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SHORT NOTES

When the tiny help the mighty: facilitation between two introduced species, a solitary ascidian and a macroalga in northern Patagonia, Argentina

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Abstract Facilitation is recognized as one of the mechanisms by which nonnative species are integrated into new assemblages. The solitary ascidian *Styela clava* and the macroalga *Undaria pinnatifida* were introduced to San Antonio Bay, Argentina, with a couple of years of difference. We studied the occurrence pattern of both species in the area and tested the hypothesis that *S. clava* facilitates *U. pinnatifida* through a manipulative experiment. Our results clearly suggest a facilitation process between these species. The probability of finding *U. pinnatifida* is 30% higher in sites where *S. clava* is present and higher recruitment of *U. pinnatifida* occurred where *S. clava* is present than where it had been experimentally removed. Increased habitat complexity by the stalked ascidian *S. clava* can facilitate the establishment of *U. pinnatifida* by providing refugee from grazers, increasing surface for settlement, or providing greater access to light.

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Introduction

While negative ecological interactions, such as predation and competition, have been widely documented in the literature, positive interactions such as facilitation and mutualism, have received far less attention (Bruno et al. 2003). Many of the advances along this line of inquiry have come from the marine realm where studies with different taxa have shown the positive effects of facilitation on structuring communities (e.g. Bertness and Callaway 1994; Stachowicz 2001; Bruno et al. 2003; Bulleri and Benedetti-Cecchi 2008; Bulleri 2009; Edwards and Stachowicz 2011). For instance, different studies have considered the effects of bivalves, polychaetes and other sessile filter-feeders on macroalgae (e.g. Bracken 2004; Bracken et al. 2007; Bulleri 2009). The effect of solitary ascidians on other invertebrates by increasing habitat complexity has also been tested (e.g. Claar et al. 2011; Rimondino et al. 2015), but little is known about the process of facilitation between ascidians and macroalgae. Harder (2008), and Sellheim et al. (2010) suggested that facilitation will be more prone to occur between habitat forming and mobile epifauna, while when an epiphytic algae is involved, the relationship should be competitive. While both Monteiro et al. (2002) and Castilla et al. (2004) showed an increase of the macroalgae diversity in the clumps of the solitary ascidia *Pyura priupitalis*, none of them have specifically tested a facilitation process.

The ascidian *Styela clava,* original from the northwestern Pacific Ocean (Goldstien et al. 2011), was reported for the first time in the southern Atlantic Ocean in 2013 (Pereyra et al. 2015). Originally described from a few sites in an inner channel of San Antonio Bay (northern Patagonia, Argentina), its presence has become evident in other sites, attached to diverse hard substrates. On the other hand, the macroalga *Undaria pinnatifida*, a notorious introduced

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Fig. 1 Low intertidal from San Antonio Bay (Rio Negro, Argentina) exposing rocky flats where the experiment was set up. Hanging from the rocks can be observed highly dense clumps of *Styela clava*. *Upper right corner* shows the area of study. *SAB* San Antonio Bay, *SAO* San Antonio Oeste Town, *SAE* San Antonio Este (international port), *black star* site of study. Photograph by Juan Saad

species worldwide, was accidentally introduced in Argentina (42°45′S) in 1992 (Piriz and Casas 1994) and has further spread both south and northwards (Casas et al. 2004; Pereyra et al. 2015). Both species co-occur now alongside the coasts of San Antonio Bay (Fig. 1).

Having noted high abundance of *U. pinnatifida* in areas where *S. clava* were present or directly overgrowing it, we hypothesized that *S. clava* facilitates the occurrence of *U. pinnatifid*a. To test this, we measured the association between both species in a shallow rocky shore of the San Antonio Bay and performed manipulative experiments to test whether *S. clava* facilitates the recruitment of *U. pinnatifida*. We specifically predicted that (1) the probability of occurrence of *U. pinnatifida* is higher where *S. clava* is present; and (2) *S. clava* facilitates the recruitment of *U. pinnatifida*. In this study, and according to Rodriguez (2006), we define facilitation as an interaction between two species that results in an increase, in either number or biomass, of at least one of the two species.

