



Short communication

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



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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

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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⁻²) 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 cm²) sparse hummocks (<1 per m⁻²; Gutiérrez et al., 2015). The barnacle *Balanus glandula* dominates the high intertidal zone at this site (up to 500 in. dm⁻²; 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,

C-scores here were equivalent to the number of checkerboard units (CU) between the two species. We inferred significant *Porphyra*-barnacle association when the observed C-score (calculated from the original matrix) fell below the lower 5% percentile in the frequency distribution of C-scores of the randomly-generated matrices.

Null model analysis of co-occurrence first considered all cases of association between *Porphyra* sp. and barnacles as epibionts on individual mussels (i.e. irrespective if the alga was attached to mussel or barnacle shells; NM TEST 1) and, then, considered only those cases where *Porphyra* sp. was attached to barnacles (NM TEST 2). In this latter test, mussels fouled both by barnacles and *Porphyra* sp. but with *Porphyra* sp. attaching to mussel shells were treated as mussels fouled by *Porphyra* sp. alone. We made this decision because the presence of barnacle epibionts apparently had no influence on the probability of *Porphyra* sp. attachment to mussel shells (i.e. a comparable proportion of mussel with and without barnacle epibionts shows *Porphyra* sp. attached to their shells; see Results and Fig. 2). However, the outcome of this test would have been the same if mussels with both *Porphyra* sp. and barnacles attached to their shells had been removed from the analysis or treated otherwise (i.e. as mussels with barnacles alone or mussels without epibionts; see Table S3 in Supplementary Materials) because they represent <0.2% of all observations.

Last, we re-ran NM TEST 1 and NM TEST 2 including only mussels larger than 13 mm length in the matrices (hereafter “size-corrected” NM TESTS) because all barnacles and most *Porphyra* sp. thalli in the samples were epibionts on mussels exceeding that size (see Results and Fig. 3). Therefore, mussels shorter than 13 mm were eliminated from the matrices in the proportion indicated by their size frequency distributions (for details, see Table S2 in Supplementary Materials). This led to corrected mussel counts of 1660, 1399, and 1562 respectively for each sampling date. Size-corrected NM TESTS allowed us to test whether non-random co-occurrence between barnacles and *Porphyra* sp. might be a consequence of bias toward the fouling of larger mussels by both epibiotic species. In that case, co-occurrence of *Porphyra* sp. and barnacles as epibionts on mussels larger from 13 mm would not depart from expected under random establishment.

2.3. Relationship between *Porphyra* sp. and barnacle densities in the mussel bed

To test for association between *Porphyra* sp. and barnacle densities in the mussel bed, we quantified both epibionts were quantified at three sampling scales based on the same cores described above on Dec-2011, Dec-2012, and Jan-2014), and in 15 and 25 cm side quadrats sampled on Nov-2013 (225 and 625 cm² respectively; n = 20 each). Simple linear regression (Zar, 1984) related (a) the abundance of *Porphyra* sp. thalli in the mussel bed and, (b) the percentage of *Porphyra* sp. thalli attaching to barnacles, to the abundance of barnacles at those dates and sampling scales.

3. Results and discussion

Less than 2% of mussels were fouled by barnacles at each sampling date, however, *Porphyra* sp. fouling on mussels ranged between 3 and 7% (Table 1). Consequently, most *Porphyra* sp. thalli were attached to mussels without barnacle epibionts (91, 92, and 84% on Dec-2011, Dec-2012, and Jan-2014 respectively). Yet, *Porphyra* sp. fouling was 5–10 times higher in mussels with barnacle epibionts (32–40% depending on sampling date) than on mussels without them (3–6%; see Fig. 2). In addition, *Porphyra* sp. and barnacles significantly co-occurred as epibionts on individual mussels. Null model analyses indicated that the frequency of *Porphyra* sp. association with mussels with barnacles fell below the lower 5% percentile of randomized co-occurrence values, thus significantly departing from chance expectation (Table 2). The latter was apparent when considering *Porphyra*-barnacle co-occurrence irrespective of algal attachment site (i.e. mussel or barnacle shells, NM

