* 2011). This is a semi-enclosed area within the Argentinian shelf with particular oceanographic features (Guerrero and Piola 1997), maximum depths near 200 m in the central area (Parker *et al.* 1997) and a macrotidal regime (Servicio de Hidrografía Naval 2010). The average salinity is high (33.84) and the average annual temperature is 13.25 ± 0.20 °C with strong thermal stratification mainly in summer (Rivas 1990). The bottom type is dominated by sands with high contents of silt and clay (Parker *et al.* 1997). Oyster banks are located on sand or sand-gravel facies deeper than 10 m depth (Escofet *et al.* 1978).

Sampling

Oysters ($N = 142$) were collected in February 2009 in two natural banks located at northwest of SMG (Fig. 1), called *El Buque* (EB, 40°50'S, 65°10'W) and *Zona de Colectores* (ZC, 40°56'S, 65°06'W), at 12 and 18 m depth at low tide, respectively. Samples were taken randomly within the most densely packed zone of each bank. Oysters were placed in tanks with circulating sea water. To avoid loss of macrofauna associated to the valve, each oyster was stored individually in a plastic bag. Oyster samples were fixed in 5% seawater formalin and 15 days later they were stored in 70% alcohol.

The epibionts and associated fauna of each left/right valve and internal/external shell surface were identified. Both surfaces were mainly considered because an edge along the internal left valve was often available to organism settlement due to breakage of young lamellae of right valves.

Areas were defined on each valve to test preferential colonization. Zonification maps of both valves were used in order to recognize the frequency and distribution of encrusting taxa. This map reflects dissimilar morphological features of the valves that may influence the settlement of different marine larvae and could be used to identify those areas where epibionts may affect the development of the oyster. The external left valve was divided into six areas: apex (10%), platform (5%), anterior margin (15%), ventral margin (25%), posterior margin (15%) and center (30%). There is no platform in the right valves, so the areas were: apex (10%), anterior margin (15%), ventral margin (30%), posterior margin (15%) and center (30%). Presence/absence, abundance (*i.e.*, number of individuals) and/or coverage (*i.e.*, percentage of the area encrusted) data were recorded in standardized maps of each valve (Fig. 2). In the internal left valve, the total available surface to be colonized by epibionts was attributed to edge of

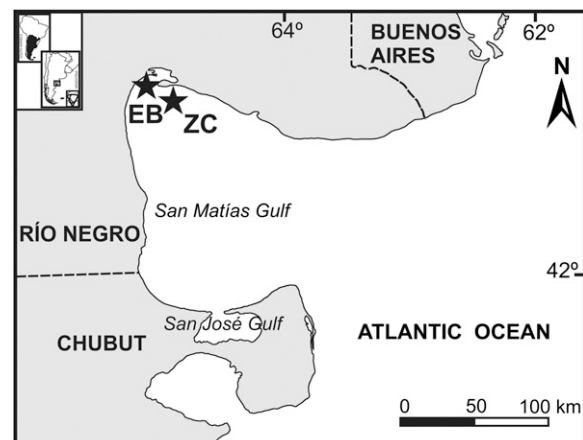


Figure 1. Location of the two oyster banks (EB and ZC) in San Matías Gulf (SMG, Argentina).

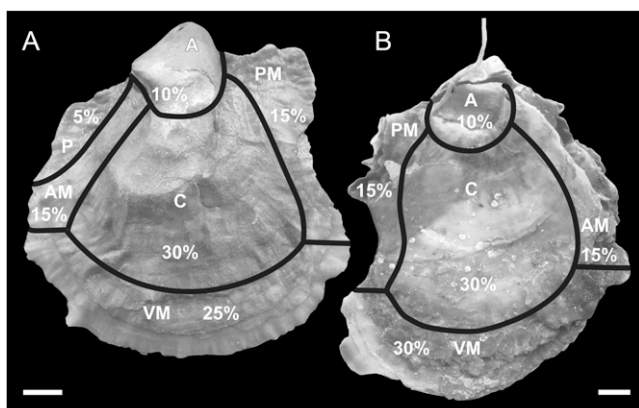


Figure 2. Zonification maps with areas selected in left valves (A) and right valves (B) of *Ostrea puelchana* (external surface). A, apex, AM, anterior margin, C, center, P, platform, PM, posterior margin, VM, ventral margin. Coverage percentage is indicated in each area. Scale bars = 1 cm.

valve. This surface was divided into five areas: apex (15%), platform (15%), anterior margin (20%), ventral margin (30%) and posterior margin (20%). In the internal right valve, the preferential settlement was not evaluated due to the very low observed frequencies.

The percentages were assigned arbitrarily and were estimated for each taxon, following Ward and Thorpe (1991) and Mauna *et al.* (2005). Coverage data were registered for those taxa with colonial forms and for epibionts that can be counted as individuals but can occupy large areas of the valves.

Data analysis

Richness of associated fauna and epibiota on the oyster shells were compared using Multivariate Nonparametric Analysis (PRIMER 6.1.10, see Clarke 1993, Clarke and Warwick 2001). Multidimensional Scaling (MDS), Similarity Percentage (SIMPER) and Analysis of Similarities (ANOSIM) tests were applied to make comparisons between EB and ZC banks (presence/absence data, Jaccard similarity index). MDS and SIMPER analysis were applied to compare right/left valves and their external/internal surfaces using abundance (fourth root transformed data, Bray-Curtis index) and/or coverage (percentage data, Bray-Curtis index). The arithmetic mean of abundances was calculated to identify if right or left valves and external or internal surfaces were more frequently colonized.

Goodness of fit test and exact confidence intervals for the binomial distribution were performed in order to assess possible preference of epibionts on different areas of the valves. When more than 20% of the expected frequencies were less than five, valve areas were grouped to avoid inaccuracies.

Yates's correction for continuity was applied in those cases with only one degree of freedom, and relatively small samples (Zar 1999). The null hypothesis was that the distribution of epibionts on valves is at random on the significance level $\alpha = 0.05$.

RESULTS

Epibionts were present in all the oyster specimens ($N = 142$) collected in EB and ZC banks. A total of 55 taxa belonging to 12 taxonomic groups were identified (Table 1). The highest percentage of occurrence in both banks (EB = 96.5% and ZC = 77.9%) corresponds to polychaetes of the family Cirratulidae, represented by 11 taxa. Other epibionts, including associated fauna, boring and encrusting organisms (*i.e.*, ctenostome bryozoans, skeletons of calcareous algae and barnacle basal plates) occurred only occasionally. Gnawing traces possibly made by the radulae of chitons on the external surfaces of both valves were recognized, most frequently in left (EB = 91% and ZC = 87%) than right valves (EB = 46% and ZC = 35%).