Methods

Study area

The study was carried out from May to August 2016, in a tidal channel of San Antonio Bay (40°43.6′S, 64°54.8′W; Northern Patagonia, Argentina). The bay is about 80 km^2 with patches of extensive muddy intertidal, sandy banks, rocky shores, inlets, tidal channels and rolling stone beaches (Gelós et al. 1994). It is a macrotidal environment, with little wave action (Isla et al. 2001) and a semidiurnal tidal regime with amplitude ranging between six and nine meters. San Antonio Oeste town, located along a channel to the west side of the bay, is highly urbanized. This channel shows signs of anthropic disturbance and eutrophication due to freshwater input, enriched with nitrogen, introduced via septic system from the city (in fact, the inner channel where the study was performed presented a concentration of ammonium almost fifteen times higher and the concentration of nitrates was nearly twice higher compared to a control channel; Martinetto et al. 2010). While the concentrations of nutrients are comparable and even higher than those of other of highly polluted waters (Teichberg et al. 2010), the inner channel seems to be in an initial state of eutrophication (Martinetto et al. 2011). This external input of nutrients favors and accelerates the growth rates of resident species (Teichberg et al. 2010).

Experimental work was performed at the low intertidal; on rocky flats with a homogeneous ground complexity (Fig. 1) periodically covered by sand and gravel, where both species occur (Pereyra et al. 2015). There, *U. pinnatifida* is established on many kinds of consolidated and unconsolidated substrata, but it is practically absent where turf-forming algae are present (e.g. young *Ulva lactuca*, *Hincksia* sp.). In this area, sporophytes of *U. pinnatifida* begin to sprout in early austral autumn (between April and May) after the characteristic senescent period of the previous cohort (Casas et al. 2008).

Density and co-occurrence of *Undaria pinnatifida* and *Styela clava*

To test if the probability of occurrence of *U. pinnatifida* is higher when *S. clava* is present, we sampled the density of both species in August when *U. pinnatifida*'s sporophytes were fully developed. The number of *U. pinnatifida* and *S. clava* was counted in 93 quadrats (0.25 × 0.25 m) located in an area of gentle slope of about 1200 m^2. The quadrats were haphazardly placed on the substratum at least 5 m apart and the number of quadrats in which both species occurred alone and associated was registered. An independence Chi square test with Yates' continuity correction was used to evaluate the probability of species occurring alone and associated.

Styela clava effect on *Undaria pinnatifida* recruitment

To test if *S. clava* enhances the recruitment of *U. pinnatifida* we randomly deployed 30 plots of 0.25 × 0.25 m where *U. pinnatifida* and *S. clava* co-occurred. Plots were only placed where both species were present in order to ensure that both species were able to establish. Plots were then randomly assigned to one of the following treatments ($n = 15$ plots per treatment): (1) plots where all *S. clava* were removed (SC−) and (2) plots where *S. clava* individuals were left undisturbed (SC+). In addition, all *U. pinnatifida* were removed from plots before the beginning of the experiment. The experimental plots were set up in May, when the sporophytes of *U. pinnatifida* begin to sprout, and then visited monthly for 3 months. At each visit the number of *U. pinnatifida* was registered and newly established *S. clava* removed from the SC− treatment. Due to the rapid growth of *U. pinnatifida,* 3 months were considered enough time to assess if facilitation was taking place and to avoid other processes that occur over a greater time scale (e.g. intraspecific competition) that could mask or modify the interaction of interest.

To test the effects of treatment and time on the number of *U. pinnatifida* we used generalized linear mixed models (GLMM; Crawley 2007; Zuur 2009). As no overdispersion was found ($c = 1.096$), a Poisson error distribution and log link function were used. Treatment and time were considered as fixed factors, while plot identity was considered a random factor.

Four models were considered (Table 1) and evaluated with information-theoretic procedures (Burnham et al. 2002). Akaike's information criterion corrected for small sample size (AICc) was used to compare models (Burnham et al. 2002), considering the difference between the lowest AICc value and AICc from all other models (ΔAICc). The relative likelihood that a specific model is the best of all models was evaluated with the AICc weight of each model (w_i). Only one model obtained $w_i \neq 0$; thus, parameters and their 95% confidence intervals were calculated based solely on that model. All statistical analyses were carried out using R software (R Core Team 2016).

Table 1 GLMM results for all models evaluated testing the effect of experimental treatment (EXP; 2 levels, fixed), time (TIME; 3 levels, fixed) and plot (*P*; random) on the abundance of newly settled *Undaria pinnatifida*

Candidate model	Freedom degrees	AICc	ΔAICc	w_i
EXP × TIME × *P*	5	187.88	0.0	1
TIME × *P*	4	204.15	16.27	0
EXP × *P*	3	223.64	35.77	0
P	2	239.57	51.69	0

Results

Density and co-occurrence of *Undaria pinnatifida* and *Styela clava*

Undaria pinnatifida's mean density ($X \pm$ SE) was 22.7 ± 6.3 individuals m^{-2} and *S. clava*'s mean density was 17.2 ± 8.3 individuals m^{-2}. However, when considering only quadrats where *S. clava* was present, the density of *U. pinnatifida* reached up to 58.2 ± 23.9 individuals m^{-2}.

