



Short communication

## Increased algal fouling on mussels with barnacle epibionts: a fouling cascade



Jorge L. Gutiérrez<sup>a,b,c,\*</sup>, M. Gabriela Palomo<sup>a,d</sup>

<sup>a</sup> Grupo de Investigación y Educación en Temas Ambientales (GrIETA), San Eduardo del Mar, Argentina

<sup>b</sup> Facultad de Ciencias Exactas y Naturales and CONICET, Universidad Nacional de Mar del Plata, Mar del Plata, Argentina

<sup>c</sup> Cary Institute of Ecosystem Studies, Millbrook, NY 12545, USA

<sup>d</sup> Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN-CONICET), Buenos Aires, Argentina

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### ABSTRACT

If the external surfaces of epibionts are more suitable to other fouling species than those of their basibionts, a 'fouling cascade' might occur where epibionts facilitate secondary colonization by other epibionts. Here we evaluate whether the presence of epibiotic barnacles (*Balanus glandula*) influences the probability of mussel (*Brachidontes rodriguezii*) fouling by ephemeral red algae (*Porphyra* sp.) in a Southwestern Atlantic rocky shore. Mussels with barnacle epibionts showed a higher prevalence of *Porphyra* sp. fouling (32–40% depending on sampling date) than mussels without them (3–7%). Two lines of evidence indicate that barnacles facilitate *Porphyra* sp. fouling. First, most *Porphyra* sp. thalli in mussels with barnacle epibionts were attached to barnacle shells (75–92% of cases). Secondly, *Porphyra* sp. associated with mussels with barnacle epibionts in a proportion that significantly exceeded that expected under random co-occurrence. These results suggest the occurrence of a fouling cascade where barnacle epibiosis on mussels facilitates subsequent algal fouling. Recognizing the occurrence of such fouling cascades is important because they might explain the non-random aggregation of multiple epibiotic species onto a proportionally few individuals of the host species.

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### 1. Introduction

The external surfaces of many aquatic organisms can serve as substrate for the attachment of microbes, algae, and sessile invertebrates (Wahl, 1989, 2009; Harder, 2008). The identity and abundance of these epibionts vary across host species – or basibionts – primarily because of differences in the mechanical, physical or chemical defenses located and/or operating on their external surfaces (i.e. antifouling defenses such as spines, mucous, or surface-associated compounds; see Wahl, 1989; Krug, 2006). The interactions between epibionts and basibionts have been widely investigated (see Wahl, 1989, 2009; Krug, 2006; Harder, 2008 for reviews) as well as the effects of microbial epibionts on the subsequent establishment of epibiotic macroalgae and invertebrates (see Krug, 2006; Dobretsov, 2008; Wahl et al., 2012 for reviews). Nevertheless, few studies report that epibiotic macroalgae and invertebrates cover a variable proportion of the basibiont surface with their own surfaces, which may well be more suitable to other epibiotic species (but see Wahl, 2008). If true, a fouling cascade – i.e. epibiont facilitation of secondary epibiont establishment – can be expected to occur.

Barnacles occur as epibionts on a variety of organisms including invertebrates, vertebrates, macroalgae, and rooted aquatic macrophytes (e.g., Withers et al., 1975; Ross and Underwood, 1997; Frick et al., 1998; Buschbaum and Saier, 2001). Simultaneously, barnacles can host other epibionts (e.g., Whorff et al., 1995; Mayer-Pinto et al., 2000; Yakovis et al., 2008). The external surfaces of barnacles can differ markedly from those of their basibionts in their suitability to particular epibionts. For example, barnacles may lack chemical antifouling defenses because of their primarily mineral shells (see Wahl, 1989; Mayer-Pinto et al., 2000) and no physical or mechanical antifouling defense have been described for these organisms (though collective suspension feeding in dense barnacle patches might remove the larvae or propagules of potential foulers). In contrast, previous studies have reported chemical and physical antifouling defenses in typical barnacle basibionts, such as mussels (see Scardino et al., 2003; Scardino and de Nys, 2004; Bers et al., 2006, 2010). Therefore, once epibiotic barnacles become established on mussel shells they could provide an alternative surface for the establishment of other epibiotic species with limited potential to colonize the mussels themselves.

Our study evaluates whether epibiosis by the non-native barnacle *Balanus glandula* on the mussel *Brachidontes rodriguezii* increases the probability of subsequent mussel fouling by ephemeral red algae of the genus *Porphyra* as well as the overall abundance of this seaweed in a Southwestern Atlantic intertidal mussel bed. Algae of the genus

\* Corresponding author at: Grupo de Investigación y Educación en Temas Ambientales (GrIETA), San Eduardo del Mar, Argentina.

E-mail address: [jgutierrez@grieta.org.ar](mailto:jgutierrez@grieta.org.ar) (J.L. Gutiérrez).

*Porphyra* occur widely and their thalli frequently develop epibiotically on mussels (e.g., Santelices and Martínez, 1988; Miyamoto and Noda, 2004; Aquilino et al., 2009; O'Connor, 2010) and barnacles (e.g., Barnes and Powell, 1950; Grant, 1977; Peterson, 1979; Creese, 1988). During preliminary sampling of the study area, we observed a noticeable proportion of mussels with barnacle epibionts fouled by *Porphyra* sp. thalli (Fig. 1). Thus, we predicted that barnacles might facilitate algal fouling onto their individual mussel basibionts, thereby causing a fouling cascade. To test this prediction, we therefore evaluated whether *Porphyra* and barnacles co-occur as epibionts on individual mussels in a proportion that differs from that expected by chance. We then tested the association between the densities of epibiotic barnacles and *Porphyra* sp. thalli in order to assess whether barnacles might contribute to increased *Porphyra* sp. densities in the mussel bed.