The MDS plot showed a clustering of samples from EB and ZC banks (stress = 0.19) and ANOSIM test indicated no difference in community composition (global $R = 0.099$, $P = 0.1$). SIMPER procedure (Table 2) revealed that Spirorbinae, Bryozoa, Cirratulidae and *Ostrea puelchana* were the taxa that contributed most to the average similarity within every bank (> 62%).

In EB and ZC, MDS between external and internal surfaces of both oyster valves showed two groupings of samples with abundance (stress = 0.12) and coverage (stress = 0.11) data. SIMPER results (Table 2) showed high percentages of average dissimilarity between external and internal surfaces ($\bar{\delta}_{\text{coverage}} = 88.02\%$, $\bar{\delta}_{\text{abundance data}} = 79.18\%$), being Spirorbinae, *Ostrea puelchana*, Bryozoa, Cirratulidae, Hydrozoa, Foraminifera and byssate mytilids the main taxa that contributed to differences. The external surface was more colonized than the internal one (Fig. 3).

Regarding epibiosis in left and right valves, MDS plots based on coverage (stress = 0.15) and abundance (stress = 0.13) data indicated a weak grouping of samples. SIMPER results (Table 2) showed average dissimilarities higher than 63% between left and right valves of *Ostrea puelchana* ($\bar{\delta}_{\text{coverage}} = 63.37\%$, $\bar{\delta}_{\text{abundance data}} = 64.70\%$). The taxa that most contributed to the differences were Cirratulidae, Spirorbinae, Foraminifera and *O. puelchana*. The left valve was, in general, more colonized than the right one (Fig. 4).

The preferential settlement of epibionts on different areas of left and right valves is shown in Figs. 5 and 6, respectively. On the left valve, Spirorbinae preferably colonized the platform and the center of the external surface; while the

Table 1. List of epibionts and associated taxa found on *Ostrea puelchana* sampled at EB and ZC (SMG, Argentina).

Taxa	Taxa
Algae	<i>Mytilus edulis</i> Linnaeus, 1758
calcareous skeletons	<i>Aulacomya atra</i> (Molina, 1782)
Foraminifera	<i>Chaetopleura</i> Shuttleworth, 1853
<i>Miliolinella subrotunda</i> (Montagu, 1803)	Arthropoda
<i>Quinqueloculina</i> d'Orbigny, 1826	Cirripedia (basal plates)
<i>Quinqueloculina lamarckiana</i> d'Orbigny, 1839	Bryozoa
<i>Quinqueloculina angulata</i> (Williamson, 1858)	<i>Escharoides</i> Milne Edwards, 1836
<i>Discorbina valvulata</i> (d'Orbigny, 1839)	<i>Escharoides</i> sp. 1
<i>Bolivina doniezi</i> Cushman and Wickenden, 1929	<i>Escharoides</i> sp. 2
<i>Cibicides fletcheri</i> Galloway and Wissler, 1927	<i>Microeciella</i> Taylor and Sequeiros, 1982
<i>Lobatula lobatula</i> (Walker and Jacob, 1798)	<i>Copidozoum</i> Harmer, 1926
<i>Discorbis</i> Lamarck, 1804	Cyclostomatida unidentified
<i>Planorbulina variabilis</i> (d'Orbigny, 1826)	Ctenostomatida unidentified
<i>Trochammina</i> Parker and Jones, 1859	<i>Bugula</i> Oken, 1815
<i>Pyrgo</i> Defrance, 1824	Chordata
<i>Pyrgo ringens</i> (Lamarck, 1804)	Asciacea unidentified
Porifera	
<i>Cliona celata</i> Grant, 1826	
Cnidaria	
Anthozoa unidentified	
Hydrozoa (hydrocauli)	
Nematoda	
Nematoda unidentified	
Annelida	
Serpulinae tubes	
Spirorbinae	
<i>Phyllochaetopterus</i> Grube, 1863	
Lumbrineridae	
<i>Eunice argentinensis</i> (Treadwell, 1929)	
Phyllodocidae	
Syllidae	
Maldanidae	
Spionidae	
<i>Monticellina</i> Laubier, 1961	
<i>Caulleriella</i> Chamberlin, 1919	
<i>Tharyx</i> Webster and Benedict, 1887	
<i>Cirratulus</i> Lamarck, 1801	
<i>Cirratulus</i> sp. 1	
<i>Cirratulus</i> sp. 2	
Cirratulidae unidentified 1	
Cirratulidae unidentified 2	
<i>Cirriiformia</i> Hartman, 1936	
<i>Chaetozone</i> Malmgren, 1867	
<i>Aphelochaeta</i> Blake, 1991	
Cirratulidae (multitentaculate)	
Sipunculida	
Sipunculida unidentified	
Brachiopoda	
Juvenile Brachiopoda	
Mollusca	
<i>Ostrea puelchana</i> d'Orbigny, 1842	
<i>Crepidula</i> Lamarck, 1799	
<i>Leiosolenus patagonicus</i> (d'Orbigny, 1842)	

more settled areas of the internal surface were the platform and the posterior margin. Cirratulidae were found on the external surface, preferentially on the ventral margin. *Ostrea puelchana* recruits occurred preferentially on the platform and the anterior margin of the external left valve and, on the internal one, their frequency was significantly higher than expected only on the platform. Furthermore, the platform was preferentially colonized by Bryozoa in both surfaces and only the posterior margin on the internal left valve. Hydrozoa showed preferential location in the platform, apex and margins on the external left valve and only in platform and apex on internal left valve. On the external surface of left valves Foraminifera preferentially settled on the apex, platform and center. On the internal surface of left valves, observed frequencies of *Phyllochaetopterus* Grube, 1863 were significantly higher than expected on the platform and apex. In the external right valve, Spirorbinae, Foraminifera, Cirratulidae, *O. puelchana* recruits and Bryozoa showed a nonrandom distribution between areas. Spirorbinae encrusted preferentially the apex and center,

Foraminifera bored on the apex and Cirratulidae were preferentially distributed on the margins. *Ostrea puelchana* recruits showed a preferential settlement on the center. Particularly, Bryozoa showed differential settlement only on the ventral margin with observed frequencies lower than the expected ones.

