



Royal Netherlands Institute for Sea Research

This is a pre-copyedited, author-produced version of an article accepted for publication, following peer review.

Arcángel, A.E.; Rodríguez, E.A.; de la Barra, P.; Pereyra, P.J.; Narvarte, M. (2022). Seasonal changes in facilitation between an ascidian and a kelp in Patagonia. *Mar. Ecol. Prog. Ser.* 693: 95-106. DOI:10.3354/meps14090

Published version: <https://dx.doi.org/10.3354/meps14090>

NIOZ Repository: <http://imis.nioz.nl/imis.php?module=ref&refid=354130>

[Article begins on next page]

The NIOZ Repository gives free access to the digital collection of the work of the Royal Netherlands Institute for Sea Research. This archive is managed according to the principles of the [Open Access Movement](#), and the [Open Archive Initiative](#). Each publication should be cited to its original source - please use the reference as presented.

When using parts of, or whole publications in your own work, permission from the author(s) or copyright holder(s) is always needed.

1 **Seasonal changes in facilitation between an ascidian and a kelp in Patagonia**

2 **Andrea Evangelina Arcángel^{1,2,3,*}, Emiliano Alexis Rodríguez^{1,2,3}, Paula de la Barra⁴,**
3 **Patricio Javier Pereyra^{1,2,3,*}, Maite Narvarte^{1,2,3}**

4 ¹Centro de Investigación Aplicada y Transferencia Tecnológica en Recursos Marinos Almirante
5 Storni (CIMAS), Güemes 1030, 8520 San Antonio Oeste, República Argentina

6 ²Consejo Nacional de Investigaciones Científicas y Técnicas, Godoy Cruz 2290, C1425FQB
7 Ciudad Autónoma de Buenos Aires, República Argentina

8 ³Escuela Superior de Ciencias Marinas-Universidad Nacional del Comahue, San Martín 247,
9 8520 San Antonio Oeste, República Argentina

10 ⁴Department of Marine Ecology, NIOZ Royal Netherlands Institute for Sea Research, Landsdiep
11 4 1797 SZ 't Horntje, Texel, The Netherlands

12 *Corresponding authors: Andrea Evangelina Arcángel, Patricio Javier Pereyra. Centro de
13 Investigación Aplicada y Transferencia Tecnológica en Recursos Marinos Almirante Storni
14 (CIMAS), Güemes 1030, 8520 San Antonio Oeste, República Argentina. +54 (2934) 42-2764.

15 E-mails: andrearcangel.ev@gmail.com, pereyranis@gmail.com

16 ORCID numbers:

17 Andrea Evangelina Arcángel: 0000-0001-5868-2612

18 Emiliano Alexis Rodríguez: 0000-0002-3474-9402

19 Paula de la Barra: 0000-0001-8416-5926

20 Patricio Javier Pereyra: 0000-0003-2873-9512

21 Maite Narvarte: 0000-0002-6051-4842

22 **Running header:** Seasonal changes in facilitation?

23 **Abstract**

24 Positive interactions may change in outcome over time and depending on which of the interacting
25 species is studied. We explored the seasonal patterns of facilitation between *Styela clava* and
26 *Undaria pinnatifida* by following their association for a complete sporophytic phase. In addition,
27 we investigated how the relationship affected the morphometric parameters of *U. pinnatifida*, and
28 if the association had a negative outcome for *S. clava*. We performed monthly surveys in San
29 Antonio Bay (Argentina) for nearly one year to evaluate *U. pinnatifida*'s density (both the total
30 and mature individuals exclusively) on different substrates to determine whether *U. pinnatifida*
31 was more closely associated with *S. clava* than with inert substrates (*i.e.*, consolidated and
32 nonconsolidated). Moreover, we compared the morphometry of *U. pinnatifida* between substrates
33 (*S. clava* vs. rock) and collected *S. clava* individuals overgrown by *U. pinnatifida* and classified
34 them by their holdfast's coverage to assess their condition (dead or alive). A higher total density
35 of individuals of *U. pinnatifida* was associated with *S. clava* than with other substrates from
36 autumn to spring. *Undaria pinnatifida* individuals growing on *S. clava* were smaller than those
37 growing on rock. Finally, the probability of *S. clava* dying increased for individuals with higher
38 holdfast coverage, although the scarcity of dead individuals found suggested a negligible
39 influence. Our findings suggest, whereas *U. pinnatifida* clearly benefitted from this interaction
40 by appearing earlier on the field and presenting higher densities that could benefit the population
41 when associated to *S. clava*, for *S. clava* the relationship was more neutral.

42 **Key words**

43 Facilitation-Population-level effect-Individual-level effect-Patagonia Argentina

44 **1. Introduction**

45 Negative interspecific interactions are involved in the structuring of communities (Irving &
46 Bertness 2009; Silliman & He 2018). Nevertheless, in stressful environments, positive
47 interactions may play a significant role as well (Bertness & Callaway 1994; Bruno et al. 2003).
48 Facilitative interactions are often defined as interspecific non trophic interactions that benefit one
49 species and do not harm another (Bruno et al. 2003). Furthermore, it is widely recognized that
50 the outcome of interspecific relationships could change with changing environmental or biologic
51 conditions (Silliman & He 2018; Gastaldi et al. 2020). These changes in the interactions are well
52 documented in marine environments, where habitat-forming species have a positive effect (on the
53 biomass or the diversity of species) at high intertidal areas, and neutral effects in the low intertidal
54 zone, both for other algae (Molina-Montenegro et al. 2005) and for other benthic organisms (Uyà
55 et al. 2020). In addition, the effects of interspecific interactions can vary throughout the life-cycle
56 of the interacting species (Schiffers & Tielbörger 2006, Allegrezza et al. 2016; Klanderud et al.
57 2021), but this phenomenon has seldom been considered in marine environments (Bulleri 2009).

58 In studies concerning facilitation process, it has also been interesting to document how the
59 facilitator species may affect the development or growth of the facilitated organism (*cf.* Peterson
60 et al. 1984; Bulleri 2009; Purcell et al. 2016). For example, in species with density-dependent
61 growth, if the association between those species results in a higher density of individuals
62 (Thomsen et al. 2018), that effect could translate into a limited growth of the facilitated species—
63 *i.e.*, individuals that grow more densely exhibit smaller morphometric parameters (Gao et al.
64 2014). In addition, studies of facilitative interactions have been dominated by unidirectional
65 approaches (Schöb et al. 2014b). Reciprocal effects between interacting species are well
66 documented, though mainly for plant-plant positive interactions; which, for their part, have
67 demonstrated a wide range of feedbacks (positive, negative or neutral) by facilitated species on

68 facilitators (Pugnaire et al. 1996, Armas & Pugnaire 2005, Cranston et al. 2012, Schöb et al.
69 2014b). Understanding of not only how a facilitation relationship affects population parameters
70 of the facilitated species (*e.g.*, recruitment, growth), but also how the relationship affects the
71 facilitator, is therefore essential.

72 Most facilitation studies performed in marine environments were carried out with organisms
73 capable of generating dense aggregates or entire new habitats—*e.g.*, mussels, corals, seagrasses
74 (Gribben et al. 2019). Ascidians, however, have received less attention as facilitators, despite
75 being capable of providing refuge and resources to other species (Rimondino et al. 2015). On
76 Argentine rocky shores, an interaction occurs between the solitary ascidian *Styela clava*
77 (Herdman 1881)—hereafter *Styela*—and the macroalga *Undaria pinnatifida* (Harvey) Suringer—
78 hereafter *Undaria*—in which the latter uses the former as basibiont (Pereyra et al. 2017). Through
79 a short-term experiment, Pereyra et al. (2017) provided evidence for facilitation at the start of the
80 sporophytic phase, but in the present work we aimed at discovering if shifts in this interaction
81 take place over time. In addition, since *Undaria* grows on a wide variety of substrates—*i. e.*, rock,
82 bivalve’s shells, artificial and live substrates (Wotton et al. 2004; Forrest & Blakemore 2006;
83 Thomsen et al. 2018), we were interested in how growth on *Styela* can affect the morphometric
84 parameters of *Undaria*. If *Styela* increases *Undaria*’s density as it was seen with other
85 invertebrates (Thomsen et al. 2018), the ascidian could affect *Undaria*’s growth because of the
86 kelp’ density-dependent growth (Gao et al. 2014). Finally, to study the effect of that interaction
87 on both participating species would appear essential for gaining a better understanding of the
88 possible outcomes in the relationship between two species in this type of facilitation.

