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To cite this article: Juan López-Gappa, María G. Liuzzi & Gabriel Genzano (2016): Role of the clam *Neilonella sulculata* as substrate for the hydroid *Bougainvillia macloviana* on muddy bottoms of San Jorge Gulf (Argentina, Southwest Atlantic), *Marine Biology Research*, DOI: [10.1080/17451000.2016.1210809](https://doi.org/10.1080/17451000.2016.1210809)

To link to this article: <http://dx.doi.org/10.1080/17451000.2016.1210809>



Published online: 05 Oct 2016.



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SHORT REPORT

Role of the clam *Neilonella sulculata* as substrate for the hydroid *Bougainvillia macloviana* on muddy bottoms of San Jorge Gulf (Argentina, Southwest Atlantic)

Juan López-Gappa^{a,b}, María G. Liuzzi^{a,b}  and Gabriel Genzano^{a,c}

^aConsejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina; ^bMuseo Argentino de Ciencias Naturales, Ciudad Autónoma de Buenos Aires, Argentina; ^cEstación Costera Nágera, Instituto de Investigaciones Marinas y Costeras (IIMyC), Universidad Nacional de Mar del Plata, Mar del Plata, Argentina

ABSTRACT

The clam *Neilonella sulculata* is the dominant bivalve on muddy bottoms along the Argentine continental shelf (Southwest Atlantic). The medusa stage of the hydroid *Bougainvillia macloviana* is one of the most abundant species in the gelatinous zooplankton of the Magellan region. Two benthic surveys carried out in 2007 and 2009 in San Jorge Gulf gave us the opportunity to analyse (1) the interaction between *N. sulculata* and its epibiont, *B. macloviana*, and (2) the role of the clam as hard substrate in a depositional area characterized by silt/clay sediments. *Bougainvillia macloviana* has a high prevalence on the posterior region of live clams. The presence of gonophores shows that these small colonies are able to reproduce there. Hydroid colonies are very rare on dead valves of *N. sulculata* and also on almost all other live bivalve species in the study area. Specimens of *N. sulculata* with hydroids were slightly but significantly larger than those without them, both in 2007 and 2009. The high prevalence of *B. macloviana* on live individuals of *N. sulculata* and its almost total absence on other clam species suggest that this association may be critical at least for the epibiont and not the result of chance alone.

ARTICLE HISTORY

Received 13 May 2016
Accepted 5 July 2016

RESPONSIBLE EDITOR

Stefania Puce

KEYWORDS

Benthic infauna; bivalve; epibiosis; hard substrate islands; Hydrozoa

Introduction

In the marine environment, hard surfaces represent potential settlement sites for sessile organisms. Solid substrates are often a limiting factor and their scarcity regulates the presence and abundance of many species in environments that otherwise would be unfavourable (Wahl 1989). On soft bottoms, organisms with hard structures such as bivalves are of great importance because they provide suitable surfaces to be colonized by sessile species (Gutiérrez et al. 2003).

The epibiosis of hydroids on bivalves is an association phenomenon that occurs in all oceans around the world (reviewed in Rees 1967; Boero 1984; Gili & Hughes 1995). While it is common to find that there is no specificity in the choice of the bivalve used as substrate by the colonial polyps (e.g. Wahl & Mark 1999; Genzano et al. 2009), obligate relationships have also been reported (e.g. Jarms & Tiemann 1996; Jarms & Mühlenhardt-Siegel 1998; reviewed in Puce et al. 2008). Few hydroids are found on soft substrata, living partially buried in the sediments (digging species) or settling initially on a small hard substrate,

and then growing in size and staying erect by an anchoring system (rooting species). Most species found in soft sediments, however, live attached to stable surfaces (e.g. polychaete tubes, sponges or scallops) on which colonies can settle, grow and extend at least a few centimetres above the abrasive sand–water interface (Genzano et al. 2009).

In the Southwest Atlantic, molluscs are usually important substrate providers for hydroids, both in the intertidal zone (Genzano & Rodriguez 1998) and on subtidal rocky outcrops (Genzano et al. 2009), but information on their role as basibionts on soft substrata is scarce.

During benthic surveys conducted on the muddy bottoms of San Jorge Gulf (Argentina, Southwest Atlantic), abundant material of *Neilonella sulculata* (Gould, 1852), the dominant clam in the area (Roux et al. 1995; Liuzzi et al. 2016), was collected and colonies of the hydroid *Bougainvillia macloviana* Lesson, 1830 were found attached to its valves. This filter-feeding bivalve has a Magellanic distribution spanning the southern tip of South America, from off the Río de la Plata estuary (36°S) in the Southwest Atlantic, up to

the Chilean fjord region in the Southeast Pacific (Leonardi et al. 1996; Osorio & Reid 2004).