DISCUSSION

In this study, all the specimens of *Ostrea puelchana* examined showed epibionts. Oysters were associated with 55 taxa of sedentary and free-living organisms recorded on both valves. The dominant groups were Annelida (20 taxa), Foraminifera

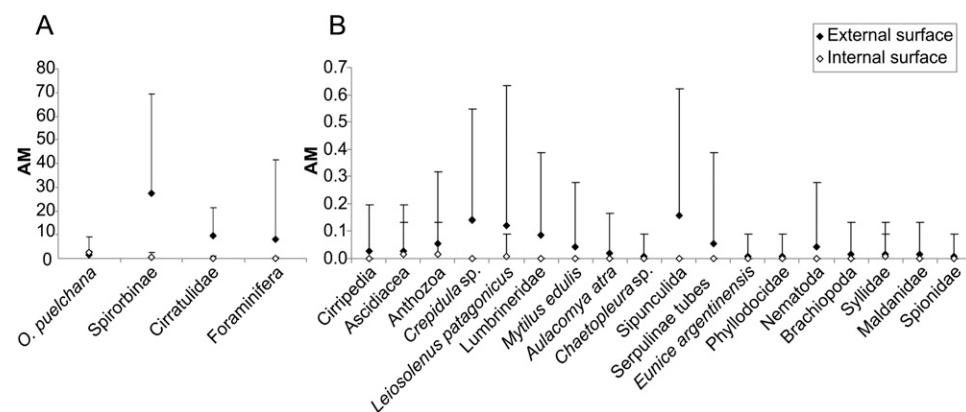
Table 2. Dissimilarity percentages between banks (EB/ZC), kind of surfaces (external/internal) and valves (left/right). Contributions percentages of each taxa higher than 3% were considered.

Taxa	DISSIMILARITY PERCENTAGES					
	EB vs. ZC		External vs. Internal Surface		Left vs. Right Valves	
	Presence/Absence	Coverage	Abundance (transformed data)	Coverage	Abundance (transformed data)	
Spirorbinae	-	37.69	34.12	19.85	26.78	
Cirratulidae	6.3	-	26.65	-	30.25	
<i>Ostrea puelchana</i>	8.58	21.55	14.88	26.62	14.65	
Foraminifera	11.73	-	11.62	-	13.4	
Bryozoa	9.87	20.61	-	24.85	-	
Hydrozoa (hydrocauli)	9.08	5.42	-	6.34	-	
byssate mytilids	8.68	5.18	-	8.36	-	
<i>Phyllochaetopterus</i> sp.	8.41	-	-	4.59	-	
Sipunculida unid.	5.6	-	-	-	-	
<i>Crepidula</i> sp.	4.64	-	-	-	-	
<i>Cliona celata</i>	4.32	-	-	-	-	
Lumbrineridae	3.34	-	-	-	-	
<i>Leiosolenus patagonicus</i>	3.3	-	-	-	-	

(13 taxa), Bryozoa (7 taxa) and Mollusca (6 taxa) in both oyster banks. Within a local biodiversity framework, the present inventory largely extends the knowledge about benthic species richness in SMG. Previous records of macro and micro-fauna associated with *O. puelchana* in natural habitats include a few mollusks (*Mytilus platensis* d'Orbigny, 1842, *Aulacomya atra* (Molina, 1782) and Calyptraeidae), together with polychaetes (*Spirorbis* Daudin, 1800), crustaceans (*Balanus* Costa, 1778), echinoderms, epizoic bryozoans, ascidians and foliulinid Protozoa (Castellanos 1957). In San José Gulf, seven similar taxa colonized *O. puelchana* but in very low percentages (Cremonte

et al. 2005). In a study of the role of chitons in the settlement of *O. puelchana* recruits on conspecific adults, Pascual (1997) reported that ascidians were the most conspicuous epibionts in the absence of grazers at natural oyster banks in SMG. Regarding composition and frequency of epibionts on oyster shells, other studies worldwide give similar results and show the presence of similar epibiotic and endolithic organisms in different marine environment from all geographic regions (Barnes 2001, Guenther *et al.* 2006, Smyth and Roberts 2010).

Boring organisms and bioerosional structures produced by boring activity upon the shells were also recorded on valves

**Figure 3.** Arithmetic mean (AM) of abundance of taxa registered on the external and internal surface. A, More frequent taxa and B) uncommon taxa. The error bars indicate the standard deviation of the data.

of *Ostrea puelchana*. Bioerosion traces attributed to Porifera—e.g., *Cliona celata* Grant, 1826, Foraminifera, Bryozoa Ctenostomatida, Polychaeta Spionidae and Bivalvia, e.g., *Leiosolenus patagonicus* (d'Orbigny, 1842)—as well as byssal etchings produced by the anchoring of bivalves to the substrate and parallel sets of straight to curved scrape marks representing gnawing traces attributed to radulae of chitons were recognized in this study. Due to the commercial value of *O. puelchana*, few studies aim to investigate the infestation produced by *Polydora rickettsi* Woodwick, 1961, *C. celata* and *L. patagonicus*

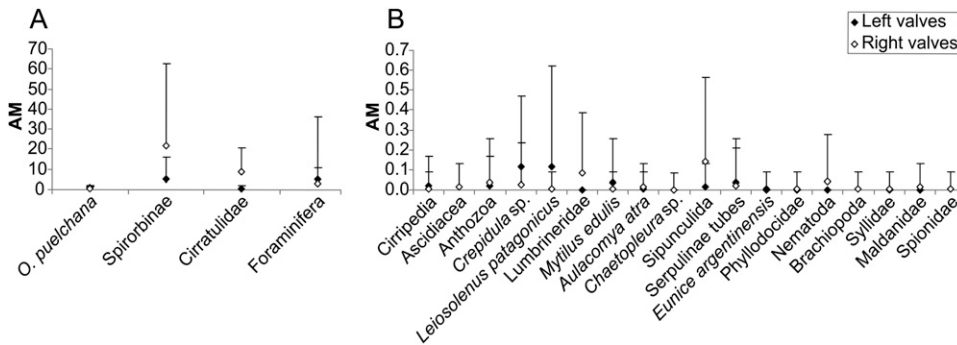


Figure 4. Arithmetic mean (AM) of abundance of taxa registered on left and right valves. **A)** More frequent taxa and **B)** uncommon taxa. The error bars indicate the standard deviation of the data.

(Mauna 2003, Cremonte *et al.* 2005, Rodríguez 2007, Diez *et al.* 2011). These taxa were frequently reported in different species of oysters (Doroudi 1996, Wesche *et al.* 1997, da Silva *et al.* 2010, Sabry *et al.* 2011).

