Aggressive interactions between the invasive anemone *Anemonia alicemartinae* and the native anemone *Phymactis papillosa*

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ABSTRACT: The distribution range expansion of species mediated by natural or anthropic mechanisms is one of the main causes of changes in biodiversity patterns. *Anemonia alicemartinae* is a cryptogenic species found along the coasts of the Southeast Pacific Ocean. This species has expanded its range by >1900 km along the Chilean coast throughout the last 50 yr. *A. alicemartinae* cohabits with the native anemone *Phymactis papillosa* in the low intertidal zone, and given the limited mobility of both species, limited space could encourage aggressive behavior between them. *P. papillosa* shows different color phenotypes, and, as in other anemone species, color is associated with its level of aggressiveness. Here, we evaluated the aggressive behavior of *A. alicemartinae* on 2 color morphotypes of *P. papillosa*. Also, intraspecific agonistic interactions were considered in individuals of *A. alicemartinae* from 2 localities. Four experiments were conducted: (1) individual vs. individual, (2) individual vs. group forming a frontal line, (3) individual vs. group surrounding the individual and (4) group vs. group. Results showed *A. alicemartinae* to be a weak competitor against *P. papillosa*. The cryptogenic species lost more contests with green *P. papillosa* than with the red phenotype. Few aggressive interactions between conspecifics of *A. alicemartinae* were found. Results suggest that the expansion success of *A. alicemartinae* could be explained by alternative strategies, such as escape behavior, asexual reproduction and high dispersal potential.

KEY WORDS: Intraspecific competition · Interspecific competition · Agonistic behavior · Invasion · Chilean coast

1. INTRODUCTION

Changes in the spatial distribution of species have become more common in the last century in the context of climate change and increased human activity (e.g. Lima et al. 2007, Lenoir et al. 2008). Species' colonization of new habitats may trigger extensive ecological shifts in the recipient habitat, with important biodiversity, economic and health impacts (Marbuah et al. 2014, Hoffmann & Broadhurst 2016). Given the increasing importance of this issue, several hypotheses have been suggested to explain the establishment success of species, driven not only by theoretical interest but also in order to establish management policies to prevent species' introduction or reduce their expansion (Kim et al. 2006, Barbier et al. 2013).

It has been suggested that the geographical range of a species is determined by a series of biological and ecological factors (e.g. Castro et al. 2004, Bozinovic et al. 2011). Among these, competitive ability could be one of the main factors determining the establishment success of a species in a recipient community (Pimentel et al. 2000, Brown et al. 2002, Svenning et al. 2014). Most studies evaluating this trait consider invasive species. For example, in an extensively studied group such as terrestrial plants, a

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hypothesis regarding high competitive ability states that exotic plants may escape from the control of natural enemies, relocating energy to growth in detriment to defense (Blossey & Nötzold 1995). However, inconsistent results have been observed in other plant groups (Vilà et al. 2003, Caño et al. 2009, Zheng et al. 2015).

In the marine realm, several studies have explored the role of competitive interactions for invasion success (e.g. Bando 2006, Shinen & Morgan 2009, Strain & Johnson 2009, Hart & Marshall 2012). Food and space availability are the main limiting resources for sessile organisms in the intertidal zone, especially for sessile and sedentary organisms with aggregated distributions (Connell 1961, Harger 1968, Dayton 1971, Menge & Sutherland 1976). In filter-feeding sedentary species, interspecific competition for sestonic food and attachment substrate has commonly been reported in the intertidal zone (Frechette & Despland 1999, Shinen et al. 2009). Several studies have suggested that species that have successfully established in a new habitat are better competitors for food and space than native species in marine coastal habitats. For example, on the rocky shore of the NW Pacific coast, the mussel invader *Mytilus galloprovincialis* is competitively dominant over the native mussels *M. trossulus* and *M. californianus*. The invader outcompetes both native species by physical interference, triggering agglomeration and suffocation and also because it uses resources more efficiently (Shinen & Morgan 2009).

The marine anemone *Anemonia alicemartinae* is a cryptic species that has expanded its distribution by >1900 km along the coast of the SE Pacific Ocean throughout the past 50 yr, with an expansion rate of 38 km yr^{-1} (Häussermann & Försterra 2001). Using molecular analyses, Canales-Aguirre et al. (2015) suggested that the current distribution of this species can be explained by an increase in population size from one small ancestral population, most likely from the south of Peru, with subsequent human-mediated southward transport, probably associated with maritime activities. In combination with maritime transport, previous studies have also suggested that adults of this anemone may show high dispersive potential given their capacity to detach from the substrate, float and drift till they find a new place to settle (López et al. 2013). In addition, asexual reproduction by fission is the main reproductive strategy of *A. alicemartinae*, which may favor a rapid population growth rate (Häussermann & Försterra 2001). It is interesting to note that *A. alicemartinae* shows the highest aggregation densities in intertidal and subtidal zones where

no other anemone species are present (Häussermann & Försterra 2001). This could suggest that other ecological traits, such as competitive capacity, in combination with other biological characteristics, could explain the expansion success of *A. alicemartinae*.