Bougainvillia macloviana has a metagenetic life cycle including a planula larva, a benthic polyp and a free-swimming medusa. Medusae of this species have often been reported in the Southwest Atlantic (Genzano et al. 2008), but reports of its benthic stages are scarce (Jäderholm 1917, as *Perigonimus repens* Wright, 1857; Blanco 1994 and references therein, as *Perigonimus octonus* (Fleming, 1823)).

The aim of this study is to analyse the role of the clam *N. sulculata* as provider of a hard substrate on muddy bottoms in San Jorge Gulf and its relationship with the epibiont hydrozoan *B. macloviana*.

Material and methods

Samples were collected during two benthic surveys carried out from the supply vessels *Martes Santo* (December 2007) and *Mr. Big* (October 2009) chartered to carry out baseline studies in the central zone of San Jorge Gulf. This zone is a depositional area characterized by silt/clay sediments with grain sizes ranging from 4 to 5 phi units (Fernández et al. 2003). Sixteen sampling stations were arranged in each of three different areas of uniform topography and granulometry called N, Z and S (Figure 1), producing a total of 96 samples (16 stations × 3 areas × 2 surveys). The depth range was 88–92 m in area N, 87–99 m in area Z, and 96–100 m in area S.

Benthic samples were collected with a 13.49 dm² Van Veen grab and washed onboard with seawater through a 1 mm mesh sieve. The material retained in the sieve was then fixed in a 5% formaldehyde solution in seawater and then preserved in 70% ethanol. All live individuals of *Neilonella sulculata* were separated, counted and their length measured with a micrometer eyepiece under a stereoscopic microscope with an error of 0.133 mm. Each individual of *N. sulculata*, either alive or dead during sample collection, was thoroughly examined in search of epibionts on its valves. The null hypothesis of independence between presence/absence of the hydroid and the status of the clam at the moment of sampling (live/dead) was tested using a Fisher Exact Test on a 2 × 2 contingency table (Zar 2010).

The null hypothesis of no difference in size between clams with or without epibionts was tested as follows: (1) variance homogeneity was tested with the Bartlett test (Zar 2010); (2) several transformations were applied on heteroscedastic data; (3) the Student's *t*-test (Zar 2010) was used on the 2007 data, which attained homogeneity after a log-transformation; (4)

as this assumption could not be met even after transformations, the 2009 data were tested with the non-parametric Mann–Whitney test (Zar 2010). Due to low clam abundances in areas Z and N, this analysis was carried out only in area S.

Data analyses were performed using the statistical programming language and computing environment R (R Development Core Team 2011).

The prevalence of epibionts (%) was calculated only for stations with more than 100 ind m⁻². The shell surface of three other relatively scarce clam species was also examined in search of epibionts. The epibiosis on *Thyasira patagonica* Zelaya, 2010, however, was not analysed because of its small size.

Results

Besides the dominant clam *Neilonella sulculata*, other infaunal bivalves were found in low densities: *Ennucula puelcha* (d'Orbigny, 1842), *Malletia cumingii* (Hanley, 1860), *Pandora braziliensis* G.B. Sowerby II, 1874 (as *P. cistula* in Liuzzi et al. (2016), see Güller & Zelaya (2016)) and *Thyasira patagonica*.

A total of 5136 live and 2520 dead *N. sulculata* were found in the samples. Clams were absent or were fewer than 100 ind m⁻² per station in area N. The hydroid *Bougainvillia macloviana* was the only macroscopic epibiont found on the valves and was present at all stations with live clams, which ranged from 1.9 to 15.1 mm. Its prevalence was very high on live clams (2007: 86.1%, 2009: 85.6%), but very low on empty valves (2007: 2.7%, 2009: 0.8%). Hence, the presence of the hydroid was not independent of the status (live/dead) of the clam (Fisher Exact Test: $P_{2007} = 2.2 \times 10^{-16}$, $P_{2009} = 2.2 \times 10^{-16}$). The few hydroid colonies on dead clams were mostly found in cases where the left and right valves were still joined by the ligament and the periostracum was intact.