Marine organisms that colonize both biogenic and abio-genic hard substrates often exhibit a pattern of uneven distribution between exposed and less exposed or cryptic surfaces (Palmer and Fürsich 1974, Ward and Thorpe 1991, Nebelsick *et al.* 1997, Glasby and Connell 2001, Schejter and Bremec 2007a, 2007b). On the “puelche oysters”, the external surface of valves supported a high coverage of epibionts. Particularly, recruits of *Ostrea puelchana* showed greater percentage of coverage on external than on internal surfaces, although higher numbers were recorded on the internal surface, mainly in the platform and anterior margin of left valves. Considering that the oysters were collected in breeding season, the preferential settling of juveniles probably reflects the carriage of dwarf males by adult females, as described only in *O. puelchana* (Calvo and Morriconi 1978, Pascual 1997). The non-random distribution of these juveniles was attributed to some kind of chemical interaction female-epibionts (Calvo and Morriconi 1978, Pascual and Zampatti 1995). Besides, Pascual (1997) proposed that this non-random distribution, at least in part, is a consequence of the increased survival rate of epibionts settled on the platform of adult females, which operates as a refuge from grazing by chitons. In this study, although chitons were occasionally found, gnawing traces were registered at high frequencies, mostly on the external surfaces of left shells. Left valves of *O. puelchana* exhibited a greater coverage and number of epibionts than right valves. Nevertheless, some taxa (Anthozoa, Nematoda, Sipunculida, Bryozoa, Polychaeta Spirorbinae and Cirratulidae) were most conspicuous on right valves, most of them in the shell margins and associated to lamellae. Rosso and Sanfilippo (1991) report similar results in the scallop *Zygochlamys patagonica* (King and Broderip, 1832) from the Beagle Channel, with increased coverage of epibionts on the left valves and a greater colonization of epibionts and associated fauna on the margins of right valves, without contact

with the substrate. In contrast, Smyth and Roberts (2010) reported similar degree of epibiosis in both valves of *Ostrea edulis* Linnaeus, 1758, probably because the oysters settled at nearly 45° on the bottom. The life position of *O. puelchana* provides stability in a highly hydro-dynamic environment as it lies with the right valve in contact with the substrate (Pascual 1993). The lifestyle of the “puelche oyster” favors a preferential settlement of epibionts on different valves and areas within the valves.

Additionally, the texture of a colonized surface is an important factor that can influence the settlement of larvae of benthic invertebrates (Eckman 1990, Hoover and Purcell 2009). The preferential settlement in cryptic habitats is common to most marine invertebrate larvae and may primarily be an evolutionary adaptation to prevent mortality by solar radiation, and secondly, to avoid mortality by sedimentation and predation (Svane and Dolmer 1995). Rough and irregular surfaces are more attractive than smooth surfaces for the settlement of organisms (Warner 1997). This would explain the greater coverage and number of epibionts, not susceptible to grazing, on the rough left valves than on the smooth right valves. Small scale substratum heterogeneity (*e.g.*, 1 mm) affects the larval settlement and subsequent development of epibenthic community (Lapointe and Bourget 1999) and habitats of great complexity will increase the biodiversity of the assemblages that occur within them (Huston 1997, Tilman *et al.* 1997, Tilman 1999). The imbricate concentric lamellae on right valves of *Ostrea puelchana* seem to be a good example at individual scale. Lamellae form a fringe around the margin of the shell and generate microhabitats available for colonization. These microhabitats harbored 11 taxa of Cirratulidae and others less abundant. In accordance with these results, Kalyanasundaram *et al.* (1974) found that protected areas and cavities on valves of Ostreidae were habitats of *Cirratulus cirratus* (Müller, 1776). Liñero-Arana and Diaz (2006) also indicated the presence of polychaetes Cirratulidae and Sabel-lidae on the mollusk *Spondylus americanus* Hermann, 1781, which build their galleries with the sediment accumulated between the spines of the mollusk. Similarly, lamellae developed in right valves seem to be used as habitats that give refuge from predators and brooding care. Brooding care behavior, like the deposition of eggs in mucus on rocks and shells, is a usual strategy in Cirratulidae (Petersen 1999).

The gregarious behavior of settled organisms on marine hard substrates is a common phenomenon. Aggregation is a pattern that shows a variety of different processes,