The probability of co-occurrence was of 0.63, while the probability of finding *U. pinnatifida* in quadrats where *S. clava* was absent was of 0.33 (Fig. 2). Thus, the probability of finding *U. pinnatifida* was 0.30 higher in plots where *S. clava* was present ($\chi^2 = 5.01$, $P = 0.02$).

Styela clava effect on *Undaria pinnatifida* recruitment

During the experiment some plots were lost leaving 27 plots at time 1 ($n_{SC+} = 13$, $n_{SC-} = 14$), 26 at time 2 ($n_{SC+} = 13$, $n_{SC-} = 13$) and 20 at time 3 ($n_{SC+} = 8$, $n_{SC-} = 12$). In SC− plots, the abundance of *U. pinnatifida* was rarely higher than zero, irrespective of sampling time (2.08 ± 1.12 individuals m^{-2}, range = 0–2; $n = 39$; Fig. 3). On the other hand, in SC+ plots, *U. pinnatifida*'s mean

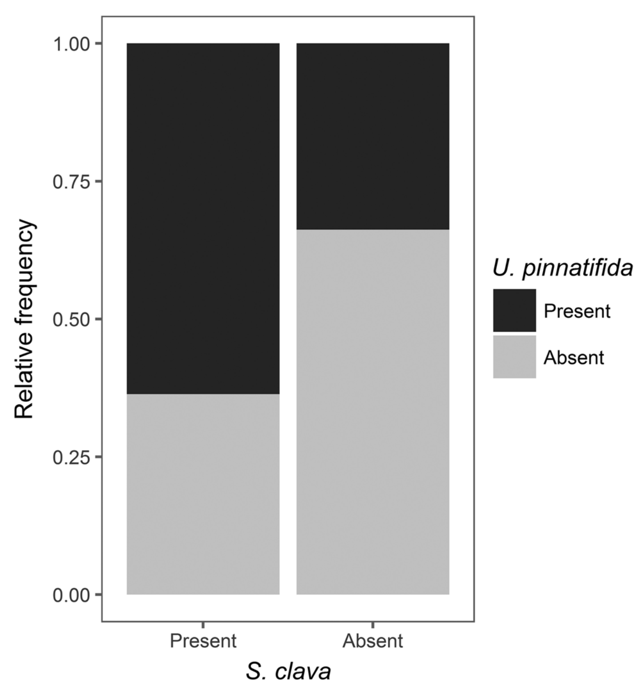

Fig. 2 Relative frequency of *Undaria pinnatifida* in quadrats where *Styela clava* was present ($n = 22$) and where *S. clava* was absent ($n = 71$)

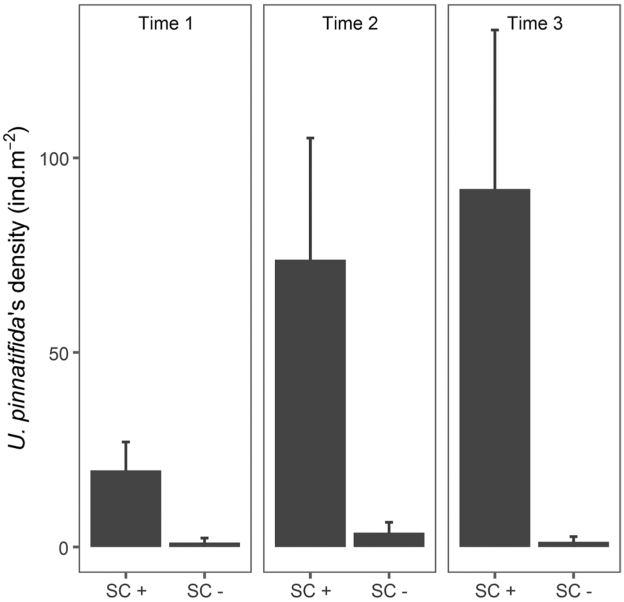

Fig. 3 Density of *Undaria pinnatifida* (mean ± SE) in plots with *Styella clava* (SC+) and plots where *S. clava* was removed (SC−). Time is expressed in months since the beginning of the experiment, where *1*, *2* and *3* represent June, July and August, respectively

Table 2 Parameter estimates (±SE) from GLMM describing variation in the abundance of *Undaria pinnatifida*

Explanatory variable	Parameter estimate ± SE	CI	
		Lower	Upper
Intercept	−0.59 ± 0.49	−1.56	0.38
EXP (SC−)	−3.45 ± 0.81	−5.06	−1.85
TIME (2)	1.31 ± 0.27	0.77	1.86
TIME (3)	1.58 ± 0.30	0.99	2.18

abundance showed a constant increase (Fig. 3) and by the end of the experiment, all plots had at least one individual of *U. pinnatifida*.