89 We conducted field sampling for 11 months from the time that the first sporophytes appeared in
90 the area until most became senescent—hereafter called the sporophytic phase—with the objective
91 of assessing changes in the sign of the facilitation between *Styela* and *Undaria*, and how that

92 interaction affects both species. We hypothesized that seasonal changes occur in the facilitative
93 interaction between *Styela* and *Undaria* throughout the sporophytic phase of the macroalgae. In
94 this context, we predicted that (1) the density of *Undaria* on *Styela* would be higher than on other
95 available substrates at the beginning of *Undaria*'s sporophytic phase but that the pattern would
96 be the opposite when *Undaria* reach maturity, (2) *Undaria* growing on *Styela* would be smaller
97 than those growing on rock, and (3) the probability of *Styela* of dying would be greater as the
98 level of coverage by *Undaria* increases.

99 **2. Materials & Methods**

100 **2.1 Study area and species investigated**

101 The study was performed in San Antonio Bay, a protected marine area of 80 km², located in the
102 San Matias Gulf, northern Argentine Patagonia (40° 46' S, 64° 54' W). San Antonio Bay is
103 dominated by tidal currents, with a semidiurnal macrotidal regime (up to 9-m amplitude; Alliota
104 et al. 2000) and is characterized by its high diversity of benthic species, mainly mollusks (Güller
105 & Zelaya 2017). Among the Mollusca, mytilids, such as *Brachidontes rodriguezii* and
106 *Perumytilus purpuratus*, are the dominant species on the rocky shores; but ophiuroids, crabs,
107 snails, sea stars, and sea urchins in addition to algae such as *Corallina officinalis*, *Ulva* sp., and
108 *Dictyota* sp. are also common although their distribution is patchier (Narvarte et al. 2006). We
109 carried out the study near the mouth of the bay, a sector that is characterized by a substrate of a
110 wide range of grain sizes—silt, sand, and gravel; including granules, pebbles, and cobbles (Salas
111 et al. 2016). In this location, the interaction between the studied species was documented for the
112 first time, with both species being found in relatively high abundances (Pereyra et al. 2015).
113 *Undaria* (Phaeophyceae, Laminariales) has a biphasic life-cycle with a heteromorphic alternation
114 of generations, a microscopic gametophyte, and a macroscopic sporophyte (Epstein & Smale

115 2017). *Styela* is a solitary ascidian with an elongated oval body and a long tapering peduncle
116 terminating in a discoid holdfast (Lützen 1998).

117 **2.2 Facilitation throughout *Undaria pinnatifida*'s sporophytic phase**

118 To evaluate the facilitation between *Undaria* and *Styela*, we performed monthly surveys during
119 low tide in the intertidal and shallow subtidal (up to 0.5 m deep), from March 2018 through
120 January 2019. Sampling was carried out using quadrats of 30 x 30 cm, arranged in a random,
121 stratified manner. We divided the study area into two sectors, according to the dominant
122 substrate—the first, a consolidated substrate sector (dominated by rocky outcrops); the second, a
123 nonconsolidated substrate sector (dominated by sand and cobble in different proportions)—and
124 randomly deployed 50 quadrats in each one every month. For each quadrat, we counted the
125 number of individuals of *Undaria*, and registered the occurrence of *Styela* in order to obtain the
126 number of *Undaria* growing in quadrats with and without *Styela* in each sector. We collected all
127 the individuals of *Undaria* in the quadrats for further processing in the laboratory. All the
128 individuals were preserved in aquaria with aerated seawater until further processing (from 5 to
129 10 h). Each *Undaria* was classified by its developmental stage after Casas et al. (2008): stage 0,
130 no stipe or defined holdfast; stage 1, poorly developed holdfast; stage 2, sporophyll not yet
131 developed; stage 3, fully developed sporophyll.

132 We evaluated the total density of *Undaria* and the density of the mature macroalga (stage 3)
133 relative to the substrate throughout the sporophytic phase. The variable substrate was defined as
134 having three levels: (1) *Styela*, quadrats from the consolidated sector containing *Styela*
135 individuals; (2) consolidated substrate, quadrats from the consolidated sector with no *Styela*; and
136 (3) nonconsolidated substrate, quadrats from the nonconsolidated sector with no *Styela* present
137 (Fig. 1). Because we found only 4 quadrats from the nonconsolidated sector containing *Styela*,
138 we excluded this circumstance as a fourth level from the analysis. We used a Scheirer-Ray-Hare

139 test, an extension of the Kruskal-Wallis test (Sokal & Rohlf 1995) because the data was zero-
140 inflated and presented highly heterogeneous variances (Levene test, $P < 0.001$) and thus did not
141 conform the parametric-test assumptions that could be corrected by data transformation. The
142 Scheirer-Ray-Hare test was performed with the function `scheirerRayHare` of the R package
143 “`rcompanion`” (Mangiafico 2021) in a crossed design involving ‘sampling month’ and ‘substrate’
144 as independent variables, and the number of *Undaria* individuals as the response variable.

145 To further assess, we compared the number of *Undaria* individuals between substrates and
146 months. We compared *Styela* vs. consolidated substrate to evaluate the use of *Styela* as substrate.
147 In addition, we compared the use of consolidated vs. nonconsolidated substrate to determine if
148 *Undaria* was more closely associated with hard substrates, as is usually described for the species
149 (Epstein & Smale 2017). These analyses were performed with Kruskal-Wallis tests through the
150 use of the `Kruskal-test` function of the R package “`stats`” (R Core Team 2020).

151 **2.3 Morphometric differences in *Undaria pinnatifida***

152 To evaluate the potential effect of *Styela* as a basibiont on the morphometry of *Undaria*, we
153 randomly collected mature individuals (stage 3) of *Undaria* growing atop *Styela* and on rock (n
154 = 14, on each substrate) in July 2018. Of each *Undaria* individual we measured (in mm) lamina
155 length, lamina width, stipe length, stipe width and sporophyll width with a measuring tape. In
156 addition, the total wet and dry weights and the sporophyll wet weight (in g) were registered. For
157 the dry weight, individuals were weighed after drying in an oven at 60 °C for 48 h. The different
158 measurements used in this study are those that are usually considered in ecological and
159 commercial studies to characterize algal growth (Casas et al. 2008; Gao et al. 2014; de Leij et al.
160 2017).

161 Morphometric variables were compared between *Undaria* growing on *Styela* and on a rocky
162 substrate with a multivariate permutational analysis of variance (PERMANOVA) by means of
163 the adonis function of the R package “vegan” (Oksanen et al. 2019), through the use of Euclidean
164 distances and 999 unrestricted permutations of the raw data. The variables were standardized after
165 Becker et al. (1998), with the scale function from the R base package (R Core Team 2020). The
166 assumption of multivariate homogeneity of group dispersion (variances) was tested with
167 permutest function (Anderson 2017), from the package “vegan” (Oksanen et al. 2019). As a *post-*
168 *hoc* test, a SIMPER analysis was used to identify the main morphometric-response variables
169 contributing to the dissimilarity by means of the simper function of the R package “vegan”
170 (Oksanen et al. 2019).

171 **2.4 *Undaria pinnatifida*'s holdfast coverage on *Styela clava***

172 To assess the effect of *Undaria* overgrowth on *Styela*, individuals of *Styela* that were overgrown
173 by *Undaria* were randomly collected every month during low tide, from April 2018 through
174 January 2019 (throughout *Undaria*'s sporophytic phase). Colonized individuals of *Styela* were
175 collected in a different shallow subtidal zone (up to 0.5 m deep) from the one used for section
176 2.2, to avoid a potential disturbance in the sampling area. Individuals of *Styela* were classified in
177 the following manner in accordance with their overgrowth (*i.e.*, the percent coverage) by
178 *Undaria*'s holdfast (I) 0–25%, *Styela* with a small *Undaria* individual without a holdfast; (II) 25–
179 50%, *Undaria*'s holdfast covering up to half of *Styela*'s surface; (III) 50–75%, the holdfast
180 covering more than half of *Styela*'s surface, but the siphons remaining uncovered; (IV) 75–99%,
181 *Styela*'s peduncle being the only part free from the holdfast; (V) 100%, *Styela* totally covered;
182 see Electronic Supplement S1). The condition of *Styela* upon collection (*i.e.*, dead vs. live) was
183 also assessed. The individuals that responded to being pricked with a probe, either by opening

184 and closing the siphons or the expulsion of water through the siphons or by remaining turgid
185 when squeezed, were considered alive; otherwise, they were regarded as dead.