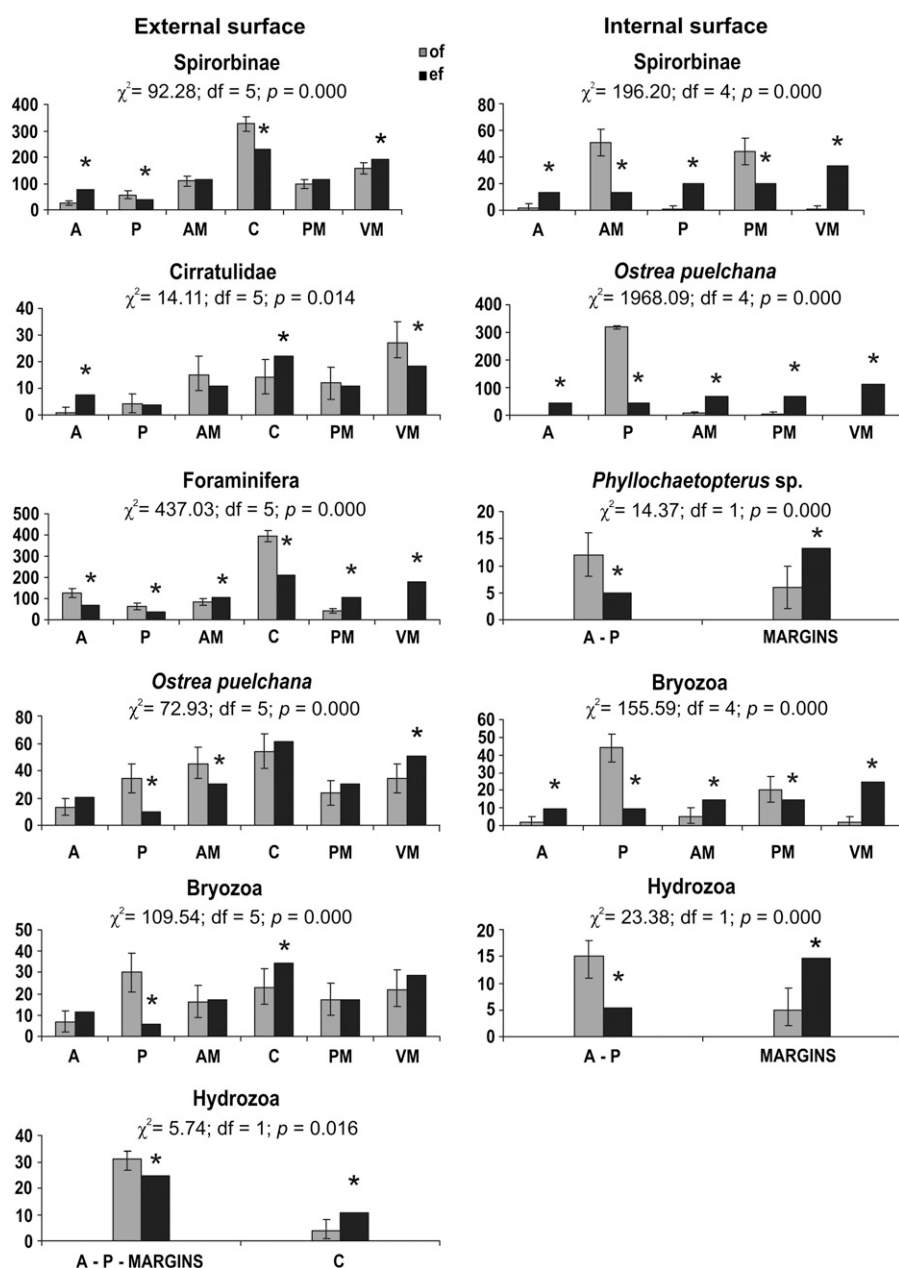


Figure 5. Preferential settlement of epibionts on different areas within external and internal surfaces of left valves. Asterisks indicate significant differences between expected frequencies (ef) and observed frequencies (of) for each area. A, apex, AM, anterior margin, C, center, MARGINS, includes anterior margin, posterior margin and ventral margin grouped, P, platform, PM, posterior margin, VM, ventral margin.

including differential early mortality of those individuals that settle more distantly from others, variations in the topography of the substrate surface which attract larvae, limited substrate availability and active larval selection of sites close to adults of the same species (Taylor and Wilson,

2003). Oyster larvae exhibit a gregarious behavior in response to water-soluble signals produced by conspecific adults and congeners (Hidu *et al.* 1978, Tamburri *et al.* 2008). Also, Bryozoa larvae (Wendt and Woollacott 1999, McKinney and McKinney 2002) and Serpulidae larvae (Knight-Jones 1951, James and Underwood 1994) settle on shadowy areas and show a gregarious behavior. Moreover, protection against predation and turbulence is one of the reasons for the endolithic behavior of Foraminifera (Véneç-Peyré 1996, Bromley and Heinberg 2006), drilling preferably flat areas on shells of gastropods (Smith 1988). These arguments could explain the preferential colonization on the oyster right valves.

Most of the taxa associated with *Ostrea puelchana* were selective suspension and deposit feeders. Selective deposit feeders were mainly associated with the ventral margin (e.g., Cirratulidae), while selective suspension feeders (e.g., Bryozoa, Spirorbinae and *O. puelchana* recruits) were preferably distributed on the dorsal areas of both valves. This differential colonization of functional groups in the areas of the valves supports the assumption that ventral margins are frequently covered by sediment.

In conclusion, this study extends the knowledge about benthic species richness at a local scale and shows that *Ostrea puelchana* possesses biogenic engineering qualities. In soft bottom environments, subjected to current action and resuspension of sediments, the substrate and microhabitats provided by *O. puelchana* increase species richness and allow the establishment and protection of mobile small individuals. Epibionts include boring and encrusting organisms, and together with other associated taxa, show

a variety of living habits and trophic guilds. The lifestyle and substratum heterogeneity (*i.e.*, rough/smooth surfaces and lamellae) of “puelche oyster” favor a preferential settlement of epibionts on different valves and areas within the valves.

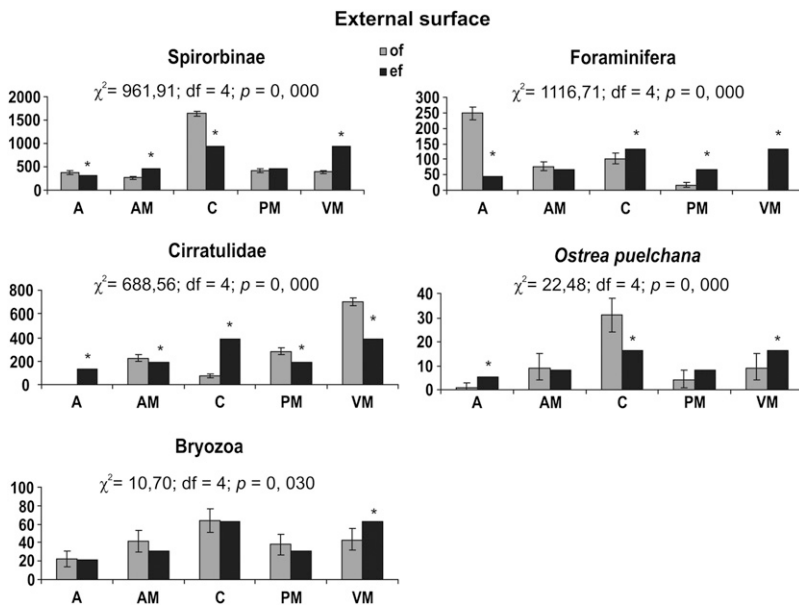


Figure 6. Preferential settlement of epibionts on different areas within external surfaces of right valves. Asterisks indicate significant differences between expected frequencies (ef) and observed frequencies (of) for each area. A, apex, AM, anterior margin, C, center, P, platform, PM, posterior margin, VM, ventral margin.

ACKNOWLEDGMENTS

We are grateful to R. Elías and M. S. Rivero, L. Ferrero, P. Taylor and L. Schejter for the identification of Cirratulidae, Foraminifera, Bryozoa and Porifera, respectively, and to the staff of Instituto de Biología Marina y Pesquera Almirante Storni (Rio Negro) for helping with the sampling work. This is Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP) Contribution N° 1799. Financial support PICT 2007-02200 and PIP 112-201101-00566. This research was supported by a Ph.D. fellowship from Consejo Nacional de Investigaciones Científicas y Tecnológicas (CONICET) to M. V. Romero.