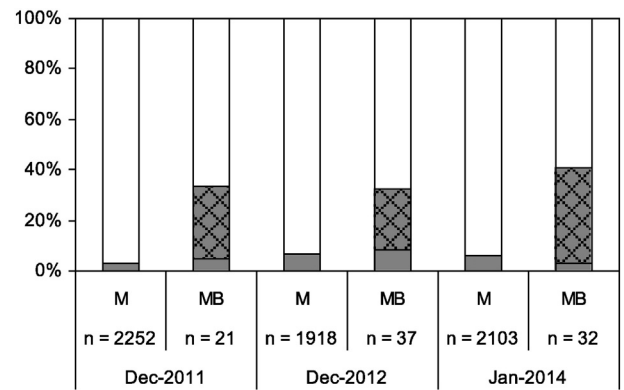


Fig. 2. Percentages of mussels with (MB) and without barnacle epibionts (M) fouled by *Porphyra* sp. (gray shading) and unfouled (white bars) in core samples taken on three sampling dates. For mussels with barnacle epibionts, the crosshatched portion of gray-shaded areas indicate the proportion of *Porphyra* sp. attaching to barnacle shells.

TEST 1) and when considering only those cases where the algae was attached to barnacle shells (NM TEST 2). Furthermore, we observed significant, non-random co-occurrence of *Porphyra* sp. and barnacles as epibionts on individual mussels despite variations in barnacle and algal abundance across sampling dates (see Fig. 2).

All barnacles and most *Porphyra* sp. thalli in the samples (76 to 84% depending on sampling date) were epibionts of mussels larger than 13 mm length (Fig. 3). However, non-random co-occurrence between *Porphyra* sp. and barnacles does not result from increased fouling of larger mussels by both species. In this regard, co-occurrence between

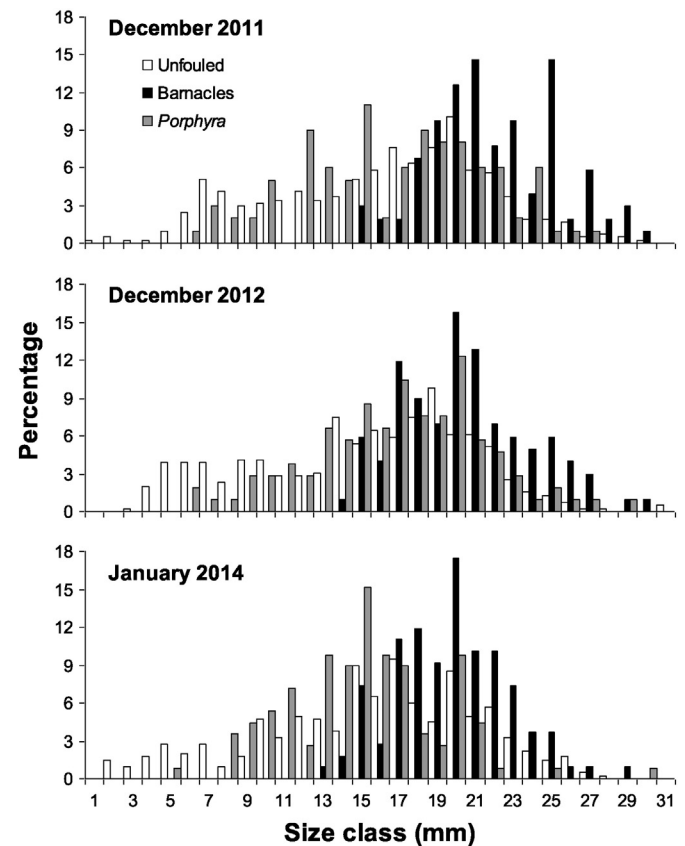


Fig. 3. Size-frequency distributions of mussels fouled by barnacles (either with or without *Porphyra* sp.), mussels fouled by *Porphyra* sp. (either with or without barnacles, *Porphyra* sp. attaching to mussel shells), and unfouled mussels on Dec-2011 (n = 206, 200, 204 respectively), Dec-2012 (n = 207, 212, 205 respectively), and Jan-2014 (n = 215, 224, 211 respectively).

Table 1
Percentage of fouled and unfouled mussels on each sampling date.