## 2. Materials and methods

### 2.1. Study site and organisms

We studied the mid intertidal zone of Punta Cantera (Mar del Plata, Buenos Aires Province, Argentina; 38°05' S, 57°32' W). Low-amplitude tides (Mean, 0.80 m) and quartzitic rock substrate (orthoquartzite) both in the form of boulders (up to 4 m maximum length) and continuous platforms interspersed by channels and tidal pools characterize this site (Gutiérrez et al., 2015). *Brachidontes rodriguezii* forms extensive beds at this site. This relatively small mytilid (up to 55 mm length, most individuals <30 mm length) occurs at high densities (up to 2000 in. dm<sup>-2</sup>) in the mid intertidal zone of Argentinean rocky shores located North of San Matías Gulf (41°S; Penchaszadeh, 1973; Arribas et al., 2013). Their beds are primarily single-layered with multilayered areas restricted to protected vertical rock surfaces and small-sized (<50 cm<sup>2</sup>) sparse hummocks (<1 per m<sup>-2</sup>; Gutiérrez et al., 2015). The barnacle *Balanus glandula* dominates the high intertidal zone at this site (up to 500 in. dm<sup>-2</sup>; pers. obs.) but also occurs at the mid



Fig. 1. Algae (*Porphyra* sp.) fouling a barnacle (*Balanus glandula*) that has settled onto a mussel (*Brachidontes rodriguezii*). The scale is in centimeters.

intertidal zone either as an epibiont on surfacing mussels or as colonizers of bare rock patches that form after mussel dislodgement (see Table S1 in Supplementary Materials for densities at the study site and nearby locales). This native Pacific North American species was first reported in the Mar del Plata area in the early seventies and currently occurs all along the Argentinean Coast (San Clemente del Tuyú to Ushuaia, 36 to 54°S; Schwindt, 2007). Thalli of red algae of the genus *Porphyra* occurs at this site during spring and summer (maximum densities occur between late October and early January; pers. obs.) and can cover a substantial proportion of the mussel bed when laying flat during low tides (e.g., 85% mean cover on Dec-2011, up to 97% cover in some plots; Authors unpublished data). In previous studies, *Porphyra* specimens collected in the Mar del Plata area and nearby towns were either reported as *Porphyra umbilicalis* (Penchaszadeh, 1973), *P. leucosticta* (López Gappa et al., 1990), or *P. pujalsiae* (Boraso and Zaixso, 2011). Given apparent taxonomic uncertainties as well as frequent phenotypic variation within *Porphyra* species (see Varela-Alvarez et al., 2007 and citations therein), we classify the specimens found at this site as *Porphyra* sp. (see also Becherucci et al., 2014). *Porphyra* sp. and *B. glandula* were effectively the only mussel epibionts at this site during the sampling season (i.e. spring to early summer). Other epibionts are numerically important at this site at other times of the year (e.g., ulvoid algae) or occur in very low numbers and/or lower in the intertidal slope (e.g., bryozoans, hydrozoans, encrusting coralline algae; pers. obs.).

### 2.2. *Porphyra*-barnacle association on individual mussels

We evaluated the prevalence of *Porphyra* sp. fouling on mussels with and without barnacle epibionts on Dec-2011, Dec-2012, and Jan-2014. Mussels with and without barnacle epibionts and the fraction of them showing *Porphyra* sp. fouling were counted from cylindrical core samples (10 cm diameter) taken from mussel-covered rock surfaces extending ca. 200 m along the coastline (5–20 m distance between samples). In the case of mussels fouled both by barnacles and *Porphyra* sp., we also noted the surface of algal attachment (i.e. mussel or barnacle shell). Ten core samples were randomly taken at each date yielding total mussel counts of 2273, 1955, and 2135 respectively. In addition, we used Vernier calipers to measure length in unfouled mussels (ca. 200 individuals subsampled at random from those in the cores), mussels fouled by barnacles (either with or without *Porphyra* sp.; ca. 200 individuals including all those found in the cores and individuals collected ad hoc), and mussels fouled by *Porphyra* sp. (either with or without barnacles, *Porphyra* sp. attaching to mussel shells; ca. 200 individuals including all those found in the cores and individuals collected ad hoc) (Precision = 0.1 mm; see Table S2 in Supplementary Materials for exact sample sizes at each date).

A null model approach (Harvey et al., 1983) was used to evaluate whether coexistence between *Porphyra* sp. and barnacles on individual mussels occurs in a proportion that differs from that expected by chance. We created a presence-absence matrix in which columns were individual mussels and rows were epibiotic species (i.e. *Porphyra* sp. or barnacles) in the original data and then randomized the matrix using Poptools (Hood, 2010) to generate 10,000 random matrices of the same size. A co-occurrence index – the C-score (Stone and Roberts, 1990) – was calculated for the original and each of the randomized matrices. C-scores correlate negatively with species co-occurrence and measure the average number of checkerboard units (CU) between all possible pairs of species in a species presence-absence matrix. CUs are samples in which one of the species in the pair occurs and the other does not, and are calculated as,

$$CU = (r_i - S)(r_j - S)$$

where  $S$  denotes the total number of samples in which both species co-occur and  $r_i$  and  $r_j$  are the row totals for species  $i$  and  $j$ . Because co-occurrence analysis in this study involved just one pair of species,

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