LITERATURE CITED

- Barnes, D. K. A. 2001. The contribution of secondary space to benthic taxon richness of a coral reef: Colonisation of *Dendrostroma* (Mollusca). *Marine Ecology* **22**: 189–200.
- Barnes, D. K. A. and A. Clarke. 1995. Epibiotic communities on sublittoral macroinvertebrates at Signy Island, Antarctica. *Journal of the Marine Biological Association of the United Kingdom* **75**: 689–703.
- Borges, M. E. 2006. *Ecología de las Ostras en Ambientes del sur Bonaerense: Cultivo y Manejo de sus Poblaciones*. Ph.D. Dissertation, Universidad Nacional del Sur, Bahía Blanca, Argentina. [In Spanish].

Bromley, R. G. and C. Heinberg. 2006. Attachment strategies of organisms on hard substrates: A palaeontological view. *Palaeogeography, Palaeoclimatology, Palaeoecology* **232**: 429–453.

Calvo, J. and E. R. Morriconi. 1978. Epibiont and protandry in *Ostrea puelchana*. *Haliotis* **9**: 85–88. [In French].

Carranza, A., O. Defeo, and M. Beck. 2009. Diversity, conservation status and threats to native oysters (Ostreidae) around the Atlantic and Caribbean coasts of South America. *Aquatic Conservation: Marine and Freshwater Ecosystems* **19**: 344–353.

Castellanos, Z. J. A. 1957. *Contribución al Conocimiento de las Especies de Ostras del Litoral Argentino* (*Ostrea puelchana* y *O. spreta*). Ministerio de Agricultura y Ganadería. Departamento de Investigaciones Pesqueras, Buenos Aires, Argentina. [In Spanish].

Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* **18**: 117–143.

Clarke, K. R. and R. M. Warwick. 2001. *Change in Marine communities: An approach to statistical analysis and interpretation*. Plymouth Publishers, PRIMER-E, United Kingdom.

Cook, J. A., J. C. Chubb, and C. J. Veltkamp. 1998. Epibionts of *Asellus aquaticus* (L.) (Crustacea, Iso-poda): An SEM study. *Freshwater Biology* **39**: 423–438.

Cremonte, F., A. Figueras, and E. M. Burreson. 2005. A histopathological survey of some commercially exploited bivalve molluscs in northern Patagonia, Argentina. *Aquaculture* **249**: 23–33.

da Silva, P. M., A. L. L. Leal, A. R. M. Magalhães, and M. A. Barracco. 2010. Pathological survey on the commercial edible bivalve species from Santa Catarina (South Brazil). In: S. E. Shumway, J. Nickum, M. Masser, and B. Hart, eds., *Abstracts of the triennial meeting of the National Shellfisheries Association, Fish Culture Section of the American Fisheries Society, and the World Aquaculture Society, Aquaculture 2010*, San Diego, California. P. 244.

Dauer, D. M., G. H. Tourtellotte, and R. M. Ewing. 1982. Oyster shells and artificial worm tubes: The role of refuges in structuring benthic infaunal communities. *Internationale Revue Der Gesamten Hydrobiologie* **67**: 661–677.

de Grave, S., S. J. Moore, and G. Burnell. 1998. Changes in benthic macrofauna associated with intertidal oyster, *Crassostrea gigas* (Thunberg) culture. *Journal of Shellfish Research* **17**: 1137–1142.

Diez, M. E., V. I. Radashevsky, J. M. Orensanz, and F. Cremonte. 2011. Spionid polychaetes (Annelida: Spionidae) boring into shells of molluscs of commercial interest in northern Patagonia, Argentina. *Italian Journal of Zoology* **1**: 1–8.

Doroudi, M. S. 1996. Infestation of pearl oysters by boring and fouling organisms in the northern Persian Gulf. *Indian Journal of Marine Sciences* **25**: 168–169.

Eckman, J. E. 1990. A model of passive settlement by planktonic larvae onto bottoms of differing roughness. *Limnology and Oceanography* **35**: 887–901.

Escapa, M., J. P. Isacch, P. Daleo, J. Alberti, O. Iribarne, M. Borges, E. P. Dos Santos, D. A. Gagliardini, and M. Lasta. 2004. The