Mussel status	Sampling date (Sample size)		
	Dec-2011 (2273)	Dec-2012 (1955)	Jan-2014 (2135)
Unfouled	96.13	91.87	92.83
Fouled by			
barnacle alone	0.62	1.28	0.89
<i>Porphyra</i> sp. alone	2.95	6.24	5.67
Both	0.31	0.61	0.61
Both (<i>Porphyra</i> sp. on barnacle)	0.26	0.46	0.56

Porphyra sp. and barnacles remained significant after removing mussels shorter than 13 mm from the analysis (see results of size-corrected NM TESTS in Table 2). This result demonstrates that processes other than increased settlement and/or survival of both species on the larger mussels contributed to non-random co-occurrence of *Porphyra* sp. and barnacles as mussel epibionts.

Individual mussel attributes other than size could potentially aid the joint establishment of both epibionts on the same individual (e.g., shell abrasion and periostracum damage; see Wahl et al., 1998). Nonetheless, most *Porphyra* sp. thalli in mussels with barnacle epibionts were attached not to the mussel shells but rather to the barnacles themselves (85, 75, and 92% of cases in the 2011, 2012, and 2014 samples, respectively; see Fig. 2). In addition, the percentage of mussels with barnacle epibionts with *Porphyra* sp. thalli attached to the mussel shells (i.e. the percentage of mussels with barnacle epibionts excluding those without *Porphyra* sp. and those with *Porphyra* sp. attached to barnacle shells; 3–8% depending on sampling date) was comparable to *Porphyra* sp. fouling on mussels without barnacle epibionts (2–6%; see Fig. 2). This result indicates some differences in the mussel attributes controlling *Porphyra* sp. establishment and those controlling fouling by barnacles (mussels show multiple antifouling defenses that may vary in their efficacy against distinct epibionts; Wahl et al., 1998). This result also indicates that *Porphyra*-barnacle co-occurrence does not represent a response to particular mussel shell attributes but instead results from increased *Porphyra* sp. settlement and/or survival on barnacle shells. Note that differences in mussel and barnacle surfaces as *Porphyra* sp. colonization sites excludes the possibility of *Porphyra* sp. establishment as a simple response to greater overall surface area resulting from barnacle establishment on mussel shells.

Our results indicate that epibiosis by non-native barnacles, *Balanus glandula*, on the mussel *Brachidontes rodriguezii* aids secondary fouling

Table 2
C-scores of the randomized and observed matrices at each sampling date. Co-occurrence between *Porphyra* sp. and barnacles as epibionts on individual mussels was analyzed irrespective of whether the alga was attached to mussel or barnacle shells (NM TEST 1) or considering only cases where *Porphyra* sp. was attached to barnacles (NM TEST 2). Both co-occurrence analyses were first run including all mussel sizes in the population and then limiting the analysis to mussels larger than 13 mm size (i.e.; the mussel size classes that are mostly affected by barnacle and *Porphyra* sp. fouling; "Size corrected" tests). The lower 5% percentile of the distribution of C-scores from the 10,000 randomized matrices is shown. Significant co-occurrence was found in all cases (i.e. C-score of the observed matrices is less than the lower 5% percentile in the distribution of randomized C-scores).

Analysis	NM TEST 1		NM TEST 2	
	Observed C-score	Lower 5% percentile	Observed C-score	Lower 5% percentile
<i>Uncorrected — all data</i>				
Dec-2011	938	1368	952	1296
Dec-2012	3325	4480	3400	4060
Jan-2014	2299	2856	2318	2760
<i>Size-corrected — mussels > 13 mm</i>				
Dec-2011	728	1083	742	1026
Dec-2012	2800	3658	2875	3304
Jan-2014	1748	2700	1767	2600