186 We used a generalized linear mixed model (GLMM; Bolker et al. 2009) to identify the effect of
187 the *Undaria* holdfast coverage on *Styela*. This test is an extension of generalized linear model
188 (GLM) that allows the violation of independence assumption between observations. The levels
189 of that coverage were used as the fixed factor and the condition of *Styela* as the response variable
190 with binomial error distribution. The *Undaria* holdfast coverage occurred at five levels and was
191 considered an ordered factor because the state of the holdfast overgrowth was sequential—*i.e.*,
192 the holdfast in level 5 had to have gone through levels 4 and 3 previously. To deal with temporal
193 autocorrelation, the month of collection was included as a random factor. The effects of holdfast
194 overgrowth were assessed through the use of Akaike’s Information Criterion (Burnham &
195 Anderson 2002) by means of the function `aictab` of the R package “AICcmodavg” (Mazerolle
196 2020). GLMMs were calculated through the `glmer` function of the R package “lmer4” (Bates et
197 al. 2015). All analyses were performed in R version 3.6.3 (R Core Team 2020).

198 **3. Results**

199 **3.1 Facilitation throughout *Undaria pinnatifida*’s sporophytic phase**

200 Upon evaluation of *Undaria*’s total density, the data revealed an interaction between month and
201 substrate use (Schierer-Ray-Hare test, $H_{20, 1058} = 63.230$, $P < 0.001$) suggesting that *Undaria*’s
202 density on each substrate was dependent on the month of the year (Fig. 2).

203 For simplicity, we expressed the differences in *Undaria* density by citing one month per season.
204 Those months, accordingly, were representative of the differences evidenced for the remaining
205 months of each season (*cf.* Electronic Supplement S2 for a detailed comparison of every month).
206 In autumn (April), the density of *Undaria* was 97% higher in the *Styela* quadrats than in the

207 consolidated-substrate quadrats (Kruskal-Wallis, April: $H_1 = 37.4$, $P < 0.001$; Fig. 2). Similar
208 results were found in winter (July), with a 24% higher density in the *Styela* quadrats than in the
209 consolidated-substrate quadrats (Kruskal-Wallis, July: $H_1 = 4.9$, $P = 0.026$) and 72% higher in
210 the consolidated-substrate quadrats than in the nonconsolidated-substrate quadrats (Kruskal-
211 Wallis, July: $H_1 = 5.7$, $P = 0.016$). In spring (October), the density of *Undaria* was 28% higher
212 in the *Styela* quadrats than in the consolidated-substrate quadrats (Kruskal-Wallis, October: $H_1 =$
213 4.7 , $P = 0.029$). Finally, in summer (January), we found no evidence that *Undaria*'s density in
214 the consolidated-substrate quadrats differed from that in the *Styela* quadrats (Kruskal-Wallis,
215 January: $H_1 = 3.5$, $P = 0.061$) or the nonconsolidated-substrate quadrats (Kruskal-Wallis, January:
216 $H_1 = 1.6$, $P = 0.212$).

217 Upon observing the density of the different developmental stage of *Undaria* associated to each
218 evaluated substrate, we found that it was higher in *Styela* quadrats for every developmental stage
219 (Fig. 3). Mature *Undaria* occurred from only June onwards. These results also revealed an
220 interactive effect of substrate and month on the density of mature *Undaria* (Schierer-Ray-Hare
221 test, $H_{20, 1058} = 42.3$, $P = 0.002$) implicating that the density of mature *Undaria* associated to the
222 different evaluated substrates vary throughout the evaluated months. Mature *Undaria* were
223 affected by substrate only during June and August exhibiting a 35% and 39% higher density in
224 the consolidated-substrate quadrats than in the nonconsolidated-substrate quadrats (Kruskal-
225 Wallis, June: $H_1 = 4.8$, $P = 0.027$; August: $H_1 = 4.3$, $P = 0.02$; cf. Electronic Supplement S2 for
226 details). Throughout the study period the densities of the mature *Undaria* were not significantly
227 different between the *Styela* and the consolidated substrates (cf. Electronic Supplement S2 for
228 details).

229 **3.2 Morphometric differences in *Undaria pinnatifida***

230 Our data revealed that *Undaria* individuals growing on *Styela* were morphometrically different
231 from those growing on rock (PERMANOVA, $F_{1,28} = 9.9$, $P = 0.001$). *Undaria* growing on *Styela*
232 were smaller than those growing on rock with respect to all the metrics used (Fig. 4), and all the
233 morphometric variables evaluated contributed to the dissimilarity (SIMPER, $P \leq 0.01$), except
234 the stipe width (SIMPER, $P = 0.05$).

235 **3.3 *Undaria pinnatifida*'s holdfast coverage on *Styela clava***

236 We examined 270 individuals of *Styela* with different levels of coverage of *Undaria*'s holdfast.
237 Only 12 of the *Styela* individuals collected (4.4%) were dead (Fig. 5). The data, however, revealed
238 an association between *Undaria* holdfast coverage on the condition of *Styela* (Table 1), although
239 the size of the effect was very small since only 13% of the individuals from categories IV or V
240 were dead (Fig. 5).

241 **4. Discussion**

242 The results suggest that, although the facilitation between *Styela* and *Undaria* is maintained
243 throughout the sporophytic phase, changes occur in that interaction. *Undaria* sporophytes are
244 found in the substrates in a differing fashion during the year-long phase, with the total density of
245 *Undaria* in *Styela* quadrats being higher for almost the entire time—except in summer, when this
246 pattern changes and the total densities become similar on all the substrates evaluated. In addition,
247 from the first half of the sporophytic phase until the end, the density of mature individuals of
248 *Undaria* is higher in quadrats with *Styela* than on any other substrate quadrats. Our observations
249 indicate that *Styela* facilitates *Undaria* during the entire sporophytic phase—first with higher
250 density of juveniles of *Undaria* and then with a greater proportion of mature individuals—by
251 serving as a beneficial substrate. Nevertheless, *Undaria* growing on *Styela* ends up being smaller
252 than when growing on a rocky substrate, a difference which might be interpreted as a negative
253 effect of this relationship. In addition, our results did not suggest any negative effect from the

254 interaction on *Styela* because, although the higher proportion of dead *Styela* individuals presented
255 high degree of coverage by *Undaria*, the number of dead individuals of *Styela* found in the current
256 study was still quite low.

257 **4.1 Facilitation throughout the sporophytic phase of *Undaria pinnatifida***

258 *Undaria* was more associated to *Styela* during the first half of the sporophytic phase (autumn to
259 early spring), but then this decreased at the end of the sporophytic phase to the point of being
260 indistinguishable from other substrates by summer. Nonetheless, an evaluation of the number of
261 individuals of *Undaria* reaching maturity indicated that *Styela* quadrats still had the highest
262 densities of mature *Undaria*.

263 The presence of *Undaria* almost exclusively in *Styela* quadrats at the beginning of the sporophytic
264 phase could favor the kelp competitively (Thompson & Schiel 2012). *Undaria* is considered a
265 poor competitor for space and in the presence of other canopy-forming macroalgae cannot readily
266 become established in new environments (Thompson & Schiel 2012). If that establishment does
267 occur, it is only transient (South et al. 2016). Thus, growing associated with *Styela* could give
268 *Undaria* a competitive advantage by providing an opportunity to emerge before other algae. In a
269 similar study, Thomsen et. al. (2018) reported that mussels could facilitate *Undaria*, thus resulting
270 in the maintenance of the kelp's cover through the sporophytic phase. Something similar may
271 occur in the present study site, with *Styela* benefitting *Undaria* by facilitating it in periods when
272 the cover or abundance of the kelp is negligible. Since solitary tunicates have the ability to
273 increase organic matter deposits—*i.e.*, via biodeposition (Qi et al. 2015), the high density of
274 recruits of *Undaria* found growing in *Styela* quadrats at the beginning of the sporophytic phase
275 could be due to the biologic properties of *Styela* as opposed to bare substrate (Qi et al. 2015;
276 Pereyra et al. 2021).