The position of the live clams in the muddy substrate was usually seen by a sharp change in colour, with a darker posterior area of the valves protruding over the sediment surface and a clearer one within the mud (Figure 2). Most hydroid colonies were growing on the darker area of both valves. In some individuals, however, the hydroid colony was spreading over most of the valve surfaces. Gonophores were observed in colonies from areas Z and S during October 2009, showing that these small, attached colonies consisting of hydrorhizae and a few hydranths were able to reach reproductive maturity on the bivalve.

Although the differences were small (2007: 0.3 mm, 2009: 0.8 mm), the size of clams with *B. macloviana* was significantly higher than that of clams without hydroid

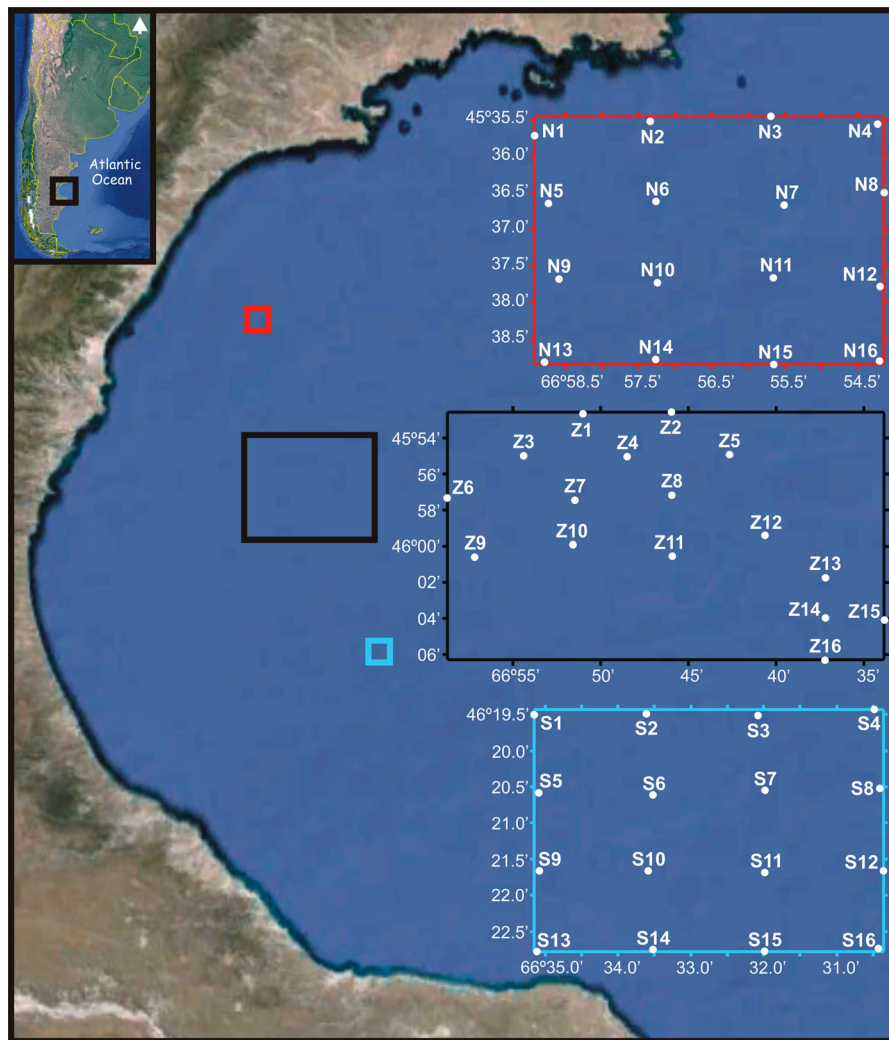


Figure 1. Distribution of stations in San Jorge Gulf.



Figure 2. The hydroid *Bougainvillia macloviana* growing on the posterior area of an individual of *Neilonella sulcata*, showing position in life.

colonies (2007, with: 8.26, without: 7.97 mm; 2009, with: 9.21, without: 8.40 mm; Student's *t*-test, 2007: $t = 4.758$, $P = 2.83 \times 10^{-6}$; Mann-Whitney test, 2009: $U = 759776$, $P < 2.2 \times 10^{-16}$; Figure 3).

Bougainvillia macloviana was absent on the shell surfaces of *M. cumingii* ($n = 5$) and *P. braziliensis* ($n = 5$), and was extremely rare on *E. puelcha* (1/70, 1.4%).