by *Porphyra* sp. By covering part of the mussel shells with their bodies, epibiotic barnacles provide an alternative surface that ostensibly favors *Porphyra* sp. establishment and/or survival. This may result from differences between mussels and barnacles in their defenses against *Porphyra* sp. fouling – given expected differences between barnacle and mussel antifouling defenses with weaker defenses expected in barnacles (see Wahl, 1989; Mayer-Pinto et al., 2000; Scardino et al., 2003; Scardino and de Nys, 2004; Bers et al., 2006, 2010). The crevices between barnacle shell plates might also provide sites of enhanced spore settlement (see Barnes, 2000). Moreover, algal spores and germlings attached to the relatively small and rugged barnacle shells might be less accessible to grazers (pulmonate limpets, *Siphonaria lessonii*, are numerically important in at the study area; see Penchaszadeh, 1973) thus reducing algal mortality relative to those in relatively smoother and larger mussel shells (Hawkins, 1981; Lubchenco, 1983; Barnes, 2000). The globally widespread occurrence of barnacles as epibionts of mussels (e.g., Laihonen and Furman, 1986; Lee and Ambrose, 1989; Buschbaum and Saier, 2001; Palomo et al., 2007) and *Porphyra* species as epibionts of barnacles (e.g., Barnes and Powell, 1950; Grant, 1977; Peterson, 1979; Creese, 1988) suggests that similar fouling cascades might occur elsewhere as long as barnacle surfaces show less effective antifouling defenses and/or lower exposure to grazers than those of their mussel basibionts.

In general, fouling cascades may be expected to occur whenever epibionts cover basibiont surfaces with their own surfaces or otherwise modify them (e.g., via damage) thus increasing their suitability for recruitment and survival of other epibionts. Fouling cascades may be of particular interest when the presence of intermediary epibionts (i.e. barnacles in this example) has reverberating positive impacts on populations of other epibionts. This pattern appears not to be the case here. Indeed, the density of *Porphyra* sp. thalli within the mussel bed was not significantly related to barnacle density (see Table 3A for evidence from different sampling dates and scales). This finding suggests (a) that the prevalence (<2%; see above) and density (<14 in. dm⁻²; see Table 3) of epibiotic barnacles in the mussel bed was not sufficient to cause an overall positive effect on *Porphyra* sp. densities and/or (b) that factors other than the availability of colonizable surface limit the abundance of *Porphyra* sp. thalli in this system (e.g., propagule supply, intraspecific competition for space and/or light). Furthermore, our data show an increased proportion of algal thalli attaching to barnacles with increased barnacle densities (see significant positive relationships between the proportion of *Porphyra* sp. thalli attaching to barnacles and barnacle densities in Table 3B), which suggests that barnacles influence the location of individual *Porphyra* sp. thalli in the mussel bed despite no impact on algal densities.

Summing up, our results indicate that *Porphyra* sp. foul individual mussels with epibiotic barnacles more frequently because they offer alternative, and likely more suitable surfaces for algal colonization. Nonetheless, this preference apparently does not translate into increased densities of algal thalli in the mussel bed. Barnacles may thus be hot spots in the mussel bed for the establishment and/or survival rates of individual *Porphyra* sp. thalli, though they would have little effect, if any, on algal demography and production. Furthermore, fouling cascades affect a minor proportion of mussels (i.e. <1%, see Fig. 2) and the same may apply to barnacles given that most of them occur outside from mussel beds in the high intertidal zone where little *Porphyra* sp. colonization occurs (pers. obs., see also Penchaszadeh et al., 2007). Therefore, algal fouling has potential consequences for the growth and survival of individual mussels and barnacles (e.g., due to increased drag, altered predation risk, interference with filter feeding, shading and decreased desiccation; Witman and Suchanek, 1984; Wahl, 1989; Laudien and Wahl, 1999; Thielges, 2005) but negligible impacts on mussel and barnacle populations.

A putative lack of effects on epibionts and/or basibionts populations in no way precludes the possibility of a fouling cascade. We define

Table 3

Summary of simple linear regression analyses evaluating the potential linear relationships between (A) the densities of *Porphyra* sp. thalli in the mussel bed (A) and the proportion of *Porphyra* sp. thalli attaching to barnacles (B) to the density of epibiotic barnacles. Sampling scales (i.e. 78.5, 225, and 625 cm² sampling units) and the range of values of the independent variable (barnacles per sampling unit; i.e. IV range,) at each sampling date are shown in parentheses. Intercepts in (B) were set to zero since non-zero values are logically impossible.