277 The density of *Undaria* in *Styela* quadrats decreases from the middle to the end of the sporophytic
278 phase. This pattern may be related to the high mortality of recruits in kelps, which may be even
279 higher when initial densities are high (Schiel & Foster 2006). In addition, kelp fecundity and
280 recruitment are considered high, but the survival of recruits is extremely low (Primo et al. 2010).
281 Nevertheless, the decrease in *Undaria*'s population density could be due to the natural death of
282 individuals as mortality is usual in summer as a result of rising temperatures (Thornber et al.
283 2004; Casas et al. 2008).

284 Looking our results, this interaction could be understood as a zero-sum game, where the benefits
285 of the first half of the sporophytic cycle are canceled by the end of the cycle. Notwithstanding,
286 even if the total density of individuals of *Undaria* growing on *Styela* quadrats decreased to
287 become equal to density values of the other substrates, the proportion of mature individuals was
288 still higher on *Styela* quadrats than on any other substrate quadrats, a difference that implies *Styela*
289 presence leads to more individuals with the ability to reproduce. Considering all these different
290 aspects, we would conclude that *Undaria* benefits from *Styela* from the standpoint of the kelp's
291 overall population level during the entire sporophytic phase.

292 **4.2 Morphometric differences in *Undaria pinnatifida***

293 *Undaria* individuals that grew on *Styela* were smaller than those growing on rock. That difference
294 was expected because kelp species typically exhibit a high morphologic plasticity (Fowler-
295 Walker et al. 2005; Wernberg & Thomsen 2005), and higher densities of *Undaria* growing on
296 *Styela* might translate into smaller morphometric structures as the result of limited space (Schiel
297 & Foster 2006; Gao et al. 2014). Competition for space could have consequences not only for
298 *Undaria*'s individual growth, but also for its reproductive success (de Leij et al. 2017). The
299 sporophyll is *Undaria*'s reproductive structure; and, as spore production is correlated with
300 sporophyll area (Primo et al. 2010), the smaller sporophylls of *Undaria* growing on *Styela* may

301 have lower fitness (or spore production) than those growing on rock. Nevertheless, to speculate
302 how this difference would affect the reproductive potential of *Undaria* would be premature, and
303 should be done carefully until the effect on the fitness of the kelp is evaluated. Another likely
304 explanation for the reduced size of *Undaria* on *Styela* (vs. rock) may be a selective dislodgement
305 process by the great tidal currents in the main channel, which affects mainly large individuals (cf.
306 Thomsen 2004). However, we did not see dead individuals of *Undaria* attached to *Styela* when
307 they are dislodged following the greatest spring tide. For this reason, we do not seem likely that
308 *Undaria* is dislodged more when attached to *Styela* than to other substrates.

309 Otherwise, while growing on *Styela* could be detrimental for individual growth of *Undaria*, the
310 higher densities on that substrate could be beneficial for the *Undaria* population (Schiel & Foster
311 2006). For kelps, high population density may increase dispersal distances as well as spore and
312 gametophyte densities, enhance fertilization, reduce physical stress in intertidal habitats, and
313 suppress the recruitment and growth of competitors (McConnico & Foster 2005; Schiel & Foster
314 2006, Tatsumi et al. 2018). Our results suggest that, even when the *Undaria* individuals growing
315 on *Styela* were smaller, the density of the mature stages was higher on *Styela* than on other
316 substrates, implying that *Styela* could boost the population growth of *Undaria*. We note that the
317 sample size for comparing the morphometry of *Undaria* growing on *Styela* and rock was small
318 ($n = 14$ per substrate), and thus the conclusions accepted with caution. The estimation of the effect
319 size, however, has a high certainty (Baguley 2004) because the differences between the groups
320 were unquestionably evidenced and verified statistically.

321 **4.3 *Undaria pinnatifida* holdfast coverage on *Styela clava***

322 Our study reveals a higher proportion of dead individuals occurred when *Undaria*'s holdfast
323 covered *Styela* completely. Despite this, in view of the low proportion of dead *Styela* found, we
324 conclude that the ascidian tolerates being covered by the *Undaria* holdfast, contrary to what was

325 originally hypothesized by Pereyra et al. (2017). As result, we propose that, with respect to
326 lethality, the outcome of the interaction for *Styela* was essentially neutral.

327 Although ascidians could have defenses against epibiosis like the presence of antifouling
328 compounds, such as vanadium, on their tunics (Stoecker 1978; Hirose et al. 2001), they are
329 capable of survive overgrowth by epibionts if the ascidian's siphons are not covered (Claar et al.
330 2011). Despite this, we found live *Styela* individuals with their siphons fully covered by
331 *Undaria*'s holdfast. The high degree of epibiosis that *Styela* presents (Rodriguez 2020) could be
332 due to the very low concentration of vanadium and consequently, its antifouling defenses are also
333 low (Curtin et al. 1985). In addition, *Styela* has irregular longitudinal wrinkles and grooves in the
334 tunic, features that would favor the accumulation of organic matter and thus facilitate even more
335 the settlement of epibionts (Filip 2020).

336 Despite of what it was mentioned above, the possible outcomes of the interaction for *Styela* need
337 to be experimentally tested. While we only examined lethal outcomes of the coverage by
338 *Undaria*, *Styela* could experience a reduction in fitness if, for example, their reproductive output
339 is compromised by affecting gonad development, spawning and recruitment (Bourque et al.
340 2007). In addition, other aspects as the dislodgment of *Styela* should be tested, because this could
341 be modified (as the strength of attachment) by the epibiosis of *Undaria*. It is important to note
342 that our survey do not allow to determine the cause of death of *Styela*. For example, the age of
343 the *Styela* individuals could have an influence in our results, but we think this is unlikely, since
344 *Styela* has a relatively short life-cycle (up to 2 years; Morris et al. 1980, Lambert and Lambert
345 1998) and a relatively low growth rate (1–15 mm per month; Morris et al. 1980). Thus, since the
346 *Styela* individuals collected were about the same size, their belonging to different cohorts was
347 unlikely. Lastly, positive effects on *Styela* should be tested too. Positive outcomes for the
348 basibiont have been described before in marine environments (Thomsen et al. 2022, and

349 references therein). *Styela* could benefit from the interaction by the reduction of predation or
350 physical stress that *Undaria* may offer. Ascidians are commonly predated on (Giachetti et al.
351 2022), and we have observed regularly in the field death individuals of *Styela* with marks of
352 predation, but this is not the case of those individuals tested here. A possibility that remains to be
353 explored is that *Undaria* offers protection against predation to *Styela* by growing over it, as it was
354 documented for similar cases—*e.g.*, *Microcosmus sabatieri* overgrown by an encrusting sponge
355 (Voultsiadou et al. 2010). Thus, to determine the net effect of the interaction for *Styela* we need
356 to gather a better understanding of the effects on the ascidian, both positive and negative, beyond
357 lethal effects.

358 **4.4 Varied outcomes of the interaction**

359 The current study adds evidence documenting changes in outcome and magnitude of the effect
360 occurring in the facilitation relationship between *Styela* and *Undaria* over time, related to biotic
361 or abiotic context.

362 Nevertheless, a gap still remains in our understanding on how this interaction results at other
363 marine sites because context dependency could well be related not only to time but also to the
364 site where the interaction occurs (Catford et al. 2022). *Undaria* using *Styela* as basibiont has been
365 documented in other locations, but the interaction was not the focus of the study (Thornber et al.
366 2004) or was studied as competition (Farrel and Fletcher 2006). In general, our results provide
367 evidence for how facilitation changes over time in a marine system, at least for *Undaria*, and
368 contribute new observations with respect to how the interaction affects both species. *Undaria*
369 seems to benefit from its association with *Styela*, although the effects on reproductive outcome
370 will need further investigation. *Styela* does not seem to be harmed by *Undaria*, although possible
371 negative effects not tested in this study should be further evaluated. Since the two species have
372 only recently been introduced into San Antonio Bay, *Undaria* and *Styela* are still adapting to their

373 interactions with resident species, as well as to the new abiotic environment. Perhaps the plasticity
374 of *Undaria* and the facilitative interaction with *Styela* are only two adaptive responses to this new
375 set of selective pressures among others that can aid the two species in the successful invasion of
376 this new environment in the Patagonia.