Discussion

Shell production affects the structure of benthic habitats by modifying their heterogeneity and complexity. This process is particularly important on soft bottoms, which otherwise have only mud particles as structural elements (Gutiérrez et al. 2003). Hydroids are greatly diverse and abundant on firm or hard substrata (Calder 1991). Colonies usually live as epibionts on invertebrates, but some species attach directly to

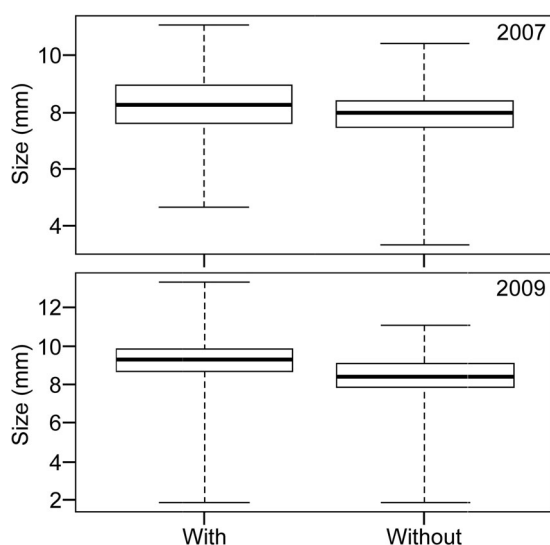


Figure 3. Size of *Neilonella sulculata* with and without colonies of *Bougainvillia macloviana*. The solid lines inside the boxes indicate the medians, the upper and lower limits of the boxes show the 25th and 75th percentiles, and the vertical segments represent the ranges.

rocks. The occupation of cryptic habitats often reduces the likelihood of finding the sessile stages of some hydrozoan species. In the southern part of San Jorge Gulf other hydroid species have been found previously on kelps, sponges, hydroids, mytilids and scallops (Genzano et al. 1991). However, these organisms are absent on the muddy central area of the gulf surveyed in the present study. We mostly found colonies of *Bougainvillia macloviana* on living clams, suggesting that the presence of shells is not enough for the hydroid, which needs a living substrate to persist on the bottom. Dead clams with hydroid colonies on them were mostly cases where both valves had an undamaged periostracum and were still joined by the ligament, suggesting recent deaths. Jarms & Mühlenhardt-Siegel (1998) also found that the hydroid *Monobrachium parasitum* Mereschkowsky, 1877 decreased and finally died after the death of the host, a small clam of the genus *Thyasira*. In addition to finding a suitable substrate, it is possible that *B. macloviana* derives a nutritional advantage from the water currents maintained by the clam. Another possible explanation for this fact could be that live clams may position themselves on the sediment surface, i.e. in a way that is advantageous to the hydroid, whereas dead clams may become buried, leaving no exposed surface for the hydroids. Both ecological processes have been postulated by Cerrano et al. (1997) for the interaction between the hydroid of *Zanclaea costata* Gegenbaur, 1857 and the bivalve *Chamelea gallina* (Linnaeus, 1758). Because the study

area is characterized by the deposition of silt–clay sediments (Fernández et al. 2003), rapid shell burial after clam death is to be expected.

Bougainvillia macloviana is an anthomedusan frequently found in plankton samples from cold temperate waters of the Southwest Atlantic, having been reported from the Valdés Peninsula to Tierra del Fuego (i.e. 42–56°S, Genzano et al. 2008). It has been regarded as the most abundant species in the gelatinous zooplankton because it was collected at almost all stations during the ‘Victor Hensen’ campaign to the Magellan Straits (Pagès & Orejas 1999). On the other hand, its small polyp stage has only been reported for the Malvinas (Falkland) Islands, the Magellan Strait, and south of Tierra del Fuego, where it has not been recorded again for almost one century (Jäderholm 1917, and references in Blanco 1994). The present finding of the *B. macloviana* polyp stage agrees with the distribution of its medusae in the Southwest Atlantic. This species is found in cold temperate waters of the continental shelf, unlike *Bougainvillia muscus* (Allman, 1863) and *Bougainvillia pagesi* Nogueira et al., 2013, which have so far been found in warm-temperate waters north of 42°S (Genzano et al. 2008; Nogueira et al. 2013).

Our study shows that the polyp stage of *B. macloviana* uses living individuals of *Neilonella sulculata* as islands of hard substrate resting in a sea of soft sediment to complete the benthic phase of its life cycle. Hydroids tend to be substrate generalists, although a few species exhibit preferences as to their basibionts, being more frequent on a particular living substrate than elsewhere (see Boero et al. 1997; Genzano et al. 2009). The high prevalence of *B. macloviana* on live *N. sulculata* and its almost total absence on other clam species suggest that this association may be critical, at least for the epibiont, and not the result of chance alone.