The best model explaining the variation in *U. pinnatifida*'s abundance included experimental treatment and time as explanatory variables ($w_i = 1$; Table 1). *U. pinnatifida*'s abundance increased every month and was always higher in SC+. After 3 months the expected density of *U. pinntatifida* where *S. clava* was present was 43.0 individuals m^{-2} (CI 95%: 9.048–206.97), while in areas where *S. clava* was absent the expected density resulted in 1.3 individuals m^{-2} (CI 95%: 0.057–32.54) (Table 2).

Discussion

Our results support the hypothesis that the solitary ascidian *Styela clava* facilitates the occurrence of the macroalga *Undaria pinnatifida*. Through the study of their distribution pattern we observed a higher probability of finding *U. pinnatifida* when *S. clava* was present; additionally, through manipulative experiments, we observed a higher recruitment of *U. pinnatifida* where *S. clava* was present. While both species share their native area (e.g. http://www.marinespecies.org), to our knowledge, this is the first time that an interaction of this nature is tested between these two species.

It is well established in the literature that sessile organisms enhance habitat suitability, adding heterogeneity and complexity to the landscape (e.g. Monteiro et al. 2002; Gutiérrez et al. 2003). In intertidal environments, facilitation can occur via wave protection, continuous provision of food, refuge against consumers (e.g. Thompson et al. 1996; Castilla et al. 2004; Bulleri and Benedetti-Cecchi 2008; Claar et al. 2011) or by providing a heterogeneous and hard surfaces for settlement (e.g. Maida et al. 1994; Harder 2008). In our study system, protection against wave action is not a likely mechanism as San Antonio Bay is sheltered and enclosed with very little wave action (Isla et al. 2001). Facilitation through nutrient supply is also hardly the case here because the channel where the experiments were conducted has the highest nutrient input in the area (Martinetto et al. 2010). Regarding the effect of algal grazers on *U. pinnatifida*'s populations, contrasting results have been found among studies performed around the world. In Tasmania and New Zealand grazers do select *U. pinnatifida* over other algaes (Suárez-Jímenez et al. 2015) and have a negative effect on *U. pinnatifida*'s abundance (Valentine and Johnson 2005), while in Argentina, grazers effect seems to be negligible and mostly affect senescent individuals (Castro et al. 2015). Whereas grazing marks were scarcely observed in fully developed *U. pinnatifida*, the effect of grazers on newly settled individuals should not be discarded. Among all, we think that the most relevant facilitation mechanism may be the addition of substrate complexity (cf. Monteiro et al. 2002). Thompson and Schiel (2012) reported a positive effect of *Corallina officinalis* on *U. pinnatifida* and suggested that greater complexity produced by *C. officinalis* allows greater moisture retention and protection from grazers, providing a safer substrate for spores to settle. This could be the case between *S. clava* and *U. pinnatifida* as well. In addition, an erected surface might improve flow dynamics (Wahl and Mark 1999; Harder 2008), increase spore settlement (Bulleri and Benedetti-Cecchi 2008) and facilitates access to light (e.g. Maida et al. 1994). In this sense, good access to light is essential to *U. pinnatifida*'s establishment (Valentine and Johnson 2003, 2004) and thus *S. clava* would help *U. pinnatifida* surpass areas where it is competitively displaced (Thompson and Schiel 2012; Morelissen et al. 2016; South and Thomsen 2016). However, the mechanism of the interaction between *U. pinnatifida* and *S. clava* (whether mechanical or biological) remains to be tested.