- distribution and ecological effects of the introduced Pacific oyster *Crassostrea gigas* (Thunberg, 1793) in northern Patagonia. *Journal of Shellfish Research* **23**: 765–772.
- Escofet, A., J. M. Orensanz, S. R. Olivier, and V. Scarabino. 1978. Biocenología bentónica del Golfo de San Matías (Río Negro, Argentina): Metodología, experiencias, y resultados del estudio ecológico de un gran espacio geográfico de América Latina. *Anales del Centro de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México* **5**: 59–81. [In Spanish].
- Glasby, T. M. and S. D. Connell. 2001. Orientation and position of substrata have large effects on epibiotic assemblages. *Marine Ecology Progress Series* **214**: 127–135.
- Gristina, M., G. D'Anna, R. Parisi, S. Riggio, and M. Tocaceli. 1996. Fenomeni di epibiosi sul lamellibranco *Ostrea edulis* L., 1758. *Biologia Marina Mediterranea* **3**: 474–475. [In Italian].
- Guenther, J., P. C. Southgate, and R. de Nys. 2006. The effect of age and shell size on accumulation of fouling organisms on the Akoya pearl oyster *Pinctada fucata* (Gould). *Aquaculture* **253**: 366–373.
- Guerrero, R. and A. R. Piola. 1997. Masas de agua en la plataforma continental. In: E. E. Boschi, ed., *El Mar Argentino y sus Recursos Pesqueros Tomo 1*. Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), Mar del Plata, Argentina. Pp. 107–118. [In Spanish].
- Hay, M. E., J. D. Parker, D. E. Burkepile, C. C. Caudill, A. E. Wilson, Z. P. Hallinan, and A. D. Chequer. 2004. Mutualisms and aquatic community structure: The enemy of my enemy is my friend. *Annual Review of Ecology, Evolution and Systematics* **35**: 175–197.
- Hidu, H., G. V. William, and F. P. Veitch. 1978. Gregarious setting in European and American oysters—response to surface chemistry versus waterborne pheromones. *Proceedings of the National Shellfisheries Association* **8**: 11–16.
- Hoover, R. A. and J. E. Purcell. 2009. Substrate preferences of scyphozoan *Aurelia labiata* polyps among common dock-building materials. *Hydrobiologia* **616**: 259–267.
- Hosack, G. R., B. R. Dumbauld, J. L. Ruesink, and D. A. Armstrong. 2006. Habitat associations of estuarine species: Comparisons of intertidal mudflat, seagrass (*Zostera marina*) and oyster (*Crassostrea gigas*) habitats. *Estuaries and Coasts* **29**: 1150–1160.
- Huston, M. A. 1997. Hidden treatments in ecological experiments: Re-evaluating the ecosystem function of biodiversity. *Oecologia* **110**: 449–460.
- James, R. J. and A. J. Underwood. 1994. Influence of colour of substratum on recruitment of spirorbid tubeworms to different types of intertidal boulders. *Journal of Experimental Marine Biology and Ecology* **181**: 105–115.
- Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. *Oikos* **69**: 373–386.
- Jones, C. G., J. H. Lawton, and M. Shachak. 1997. Positive and negative effects of organisms as ecosystem engineers. *Ecology* **78**: 1946–1957.
- Kalyanasundaram, N., S. S. Ganti, K. Mangapathi Rao, and P. Ramachandra Raju. 1974. On the occurrence of *Cirratulus cirratus* O. F. Müller (Polychaeta: Cirratulidae) a new record for Indian waters. *Current Science* **43**: 789–789.
- Knight-Jones, E. W. 1951. Gregariousness and some other aspects of the settling behaviour of *Spirorbis*. *Journal of the Marine Biological Association of the United Kingdom* **30**: 201–222.
- Kochmann, J., C. Buschbaum, N. Volkenborn, and K. Reise. 2008. Shift from native mussels to alien oysters: Differential effects of ecosystem engineers. *Journal of Experimental Marine Biology and Ecology* **1**: 1–10.
- Lapointe, L. and E. Bourget. 1999. Influence of substratum heterogeneity scales and complexity on a temperate epibenthic marine community. *Marine Ecology Progress Series* **189**: 159–170.
- Lejart, M. and C. Hily. 2011. Differential response of benthic macrofauna to the formation of novel oyster reefs (*Crassostrea gigas*, Thunberg) on soft and rocky substrate in the intertidal of the Bay of Brest, France. *Journal of Sea Research* **65**: 84–93.
- Lenihan, H. S. 1999. Physical–biological coupling on oyster reefs: How habitat structure influences individual performance. *Ecological Monographs* **69**: 251–275.
- Liñero-Arana, I. and O. Díaz. 2006. Poliquetos (Annelida: Polychaeta) epibiontes de *Spondylus americanus* (Bivalvia: Spondylidae) en el Parque Nacional Mochima, Venezuela. *Revista de Biología Tropical* **54**: 765–772. [In Spanish].
- Markert, A., A. Wehrmann, and I. Kröncke. 2010. Recently established *Crassostrea*-reefs versus native *Mytilus*-beds: Differences in ecosystem engineering affects the macrofaunal communities (Wadden Sea of Lower Saxony, southern German Bight). *Biological Invasions* **12**: 15–32.
- Mauna, A. C. 2003. *Evaluación de la Bioerosión Producida por Lithophaga patagonica (d'Orbigny) sobre Ostrea puelchana d'Orbigny en el Golfo San Matías, Argentina*. Unpublished thesis. Universidad Nacional de La Pampa, Argentina. [In Spanish].
- Mauna, C., S. Casadío, A. Parras, and M. Pascual. 2005. Frequency and distribution of *Lithophaga* (Mytilidae) perforations in recent and fossil oysters: Taphonomic and paleobiological implications. *Ameghiniana* **42**: 395–405.
- McKinney, F. K. and M. J. McKinney. 2002. Contrasting marine larval settlement patterns imply habitat-seeking behaviours in a fouling and a cryptic species (Phylum Bryozoa). *Journal of Natural History* **36**: 487–500.
- Morsan, E. M. 2002. La pesquería artesanal de la almeja púrpura *Amiantis purpurata* del Golfo San Matías: Evaluación del efectivo pesquero, estrategias de explotación y rendimiento económico. Instituto de Biología Marina y Pesquera Almirante Storni. *Serie Publicaciones* **1**: 3–22. [In Spanish].
- Narvarte, M., R. González, A. Medina, and M. S. Avaca. 2011. Artisanal dredges as efficient and rationale harvesting gears in a Patagonian mussel fishery. *Fisheries Research* **111**: 108–115.
- Nebelsick, J. H., B. Schmid, and M. Stachowitsch. 1997. The encrustation of fossil and recent sea-urchin tests: Ecological and taphonomic significance. *Lethaia* **30**: 271–284.
- Oehrens Kissner, E. M., M. S. Doldan, P. C. Zaidman, and M. A. Kroeck. 2011. Bonamiosis en banco Reparó (Golfo San Matías, Patagonia Norte, Argentina): A una década de la epizootia. In: G. Bigatti and S. Van der Molen, eds., *Libro de Resúmenes del VIII Congreso Latinoamericano de Malacología, Puerto Madryn, Argentina*. P. 216. [In Spanish].
- Palmer, T. J. and F. T. Fürsich. 1974. The ecology of a Middle Jurassic hardground and crevice fauna. *Palaeontology* **17**: 507–524.
- Parker, G., M. C. Paterlini, and R. A. Violante. 1997. El fondo marino. In: E. E. Boschi, ed., *El Mar Argentino y sus Recursos*