Dependent variable Sampling scale (date/IV range)	Intercept (b ₀)	Slope (b ₁)	F (df)	P	r ²
<i>(A) Porphyra sp. abundance (No. of thalli)</i>					
Dec-2011 (78.5 cm ² /0–4 barnacles)	8.44	–0.16	0.09 (1, 8)	0.77	0.01
Dec-2012 (78.5 cm ² /1–14 barnacles)	12.10	0.65	3.18 (1, 8)	0.11	0.28
Jan-2014 (78.5 cm ² /1–12 barnacles)	12.46	0.29	0.27 (1, 8)	0.61	0.03
Nov-2013 (225 cm ² /0–23 barnacles)	19.73	–0.28	1.38 (1, 18)	0.25	0.08
Nov-2013 (625 cm ² /6–86 barnacles)	50.56	–0.40	2.49 (1, 18)	0.13	0.12
<i>(B) Porphyra sp. thalli attached to barnacles (%)</i>					
Dec-2011 (78.5 cm ² /0–4 barnacles)	0	3.63	31.78 (1, 9)	<0.01	0.78
Dec-2012 (78.5 cm ² /1–14 barnacles)	0	1.40	20.06 (1, 9)	<0.01	0.69
Jan-2014 (78.5 cm ² /1–12 barnacles)	0	2.55	43.70 (1, 9)	<0.01	0.83
Nov-2013 (225 cm ² /0–23 barnacles)	0	1.18	53.02 (1, 19)	<0.01	0.75
Nov-2013 (625 cm ² /6–86 barnacles)	0	0.45	80.97 (1, 19)	<0.01	0.81

fouling cascade as a kind of biological interaction and, as such, it denotes an inter-individual relationship rather than a population-level net effect (cf., population-level facilitation or inhibition). As with other biological interaction (e.g., predation), fouling cascades occurs independently of whether they cause population-level impacts on the involved parties (e.g., the lack of a predator effect on prey population does not rule out that predation occurs). Hence, our example illustrates that fouling cascades occur in marine benthic communities despite apparently negligible effects on epibionts and basibionts. In our view, awareness of fouling cascades is important for at least two fundamental reasons. First, cascades might be significant to basibiont and/or epibiont populations in other circumstances (e.g., when intermediary epibionts colonize a large proportion of their putative basibionts and/or release other fouling species from limited availability of suitable surfaces). Secondly, cascades might explain the non-random aggregation of multiple epibiotic species onto a few individuals in the population of the basibiotic species, which is generally ascribed to attributes of the individual basibiont (e.g., reduced antifouling defenses) rather than facilitation between epibiotic species (see Wahl, 2008). An appreciation of fouling cascades can be of particular importance when non-native epibionts providing novel colonizable surfaces and with potential to attain high prevalence are either intentionally or accidentally introduced into aquatic habitats.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.seares.2016.04.002>.

References

Aquilino, K.M., Bracken, M.E., Faubel, M.N., Stachowicz, J.J., 2009. Local-scale nutrient regeneration facilitates seaweed growth on wave-exposed rocky shores in an upwelling system. *Limnol. Oceanogr.* 54, 309–317.

Arribas, L.P., Bagur, M., Klein, E., Penchaszadeh, P.E., Palomo, M.G., 2013. Geographic distribution of two mussel species and associated assemblages along the northern Argentinean coast. *Aquat. Biol.* 18, 91–103.

Barnes, M., 2000. The use of intertidal barnacle shells. *Oceanogr. Mar. Biol. Annu. Rev.* 38, 157–187.

Barnes, H., Powell, H.T., 1950. The development, general morphology and subsequent elimination of barnacle populations, *Balanus crenatus* and *B. balanoides*, after a heavy initial settlement. *J. Anim. Ecol.* 19, 175–179.

Becherucci, M.E., Benavides, H., Vallarino, E.A., 2014. Effect of taxonomic aggregation in macroalgae assemblages in a rocky shore of Mar del Plata, Argentina, Southwest Atlantic Ocean. *Thalassas* 30, 9–20.

Bers, A.V., D'Souza, F., Klijnstra, J.W., Willemsen, P.R., Wahl, M., 2006. Chemical defence in mussels, antifouling effect of crude extracts of the periostracum of the blue mussel *Mytilus edulis*. *Biofouling* 22, 251–259.

Bers, A.V., Diaz, E.R., da Gama, B.A.P., Vieira-Silva, F., Dobretsov, S., Valdivia, N., Wahl, M., 2010. Relevance of mytilid shell microtopographies for fouling defence - a global comparison. *Biofouling* 26, 367–377.