377 **Acknowledgements**

378 AEA and EAR were supported by a doctoral scholarship granted by CONICET, Argentina. This
379 project was partially supported by the Agencia Nacional de Promoción Científica y Tecnológica
380 (ANPCyT, Grant PICT CONAE-CONICET No. 2017-3312 to PJP). Dr. Juan Saad, Yanet Toledo
381 Cabrera, Ludmila Amione and Macarena Marelló Buch provided useful help in the field. We also
382 thank Dr. Lorena Storero and Dr. Hugo Marrero for their comments on an earlier version of this
383 work. Dr. Donald F. Haggerty, a retired academic career investigator and native English speaker,
384 edited the final version of the manuscript. We are grateful of constructive criticism received from
385 the Associate Managing Editor Dr. Paul Bachem and three anonymous reviewers who greatly
386 improved early versions of this manuscript.

387 **Literature cited**

- 388 Allegrezza M, Corti G, Cocco S, Pesaresi S, Chirico GB, Saracino A, Bonanomi G (2016)
389 Microclimate buffering and fertility island formation during *Juniperus communis*
390 ontogenesis modulate competition-facilitation balance. *J Veg Sci*, 27(3), 616-627.
- 391 Alliota S, Schnack EJ, Isla FI, Lizasoain GO (2000) Desarrollo secuencial de formas de fondo en
392 un régimen macromareal. *Lat Am J Sedimentol Basin Anal* 7:95–107.
- 393 Anderson MJ (2017) Permutational Multivariate Analysis of Variance (PERMANOVA). In:
394 Wiley StatsRef: Statistics Reference Online. American Cancer Society, pp 1–15
- 395 Armas C, Pugnaire FI (2005) Plant interactions govern population dynamics in a semi-arid plant
396 community. *J Ecology* 93:978–989.
- 397 Baguley T (2004) Understanding statistical power in the context of applied research. *Appl Ergon*
398 35:73–80.
- 399 Bates D, Mächler M, Bolker B, Walker S (2015) Fitting Linear Mixed-Effects Models Using
400 lme4. *J Stat Softw* 67(1), 1–48.
- 401 Becker RA, Chambers JM, Wilks AR (1988) *The New S Language*. Wadsworth & Brooks/Cole.
- 402 Bertness MD, Callaway R (1994) Positive interactions in communities. *TREE* 9:191–193.
- 403 Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White J-SS (2009)
404 Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol*
405 *Evol* 24: 127-135.

- 406 Bourque D, Davidson J, MacNair NG, Arsenault G, LeBlanc AR, Landry T, Miron G (2007)
407 Reproduction and early life history of an invasive ascidian *Styela clava* Herdman in Prince
408 Edward Island, Canada. *J Exp Mar Biol Ecol* 342:78–84.
- 409 Bronstein JL (2009) The evolution of facilitation and mutualism. *J Ecology* 97:1160–1170.
- 410 Bruno JF, Stachowicz JJ, Bertness MD (2003) Inclusion of facilitation into ecological theory.
411 *Trends Ecol Evol* 18:119–125.
- 412 Bulleri F (2009) Facilitation research in marine systems: state of the art, emerging patterns and
413 insights for future developments. *J Ecol* 97:1121–1130.
- 414 Burnham KP, Anderson DR (2002) A practical information-theoretic approach. Model selection
415 and multimodel inference, 2nd edn. Butterfield BJ, Callaway RM (2013) A functional
416 comparative approach to facilitation and its context dependence. *Funct Ecol* 27:907–917.
- 417 Casas G, Piriz ML, Parodi ER (2008) Population features of the invasive kelp *Undaria pinnatifida*
418 (Phaeophyceae: Laminariales) in Nuevo Gulf (Patagonia, Argentina). *J Mar Biol Assoc*
419 U K 88(1):21–28.
- 420 Catford JA, Wilson JRU, Pyšek P, Hulme PE, Duncan RP (2022) Addressing context dependence
421 in ecology. *Trends Ecol Evol* 37:158–170.
- 422 Claar DC, Edwards KF, Stachowicz JJ (2011) Positive and negative effects of a dominant
423 competitor on the settlement, growth, and survival of competing species in an epibenthic
424 community. *J Exp Mar Biol Ecol* 399:130–134.
- 425 Cranston BH, Callaway RM, Monks A, Dickinson KJM (2012) Gender and abiotic stress affect
426 community-scale intensity of facilitation and its costs. *J Ecol* 100:915–922.

- 427 Curtin MA, Kustin K, Robinson WE (1985) Iron accumulation in tunicate blood cells. II. Whole
428 body and blood cell iron uptake by *Styela clava*. Biol Bull 169:152–163.
- 429 de Leij R, Epstein G, Brown MP, Smale DA (2017) The influence of native macroalgal canopies
430 on the distribution and abundance of the non-native kelp *Undaria pinnatifida* in natural
431 reef habitats. Mar Biol 164:156.
- 432 Epstein G, Smale DA (2017) *Undaria pinnatifida*: A case study to highlight challenges in marine
433 invasion ecology and management. Ecol Evol 7:8624–8642.
- 434 Farrell P, Fletcher RL (2006) An investigation of dispersal of the introduced brown alga *Undaria*
435 *pinnatifida* (Harvey) Suringar and its competition with some species on the man-made
436 structures of Torquay Marina (Devon, UK). J Exp Mar Biol Ecol 334(2):236-243.
- 437 Filip MM (2020) Epibiota comparison between two biogenic substrates: the non-native tunicate
438 *Styela clava* and the native blue mussel *Mytilus edulis*. MSc dissertation. University of
439 Bremen, Germany.
- 440 Forrest BM, Blakemore KA (2006) Evaluation of treatments to reduce the spread of a marine
441 plant pest with aquaculture transfers. Aquaculture 257:333–345.
- 442 Fowler-Walker MJ, Werneberg T, Connell SD (2005) Differences in kelp morphology between
443 wave sheltered and exposed localities: morphologically plastic or fixed traits? Mar Biol
444 148:755–767.
- 445 Gao X, Endo H, Taniguchi K, Agatsuma Y (2013) Combined effects of seawater temperature and
446 nutrient condition on growth and survival of juvenile sporophytes of the kelp *Undaria*
447 *pinnatifida* (Laminariales; Phaeophyta) cultivated in northern Honshu, Japan. J Appl
448 Phycol 25:269–275.

449 Gao X, Endo H, Taniguchi K, Agatsuma Y (2014) Effects of experimental thinning on the growth
450 and maturation of brown alga *Undaria pinnatifida* (Laminariales; Phaeophyta) cultivated
451 in Matsushima Bay, northern Japan. *J Appl Phycol* 26:529–535.

452 Gastaldi M, Firstater F, Romero MA, Pereyra PJ, Narvarte MA (2020) Seasonality dictates
453 changes in the ecological interactions among spatial dominants. *Mar Biol* 167:176.

454 Giachetti CB, Battini N, Castro KL, Schwindt E (2022). The smaller, the most delicious:
455 Differences on vulnerability to predation between juvenile and adult of invasive
456 ascidians. *Estuar Coast Shelf Sci* 268, 107810.

457 Gribben PE, Angelini C, Altieri AH, Bishop MJ, Thomsen MS, Bulleri F (2019) Facilitation
458 Cascades in Marine Ecosystems: A Synthesis and Future Directions. In: Hawkins SJ,
459 Allcock AL, Bates AE, Firth LB, Smith IP, Swearer SE, Todd PA (eds) *Oceanography
460 and Marine Biology*, 1st ed. CRC Press, pp 127–168.

461 Hirose E, Yamashiro H, Mori Y (2001) Properties of Tunic Acid in the Ascidian *Phallusia nigra*
462 (Asciidiidae, Phlebobranchia). *Zoolog Sci* 18:309–314. Irving AD, Bertness MD (2009)
463 Trait-dependent modification of facilitation on cobble beaches. *Ecology* 90(11):3042–
464 3050.

465 Klanderud K, Meiner E, Goldberg DE, Michel P, Berge A, Guittar JL, Vandvik V (2021) Vital
466 rates in early life history underlie shifts in biotic interactions along bioclimatic gradients:
467 An experimental test of the Stress Gradient Hypothesis. *J Veg Sci* 32:e13006.

468 Lützen J (1998) *Styela clava* Herdman (Urochordata, Ascidiacea), a successful immigrant to
469 North West Europe: ecology, propagation and chronology of spread. *Helgoländer
470 Meeresunters* 52:383–391.