The epibiont may not be the only species that benefits from this association. The hydroid *Lovenella gracilis* Clarke, 1882 can form large colonies on the posterior end of the infaunal clam *Donax variabilis* Say, 1822 (Manning & Lindquist 2003). By providing a stable substrate for attachment, the clam facilitates the persistence of the hydroid in the intertidal beach. The epibiotic hydroid, which possesses stinging nematocysts and projects above the surface of the sand, defends the clam against one common fish predator. The mussel *Mytilus edulis* Linnaeus, 1758 is also protected by hydroids against predation by seastars (Laudien & Wahl 1999, 2004). *Hydractinia angusta* Harlaub, 1904 protects the Antarctic scallop *Adamussium colbecki* (E. A. Smith, 1902) by detaching and ingesting

tube feet and pedicellariae from the grazing sea urchin *Sterechinus neumayeri* (Meissner, 1900) (Cerrano et al. 2000). Another example of mutualism between hydroids and bivalves is the selective ingestion of trematode sporocysts by the hydroid *Eugymnanthea inquilina* Palombi, 1936, which indicates a protective role of this epibiont against parasites of the mussel *Mytilus galloprovincialis* Lamarck, 1819 (Piraino et al. 1994).

We found that clams with hydroid colonies on their shells were slightly but significantly larger than those without hydroids. Similarly, in the coquina clam, *Donax fossor* Say, 1822, larger individuals were more likely to support colonies of the hydroid *L. gracilis* than smaller ones (Dougherty & Russell 2005). These authors found that clams without hydroid colonies were drilled more frequently by a gastropod predator than those supporting colonies of *L. gracilis*, suggesting that the clam benefits from the hydroid by predator deterrence. Predator gastropods were not found in soft bottoms of the study area (Juan López-Gappa, unpublished observation 2009), but *N. sulculata* is one of the main food items of the cockfish *Callorhynchus callorhynchus* (Linnaeus, 1758) (Sánchez & Prenske 1996) and was also occasionally found in the stomachs of the narrow-mouthed catshark, *Schroederichthys bivius* (Müller & Henle, 1838) (Sánchez et al. 2009). The red shrimp, *Pleoticus muelleri* (Spence Bate, 1888), also preys upon juveniles of *N. sulculata* in San Jorge Gulf (Roux et al. 2009). Although clams bearing hydroid colonies were significantly larger than clams without epibionts, the difference in size was very small (0.3–0.8 mm). Rather than an effect of the epibiont on the bivalve, we cannot rule out that this difference may be simply due to the time needed by the hydroid to find a suitable substratum, settle on the host and bud a colony. Jarms & Mühlenhardt-Siegel (1998) found, however, that shells of an Antarctic species of *Thyasira* bearing the hydroid *M. parasitum* were significantly smaller than those without. These authors suggested that the explanation may be that the presence of the hydroid increases the drag on the bivalve while it moves through the substrate.

This study provides ecological information about the little-known benthic polyp stage of *B. macloviana*. In species with metagenetic life cycles, the presence and abundance of planktonic medusae is a consequence of the asexual reproduction that has taken place during the benthic polyp stage. Knowledge of the ecology of both life stages is therefore critical for understanding and interpreting spatial and abundance patterns of this species in natural environments (Miglietta et al. 2008; Jaubet & Genzano 2011).

Acknowledgements

We are grateful to the crews of *Martes Santo* and *Mr. Big* for the help received during the surveys in San Jorge Gulf. Two anonymous reviewers are acknowledged for their constructive comments on an earlier version of this paper.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

Financial support was provided by Consejo Nacional de Investigaciones Científicas y Técnicas (grant nos. PIP 2010-2012 N° 0291, PIP 2013-2015 N° 0247CO to Juan López-Gappa, Res. 4541-2012 to María Gabriela Liuzzi, PIP 0152 to Gabriel Genzano), Agencia Nacional de Promoción Científica y Tecnológica (grant no. PICT-2012-1043 to Juan López-Gappa and María Gabriela Liuzzi) and Universidad Nacional de Mar del Plata (grant no. EXA 734/15 to Gabriel Genzano).

ORCID

María G. Liuzzi  <http://orcid.org/0000-0003-3421-6048>

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