Boraso, A., Zaikso, J.M., 2011. Algas marinas bentónicas. In: Boltovskoy, D. (Ed.), *Atlas de sensibilidad ambiental de la costa y el mar argentino*. Secretaría de Ambiente y Desarrollo Sustentable, Buenos Aires, pp. 1–28.

Buschbaum, C., Saier, B., 2001. Growth of the mussel *Mytilus edulis* L. in the Wadden Sea affected by tidal emergence and barnacle epibionts. *J. Sea Res.* 45, 27–36.

Creese, R.G., 1988. Ecology of molluscan grazers and their interactions with marine algae in northeastern New Zealand, a review. *N. Z. J. Mar. Freshw. Res.* 22, 427–444.

Dobretsov, S., 2008. Inhibition and Induction of Marine Biofouling by Biofilms. In: Flemming, H.C., Venkatesan, R., Murthy, S.P., Cooksey, K. (Eds.), *Marine and Industrial Biofouling*. Springer-Verlag, Berlin, pp. 293–313.

Frick, M.G., Williams, K.L., Robinson, M., 1998. Epibionts associated with nesting loggerhead sea turtles (*Caretta caretta*) in Georgia, USA. *Herpetol. Rev.* 29, 211–213.

Grant, W.S., 1977. High intertidal community organization on a rocky headland in Maine, USA. *Mar. Biol.* 44, 15–25.

Gutiérrez, J.L., Palomo, M.G., Bagur, M., Arribas, L.P., Soria, S.A., 2015. Wave action limits crowding in an intertidal mussel. *Mar. Ecol. Prog. Ser.* 518, 153–163.

Harder, T., 2008. Marine epibiosis, concepts, ecological consequences and host defence. In: Flemming, H.C., Venkatesan, R., Murthy, S.P., Cooksey, K. (Eds.), *Marine and Industrial Biofouling*. Springer-Verlag, Berlin, pp. 219–232.

Harvey, P.H., Colwell, R.K., Silvertown, J.W., May, R.M., 1983. Null models in ecology. *Annu. Rev. Ecol. Syst.* 14, 189–211.

Hawkins, S.J., 1981. The influence of season and barnacles on the algal colonization of *Patella vulgata* exclusion areas. *J. Mar. Biol. Assoc. UK* 61, 1–16.

Hood, G.M., 2010. PopTools version 3.2.5. <http://www.poptools.org>.

Krug, P.J., 2006. Defense of Benthic Invertebrates Against Surface Colonization by Larvae, a Chemical Arms Race. In: Fusetani, N., Clare, A.S. (Eds.), *Antifouling Compounds*. Springer-Verlag, Berlin, pp. 1–53.

Laihonon, P., Furman, E.R., 1986. The site of settlement indicates commensalism between blue mussel and its epibiont. *Oecologia* 71, 38–40.

Laudien, J., Wahl, M., 1999. Indirect effects of epibiosis on host mortality: seastar predation on differently fouled mussels. *Mar. Ecol.* 20, 35–47.

Lee, H., Ambrose, W.G., 1989. Life after competitive exclusion, an alternative strategy for a competitive inferior. *Oikos* 56, 424–427.

López Gappa, J.J., Tablado, A., Magaldi, N.H., 1990. Influence of sewage pollution on a rocky intertidal community dominated by the mytilid *Brachidontes rodriguezii*. *Mar. Ecol. Prog. Ser.* 63, 163–175.

Lubchenco, J., 1983. *Littorina* and *Fucus*, effects of herbivores, substratum heterogeneity, and plant escapes during succession. *Ecology* 64, 1116–1123.

Mayer-Pinto, M., Viana, M.S., Lavrado, H.P., Silva, T.A., Silva, S.H.G., 2000. Epibiosis on barnacles at Angra dos Reis, RJ, Eutrophication effects. *Nauplius* 8, 55–61.

Miyamoto, Y., Noda, T., 2004. Effects of mussels on competitively inferior species, competitive exclusion to facilitation. *Mar. Ecol. Prog. Ser.* 276, 293–298.

O'Connor, N.E., 2010. Shore exposure affects mussel population structure and mediates the effect of epibiotic algae on mussel survival in SW Ireland. *Estuar. Coast. Shelf Sci.* 87, 83–91.