471 Mangiafico S (2021) rcompanion: Functions to Support Extension Education Program
472 Evaluation.

473 Mazerolle MJ (2020) AICcmodavg: Model selection and multimodel inference based on
474 (Q)AIC(c).

475 McConnico LA, Foster MS (2005) Population biology of the intertidal kelp, *Alaria marginata*
476 Postels and Ruprecht: A non-fugitive annual. *J Exp Mar Biol Ecol* 324:61–75.

477 Molina-Montenegro M, Muñoz A, Badano E, Morales B, Fuentes K, Cavieres L (2005) Positive
478 associations between macroalgal species in a rocky intertidal zone and their effects on the
479 physiological performance of *Ulva lactuca*. *Mar Ecol Prog Ser* 292:173–180.

480 Molina-Montenegro MA, Baldelomar M, Atala C, Torres-Díaz C (2020) A tradeoff between
481 fitness-related traits mask facilitation in a semiarid ecosystem. *Oikos* oik.07156.

482 Oksanen J, Blanchet GF, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara
483 RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2019) vegan:
484 Community Ecology Package.

485 Pereyra PJ, Narvarte MA, González R (2015) The simultaneous introduction of the tunicate
486 *Styela clava* (Herdman, 1881) and the macroalga *Undaria pinnatifida* (Harvey) Suringar,
487 1873, in northern Patagonia. *BioInvasions Rec* 4:179–184.

488 Pereyra PJ, de la Barra P, Gastaldi M, Saad JF, Firstater FN, Narvarte MA (2017) When the tiny
489 help the mighty: facilitation between two introduced species, a solitary ascidian and a
490 macroalga in northern Patagonia, Argentina. *Mar Biol* 164–185.

- 491 Pereyra PJ, de la Barra P, Saad JF, Gastaldi M, Arcángel AE, Rodríguez EA, González R,
492 Narvarte M (2021) Unravelling facilitation among introduced species, a mechanistic
493 approach. *Biol Invasions*, 1-14.
- 494 Peterson CH, Summerson HC, Duncan PB (1984) The influence of seagrass cover on population
495 structure and individual growth rate of a suspension-feeding bivalve, *Mercenaria*
496 *mercenaria*. *J Mar Res* 42:123–138.
- 497 Primo C, Hewitt CL, Campbell ML (2010) Reproductive phenology of the introduced kelp
498 *Undaria pinnatifida* (Phaeophyceae, Laminariales) in Port Phillip Bay (Victoria,
499 Australia). *Biol Invasions* 12:3081–3092.
- 500 Pugnaire FI, Haase P, Puigdefabregas J (1996) Facilitation between higher plant species in a
501 semiarid environment. *Ecology* 77(5):1420–1426.
- 502 Purcell S, Conand C, Uthicke S, Byrne M (2016) Ecological Roles of Exploited Sea Cucumbers.
503 *Oceanogr Mar Biol* 54:367–386.
- 504 Qi Z, Han T, Zhang J, Huang H, Mao Y, Jiang Z, Fang J (2015) First report on in situ
505 biodeposition rates of ascidians (*Ciona intestinalis* and *Styela clava*) during summer in
506 Sanggou Bay, northern China. *Aquac Environ Interact* 6:233–239.
- 507 R Core Team (2020) R: A language and environment for statistical computing. R Foundation for
508 Statistical Computing, Vienna, Austria.
- 509 Rimondino CM, Torre L, Sahade R, Tatián M (2015) Sessile macro-epibiotic community of
510 solitary ascidians, ecosystem engineers in soft substrates of Potter Cove, Antarctica. *Polar*
511 *Res*, 34(1), 24338.

- 512 Rodríguez EA (2020) Macrofauna epibionte de la ascidia solitaria *Styela clava* (Herdamn, 1881)
513 en el 622 Golfo San Matías. (Thesis). Escuela Superior de Ciencias Marinas, Universidad
514 Nacional del 623 Comahue, San Antonio Oeste, Argentina. 1-65 pp.
- 515 Salas MC, Defeo O, Narvarte MA (2016) Attachment features of mytilids in ecosystems with
516 mobile substrate: *Brachidontes rodriguezii* in San Antonio Bay (Patagonia, Argentina). J
517 Mar Biol Assoc U K 96(7):1449–1456.
- 518 Schiel DR, Foster MS (2006) The Population Biology of Large Brown Seaweeds: Ecological
519 Consequences of Multiphase Life Histories in Dynamic Coastal Environments. Annu Rev
520 Ecol Evol Syst 37:343–372.
- 521 Schiffers K, Tielbörger K (2006) Ontogenetic shifts in interactions among annual plants. J Ecol
522 94:336–341.
- 523 Schöb C, Michalet R, Cavieres LA, Pugnaire FI, Brooker RW, Butterfield BJ, Cook BJ, Kikvidze
524 Z, Lortie CJ, Xiao S, Al Hayek P, Anthelme F, Cranston BH, García M-C, Le Bagousse-
525 Pinguet Y, Reid AM, le Roux PC, Lingua E, Nyakatya MJ, Touzard B, Zhao L, Callaway
526 RM (2014) A global analysis of bidirectional interactions in alpine plant communities
527 shows facilitators experiencing strong reciprocal fitness costs. New Phytol 202:95–105.
- 528 Silliman BR, He Q (2018) Physical Stress, Consumer Control, and New Theory in Ecology.
529 Trends Ecol Evol 33:492–503.
- 530 Sokal RR, Rohlf FJ (1995) Biometry, 3rd ed.
- 531 South PM, Lilley SA, Tait LW, Alestra T, Hickford MJH, Thomsen MS, Schiel DR (2016)
532 Transient effects of an invasive kelp on the community structure and primary productivity
533 of an intertidal assemblage. Mar Freshw Res 67:103.

- 534 Stoecker D. (1978) Resistance of a tunicate to fouling. *Biol. Bull.* 155: 615–626.
- 535 Tatsumi M, Layton C, Shelamoff V, Mabin C, Johnson CR, Wright JT (2018) Density-dependent
536 and seasonal variation in reproductive output, sporophyte production and performance in
537 the kelp, *Ecklonia radiata*. Dynamic resilience and stability of *Ecklonia radiata*: the
538 importance of density-dependent ecosystem engineering feedbacks. PhD dissertation,
539 University of Tasmania, Australia.
- 540 Thompson GA, Schiel DR (2012) Resistance and facilitation by native algal communities in the
541 invasion success of *Undaria pinnatifida*. *Mar Ecol Prog Ser* 468:95–105.
- 542 Thomsen MS, Alestra T, Brockerhoff D, Lilley SA, South PM, Schiel DR (2018) Modified kelp
543 seasonality and invertebrate diversity where an invasive kelp co-occurs with native
544 mussels. *Mar Biol* 165(10):1-14.
- 545 Thornber C, Kinlan B, Graham M, Stachowicz J (2004) Population ecology of the invasive kelp
546 *Undaria pinnatifida* in California: environmental and biological controls on demography.
547 *Mar Ecol Prog Ser* 268:69–80.
- 548 Uyà M, Bulleri F, Wright JT, Gribben PE (2020) Facilitation of an invader by a native habitat-
549 former increases along interacting gradients of environmental stress. *Ecology*
550 101:e02961.
- 551 Voultsiadou E, Kyrodinou M, Antoniadou C, Vafidis D, 2010. Sponge epibionts on ecosystem-
552 engineering ascidians: the case of *Microcosmus sabatieri*. *Estuar Coast Shelf Sci* 86, 598–
553 606.
- 554 Wernberg T, Thomsen MS (2005) The effect of wave exposure on the morphology of *Ecklonia*
555 *radiata*. *Aquat Bot* 83:61–70.