- Pesqueros Tomo 1*. Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), Mar del Plata, Argentina. Pp. 65–87. [In Spanish].
- Parras, A. and S. Casadío, 2006. The Oyster *Crassostrea*? hatchery (Ortmann, 1897), a physical ecosystem engineer from the upper oligocene-lower Miocene of Patagonia, Southern Argentina. *Palaios* **21**: 168–186.
- Pascual, M. S. 1993. *Contingencia y Adaptación en la Ecología Reproductiva de la Ostra Puelche (Ostrea puelchana d'Orbigny)*. Ph.D. Dissertation, Universidad Nacional de Mar del Plata, Argentina. [In Spanish].
- Pascual, M. S. 1997. Carriage of draw males by adult female puelche oysters: The role of chitons. *Journal of Experimental Marine Biology and Ecology* **212**: 173–185.
- Pascual, M. S. and E. A. Zampatti. 1995. Evidence of a chemically mediated adult-larval interaction triggering settlement in *Ostrea puelchana*: Applications in hatchery production. *Aquaculture* **133**: 33–44.
- Petersen, M. E. 1999. Reproduction and development in Cirratulidae (Annelida: Polychaeta). *Hydrobiologia* **402**: 107–128.
- Rios, E. C. 1970. *Coastal Brazilian Seashells*. Fundação Cidade do Rio Grande. Museu Oceanográfico de Rio Grande, Rio Grande, Brazil.
- Rivas, A. L. 1990. Heat balance and annual variation of mean temperature in the North Patagonian gulfs. *Oceanologica Acta* **13**: 265–272.
- Rodney, W. S. and K. T. Paynter. 2006. Comparisons of macrofaunal assemblages on restored and non-restored oyster reefs in mesohaline regions of Chesapeake Bay in Maryland. *Journal of Experimental Marine Biology and Ecology* **335**: 39–51.
- Rodríguez, V. S. 2007. *Bioerosión de Cliona celata Grant, 1826 sobre Ostrea puelchana (d'Orbigny, 1842) en el Golfo San Matías, Argentina*. Ph.D. Dissertation, Universidad Nacional de La Pampa, Santa Rosa, Argentina. [In Spanish].
- Rosso, A. and R. Sanfilippo. 1991. Epibionts distribution pattern of *Chlamys patagonica* (King and Broderip) of the Magellan Strait. *Memorie di Biologia Marina e Oceanografia* **19**: 237–240.
- Sabry, R. C., P. M. da Silva, T. C. Vasconcelos Gesteira, V. de Almeida Pontinha, and A. R. Magenta Magalhães. 2011. Pathological study of oysters *Crassostrea gigas* from culture and *C. rhizophorae* from natural stock of Santa Catarina Island, SC, Brazil. *Aquaculture* **60**: 43–50.
- Sacco, F. 1897. I molluschi dei terreni terziarii del Piemonte e della Liguria (Ostreidae, Anomiidae e Dimyidae). Musei di Zoologia e di Anatomia Comparata della R. Università, Torino. *Bollettino* **12**: 99–100. [In Italian].
- Schejter, L. and C. Bremec. 2007a. Benthic richness in the Argentine continental shelf: The role of *Zygochlamys patagonica* (Mollusca: Bivalvia: Pectinidae) as settlement substrate. *Journal of the Marine Biological Association of the United Kingdom* **87**: 917–925.
- Schejter, L. and C. Bremec. 2007b. Repaired shell damage in the commercial scallop *Zygochlamys patagonica* (King & Broderip, 1832), Argentine Sea. *Journal of Sea Research* **58**: 156–162.
- Servicio de Hidrografía Naval. 2010. *Tabla de Marea 5*, Armada Argentina, Argentina. [In Spanish].
- Smith, M. J. 1988. The foraminifer *Cymbdoporellu tabellueformis* (Brady) bores in gastropod shells. *Journal of Foraminiferal Research* **18**: 277–285.
- Smyth, D. and D. Roberts. 2010. The European oyster (*Ostrea edulis*) and its epibiotic succession. *Hydrobiologia* **655**: 25–36.
- Stenzel, H. B. 1971. Oysters. In: R. C. Moore, ed., *Treatise on Invertebrate Paleontology Part N, volume 3, Mollusca 6, Bivalvia*. Geological Society of America & University of Kansas Press, Kansas. Pp. 953–1197.
- Svane, I. and P. Dolmer. 1995. Perception of light at settlement: A comparative study of two invertebrate larvae, a scyphozoan planula and a simple ascidian tadpole. *Journal of Experimental Marine Biology and Ecology* **187**: 51–61.
- Tamburri, M. N., M. W. Luckenbach, D. L. Breitburg, and S. N. Bonniwell. 2008. Settlement of *Crassostrea ariakensis* larvae: Effects of substrate, biofilms, sediment and adult chemical cues. *Journal of Shellfish Research* **27**: 601–608.
- Taylor, P. D. and M. A. Wilson. 2003. Palaeoecology and evolution of marine hard substrate communities. *Earth-Science Reviews* **62**: 1–103.
- Tilman, D. 1999. The ecological consequences of changes in biodiversity: A search for general principles. *Ecology* **80**: 1455–1474.
- Tilman, D., C. L. Lehman, and K. T. Thomson. 1997. Plant diversity and ecosystem productivity: Theoretical considerations. *Proceedings of the National Academy of Sciences U.S.A.* **94**: 1857–1861.
- Véneç-Peyré, M. T. 1996. Bioeroding foraminifera: A review. *Marine Micropaleontology* **28**: 19–30.
- Wahl, M. 1989. Marine epibiosis I. Fouling and antifouling: Some basic aspects. *Marine Ecology Progress Series* **58**: 175–189.
- Wahl, M. 2008. Ecological lever and interface ecology: Epibiosis modulates the interactions between host and environment. *Biofouling* **24**: 427–438.
- Wahl, M. 2009. Epibiosis: Ecology, effects and defenses. In: M. Wahl, ed., *Marine Hard Bottom Communities*. Ecological Studies, Berlin Heidelberg, Germany. Pp. 61–72.
- Wahl, M. and O. Mark. 1999. The predominantly facultative nature of epibiosis: Experimental and observational evidence. *Marine Ecology Progress Series* **187**: 59–66.
- Ward, M. A. and J. P. Thorpe, 1991. Distribution of encrusting bryozoans and other epifauna on the subtidal bivalve *Chlamys opercularis*. *Marine Biology* **110**: 253–259.
- Warner, G. F. 1997. Occurrence of epifauna on the periwinkle, *Littorina littorea* (L.), and interactions with the polychaete *Polydora ciliata* (Johnston). *Hydrobiologia* **355**: 41–47.
- Wendt, D. E. and R. M. Woollacott. 1999. Ontogenies of phototactic behavior and metamorphic competence in larvae of three species of *Bugula* (Bryozoa). *Invertebrate Biology* **118**: 75–84.
- Wesche, S. J., R. D. Adlard, and J. N. A. Hooper. 1997. The first incidence of clionid sponges (Porifera) from the Sydney rock oyster *Saccostrea commercialis* (Iredale and Roughley, 1933). *Aquaculture* **157**: 173–180.
- Williams, J. D. and J. J. McDermott. 2004. Hermit crab biocoenoses: A worldwide review of the diversity and natural history of hermit crab associates. *Journal of Experimental Marine Biology and Ecology* **305**: 1–128.

- Zar, J. H. 1999. *Biostatistical Analysis*. Englewood Cliffs. Prentice-Hall Publishers, New Jersey.
- Zimmerman, R. J., T. J. Minello, T. J. Baumer, and M. C. Castiglione. 1989. Oyster reef as habitat for estuarine macrofauna. *NOAA Technical Memorandum* **249**: 1–249.
- Zuschin, M. and C. Baal. 2007. Large gryphaeid oysters as habitats for numerous sclerobionts: A case study from the northern Red Sea. *Facies* **53**: 319–327.
- 7th International Conference on shellfish restoration. 2005. *Journal of Shellfish Research* **24**: 309–340.

Submitted: 26 July 2012; **accepted:** 7 April 2013; **final revisions received:** 13 June 2013