- Palomo, M.G., People, J., Chapman, M.G., Underwood, A.J., 2007. Separating the effects of physical and biological aspects of mussel beds on their associated assemblages. *Mar. Ecol. Prog. Ser.* 344, 131–142.
- Penchaszadeh, P.E., 1973. Ecología de la comunidad del mejillín (*Brachidontes rodriguezii* D'Orb.) en el mediolitoral rocoso de Mar del Plata, Argentina, el proceso de recolonización. *Physis* 32, 51–64.
- Penchaszadeh, P.E., Scelzo, M.A., Palomo, M.G., Cuevas, M., Cledón, M., 2007. A review of the intertidal rocky shore community at Mar del Plata (Argentina) characterized by the mussel *Brachidontes rodriguezii* (d'Orbigny, 1846). *Publ. Seto. Mar. Biol. Lab.* 8, 115–123.
- Peterson, C.H., 1979. The importance of predation and competition in organizing the intertidal epifaunal communities of Barnegat Inlet, New Jersey. *Oecologia* 39, 1–24.
- Ross, P.M., Underwood, A.J., 1997. The distribution and abundance of barnacles in a mangrove forest. *Aust. J. Ecol.* 22, 37–47.
- Santelices, B., Martínez, E., 1988. Effects of filter-feeders and grazers on algal settlement and growth in mussel beds. *J. Exp. Mar. Biol. Ecol.* 118, 281–306.
- Scardino, A., de Nys, R., 2004. Fouling deterrence on the bivalve shell *Mytilus galloprovincialis*, a physical phenomenon? *Biofouling* 20, 249–257.
- Scardino, A., de Nys, R., Ison, O., O'Connor, W., Steinberg, P., 2003. Microtopography and antifouling properties of the shell surface of the bivalve molluscs *Mytilus galloprovincialis* and *Pinctada imbricata*. *Biofouling* 19, 221–230.
- Schwindt, E., 2007. The invasion of the acorn barnacle *Balanus glandula* in the south-western Atlantic 40 years later. *J. Mar. Biol. Assoc. UK* 87, 1219–1225.
- Stone, L., Roberts, A., 1990. The checkerboard score and species distributions. *Oecologia* 85, 74–79.
- Thieltges, D.W., 2005. Impact of an invader, epizoitic American slipper limpet *Crepidula fornicata* reduces survival and growth in European mussels. *Mar. Ecol. Prog. Ser.* 286, 13–19.
- Varela-Alvarez, E., Stengel, D.B., Guiry, M.D., 2007. Seasonal growth and phenotypic variation in *Porphyra linearis* (Rhodophyta) populations on the west coast of Ireland. *J. Phycol.* 43, 90–100.
- Wahl, M., 1989. Marine epibiosis. I. Fouling and antifouling, some basic aspects. *Mar. Ecol. Prog. Ser.* 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 Defences. In: Wahl, M. (Ed.), *Marine Hard Bottom Communities, Patterns, Dynamics, Diversity, and Change*. Springer-Verlag, Berlin, pp. 61–72.
- Wahl, M., Kröger, K., Lenz, M., 1998. Non-toxic protection against epibiosis. *Biofouling* 12, 205–226.
- Wahl, M., Goecke, F., Labes, A., Dobretsov, S., Weinberger, F., 2012. The second skin, ecological role of epibiotic biofilms on marine organisms. *Front. Microbiol.* 3, 292–313.
- Whorff, J.S., Whorff, L.L., Sweet, M.H., 1995. Spatial variation in an algal turf community with respect to substratum slope and wave height. *J. Mar. Biol. Assoc. UK* 75, 429–444.
- Withers, R.G., Farnham, W.F., Lewey, S., Jephson, N.A., Haythorn, J.M., Gray, P.W.G., 1975. The epibionts of *Sargassum muticum* in British waters. *Mar. Biol.* 31, 79–86.
- Witman, J.D., Suchanek, T.H., 1984. Mussels in flow, drag and dislodgement by epizoans. *Mar. Ecol. Prog. Ser.* 16, 259–268.
- Yakovis, E.L., Artemieva, A.V., Shunatova, N.N., Varfolomeeva, M.A., 2008. Multiple foundation species shape benthic habitat islands. *Oecologia* 155, 785–795.
- Zar, J.H., 1984. *Biostatistical Analysis*. Prentice-Hall, Englewood Cliffs, NJ, USA.