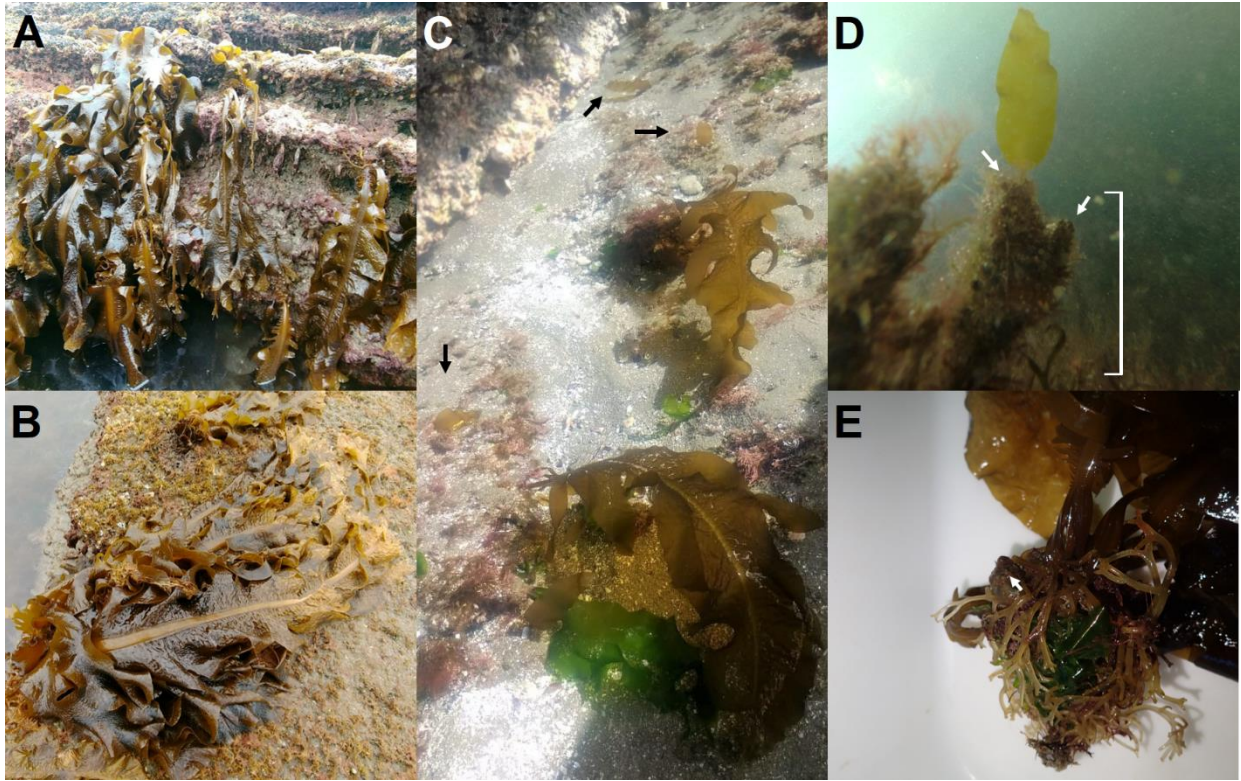
556 Wotton DM, O'Brien C, Stuart MD, Fergus DJ (2004) Eradication success down under: heat
557 treatment of a sunken trawler to kill the invasive seaweed *Undaria pinnatifida*. Mar Pollut
558 Bull 49:844–849.

559 **Tables**

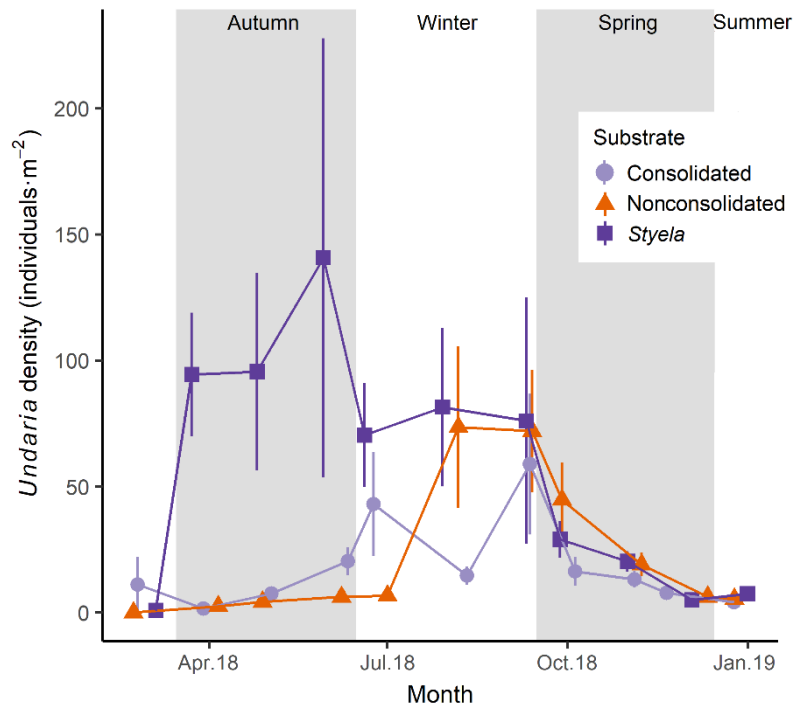
560 Table 1. Parameter estimates \pm standard errors (SE) and 95% confidence interval limits (CL) for
 561 explanatory variables describing the variation in probability of *Styela clava* individuals of dying
 562 relative to level of coverage by *Undaria pinnatifida*. The significant explanatory variables are
 563 represented in bold.

Explanatory variable	Parameter estimate \pm SE	CL	
		Lower	Upper
Coverage			
Intercept	5.405 \pm 1.149	3.69	8.65
Category II	-1.534 \pm 1.489	-4.88	1.79
Category III	-2.042 \pm 1.495	-5.44	1.28
Category IV	-3.189 \pm 1.196	-6.31	-1.15
Category V	-3.312 \pm 1.227	-6.48	-1.19

564

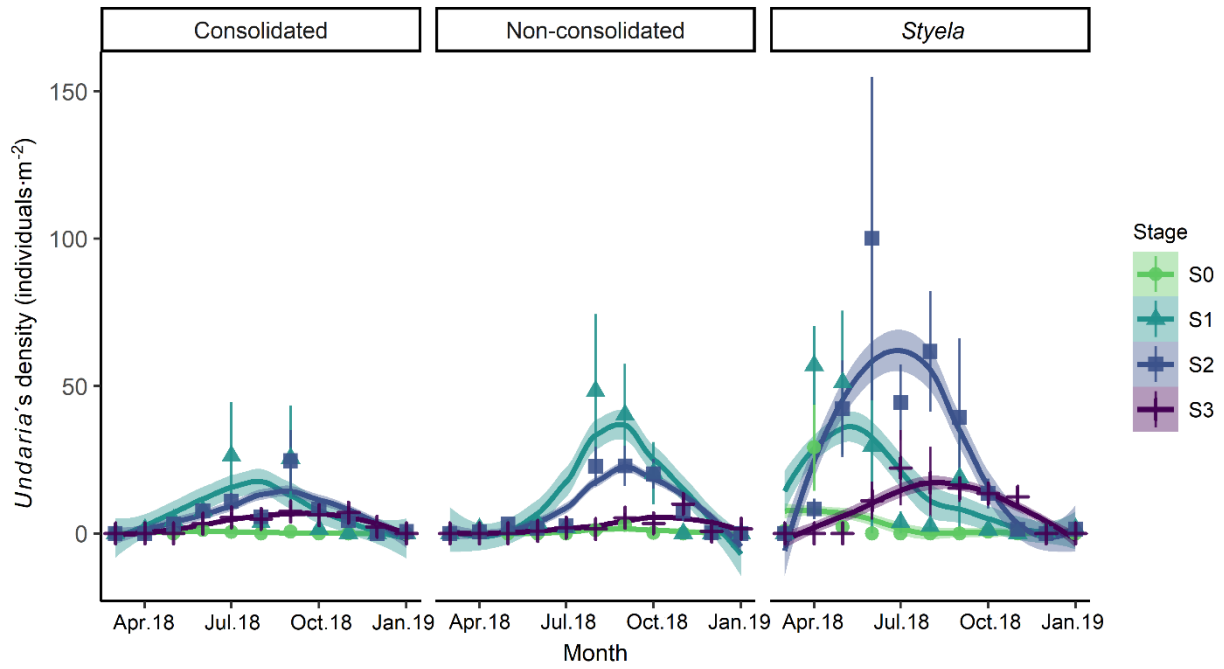


565
 566 **Fig. 1.** *Undaria pinnatifida* growing on each substrate evaluated. Panels A and B: *U. pinnatifida*
 567 growing on the consolidated substrate. Panel C: *U. pinnatifida* growing on the nonconsolidated
 568 substrate. Black arrows point to recruits. Panels D and E: *U. pinnatifida* growing on *Styela clava*.
 569 White arrows point to *S. clava*'s siphons and the white square bracket demarcates *S. clava*'s body.