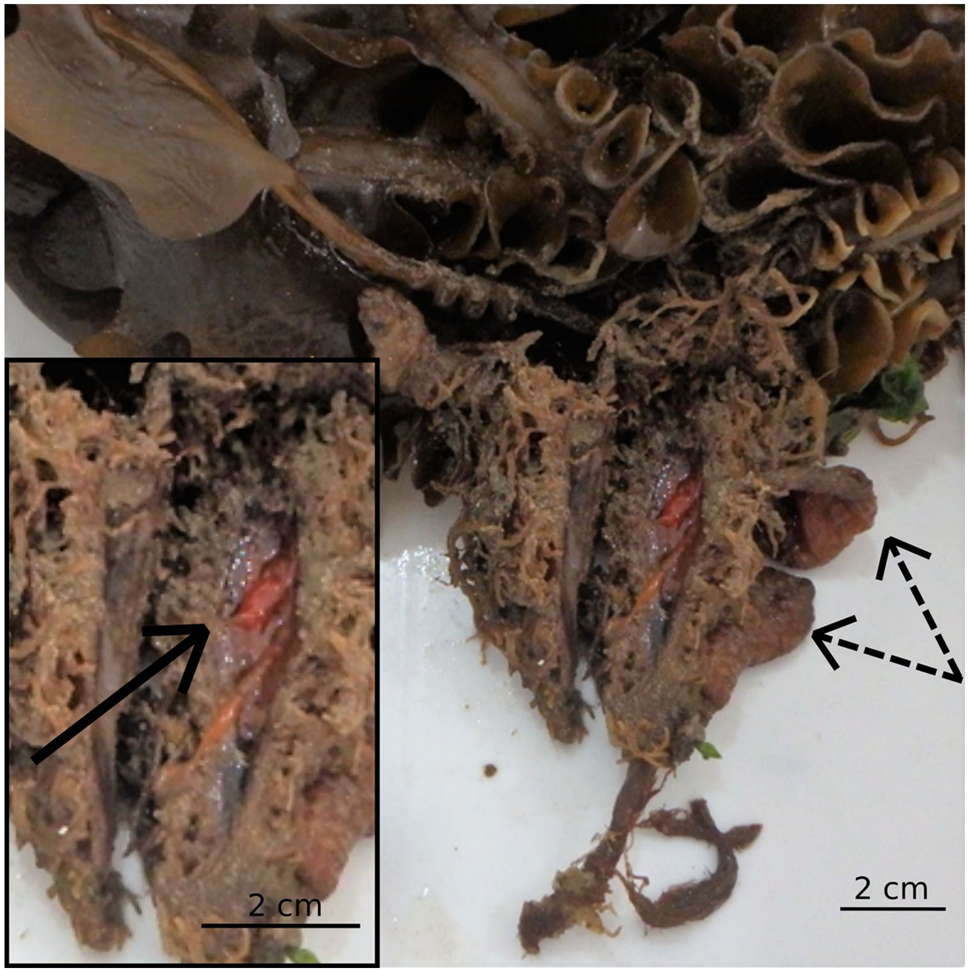

Fig. 4 *Undaria pinnatifida* overgrowing *Styela clava*. *Solid arrow* indicates the section of the stolon showing the basibiont completely covered; *dashed arrows* indicate two individuals of *S. clava* growing on the stolon of *U. pinnatifida*

While our results suggest a positive effect of *S. clava* on *U. pinnatifida*, the macroalga could negatively affect *S. clava* (e.g. Farrell and Fletcher 2006). Other ascidians can survive epibiosis when the epibiont does not preclude the siphon of the basibiont (e.g. Claar et al. 2011), but this is not the case here. After a couple of months following the establishment of *U. pinnatifida* its stolon has overgrown entirely the basibiont (Fig. 4). However, determining if this increases mortality in *S. clava* as a consequence of great pressure should be experimentally tested.

Introduced ascidians rarely colonize natural benthic habitats (Simkanin et al. 2012, 2016); thus most studies are performed in man-made environment where species are introduced (e.g. ports, harbors, marinas) (Zhan et al. 2015), and with *ad hoc* structures (e.g. Schwindt et al. 2014). However, in our study system, *S. clava* is found on intertidal rocky shores at abundances an order of magnitude higher than those reported in other natural areas (*cf.* Simkanin et al. 2012). There is little understanding on how introduced ascidians spread in natural environments (Zhan et al. 2015) and how they affect natural assemblages (but see Monteiro et al. 2002; Castilla et al. 2004). Therefore, more research is needed to understand the effects introduced ascidians may produce in natural environments. While we need detailed observation and experimentation before jumping to conclusions on the effects of both species on the biodiversity in the area, *U. pinnatifida* produces (negative) economic effects in Puerto Madryn (Piriz et al. 2003), and similar outcomes could be expected in this recently invaded area.

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Compliance with ethical standards

Conflict of interest We declare that we have no conflict of interest. All the authors consented and agreed to carry out this research. All animals have been sampled and treated according to the national legislation. All permission to work in our study area were obtained prior the start of the experiments.

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