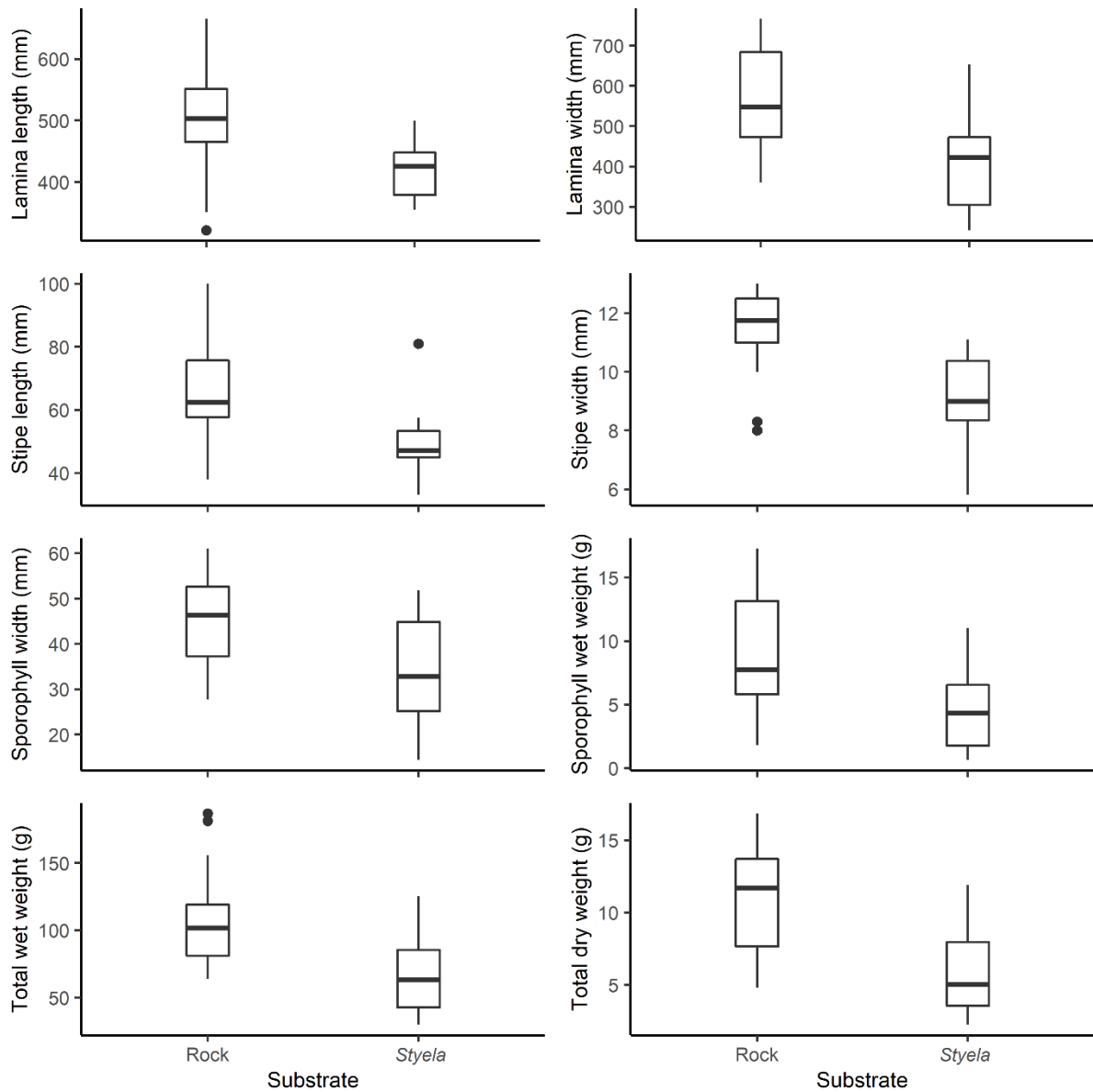
570

571 **Fig. 2.** *Undaria pinnatifida* density (individuals/m²) on different substrates through the
 572 sporophytic phase (mean ± standard error). Shaded and unshaded areas mark the seasons. The
 573 curves were plotted through the use of ‘jitter’ to reduce the overlap of points and error bars. The
 574 months on the X-axis are the ones whose results are provided in the main text. n = 1100 quadrats.

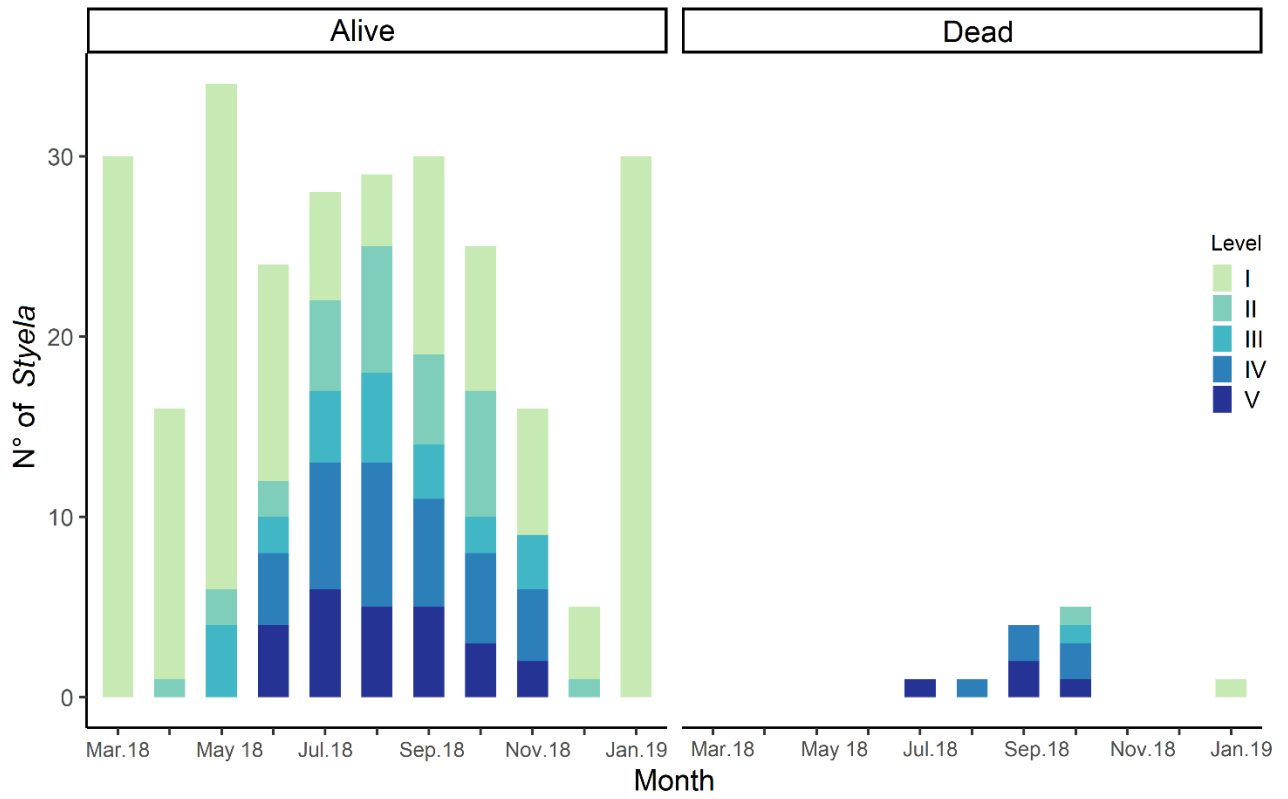


575

576 **Fig. 3.** *Undaria pinnatifida* density (individuals/m²) at each developmental stage on different
 577 substrates throughout the sporophytic phase. n = 1100 quadrats



578
 579 **Fig. 4.** Morphometric differences between *Undaria pinnatifida* growing on rock and on *Styela*
 580 *clava*. Each box represents 50% of the central data and the thick horizontal line denotes the
 581 median. The bars represent maximum and minimum values without the outliers. The black points
 582 mark the outlier values. n = 14 individuals of *Undaria pinnatifida* per substrate.



583

584 **Fig. 5.** *Styela clava* condition (alive vs. dead) in relation to the level of *Undaria pinnatifida*
 585 overgrowth represented by the *U. pinnatifida*–holdfast coverage throughout the study period.

586