The native anemone *Phymactis papillosa* Lesson, 1830 (Häussermann, 2004) cohabits with *A. alicemartinae* along the intertidal rocky shore of south-central Chile (Häussermann & Försterra 2001). This species inhabits the intertidal, mostly in sheltered areas and has limited mobility (Rivadeneira & Oliva 2001). *P. papillosa* shows 3 phenotypes: red, green and blue. In other anemone, color is related to different aggressiveness levels (e.g. Brace et al. 1979, Watts et al. 2000). For example, red-brown individuals of *Actinia equina* are more aggressive than green *A. equina* (Brace et al. 1979).

The recent distributional expansion of *A. alicemartinae* along the Chilean coast, the cohabitation of *A. alicemartinae* and *P. papillosa* in the intertidal zone, and the variety of colorations in *P. papillosa* make both species a suitable model for exploring the role of competition in order to explain species expansion under the framework of invasion ecology. In the present study, we explored the interspecific competitive ability of the cryptogenic anemone *A. alicemartinae* in relation to its aggressive behavior against the red and green phenotypes of the native anemone *P. papillosa*. We also evaluated intraspecific interactions in the cryptogenic anemone using individuals from 2 different localities in order to account for potential differences in its agonistic behavior, due to the presence of clonal individuals within localities. We specifically addressed the following hypotheses focused on *A. alicemartinae*: (1) this species demonstrates aggressive behavior against the 2 *P. papillosa* phenotypes (red and green); (2) *A. alicemartinae* shows greater competitive ability when found in aggregations relative to single individuals; (3) *A. alicemartinae* shows a higher frequency of intraspecific aggressive behavior towards individuals from other locations compared to individuals from the same locality.

2. MATERIALS AND METHODS

During the austral winter 2010 (July–August), individuals of the red and green color phenotypes of *Phymactis papillosa* were collected from the intertidal zone in the locality of Punta Hualpén (36° 02′ S, 73° 10′ W), Biobío region, Chile. To test for interspecific interactions, individuals of *Anemonia alicemartinae* were collected from the intertidal zone at Lirquén

(36° 43′ S, 72° 58′ W), Biobío region, Chile. Given that fission is the main reproductive strategy in *A. alicemartinae* (Häussermann & Försterra 2001), specimens of this species were also collected from the locality of Punta de Parra (36° 37′ S, 72° 57′ W) from the Biobío region, Chile. In this way, intraspecific aggression behaviors were evaluated in individuals from the same locality (high probability of interactions among clones) and between localities (lesser probability of interactions among clones). The pedal disk size of all specimens ranged in diameter from 3.5 to 4.0 cm. After collection, individuals were transported to the Universidad Católica de la Santísima Concepción's Marine Biological Station Abate Juan Ignacio Molina to run the experiments. In the laboratory, individuals were maintained in aquaria, and *ad libitum* fed with fresh mussels (*Perumitylus purpuratus* and *Semimytilus algosus*). Prior to experiments, all specimens were acclimated for 48 h in continuous aeration and seawater circulation.

2.1. Experimental treatments

Interspecific and intraspecific aggressive behaviors were evaluated in contests between individuals, aggregations and individual vs. aggregation (see Table 1 for treatment combinations). To arrange experiments, each individual was induced to adhere to a 5 cm^2 ceramic plate to facilitate manipulation. Anemones attached to plates were acclimated for 24 h prior to the experiments in tanks with constant aeration and circulation of seawater (salinity ~34 psu and 14 ± 1°C). For single interactions, single individuals were confronted (Fig. 1a). Aggregations of conspecifics of both species are commonly observed in the field. Therefore, aggregations of individuals were arranged as groups in a line facing the individual (lineal aggregation) and in a circle surrounding the individual (surrounding aggregation) (Table 1, Fig. 1b–d). Five individuals were used in each aggregation, in order to cover the whole perimeter surrounding the focal individual

Table 1. Combination of treatments to evaluate intra- and interspecific aggressive behaviors between the non-native anemone *Anemonia alicemartinae* (Aa; light red) and the native *Phymactis papillosa* (Pp) of different color types (G: green, R: darker red). Species were confronted individually and in lineal and surrounding aggregations. Individuals of *A. alicemartinae* from 2 localities (Lirquén and Punta de Parra; solid and striped, respectively) were considered. Symbols are included to represent each treatment

Interspecific interactions			Symbol
1 G-Pp	vs	1 Aa-Lirquén	
1 R-Pp			
1 G-Pp - surrounding	vs	5 Aa-Lirquén	
1 G-Pp - lineal			
1 R-Pp - surrounding			
1 R-Pp - lineal			
5 G-Pp - lineal			
5 R-Pp - lineal			
Intraspecific interactions			
1 Aa-Punta de Parra	vs	1 Aa-Lirquén	
1 Aa-Lirquén			
1 Aa-Punta de Parra - surrounding	vs	5 Aa-Lirquén	
1 Aa-Punta de Parra - lineal			
1 Aa-Lirquén - surrounding			
1 Aa-Lirquén - lineal			
5 Aa-Lirquén - lineal	vs	5 Aa-Lirquén	
5 Aa-Punta de Parra - lineal			

in surrounding configurations, and in lineal configurations facing the individual. Only *A. alicemartinae* specimens from Lirquén were used for interspecific experiments, while individuals from Lirquén and Punta de Parra were utilized in intraspecific experiments. For each treatment combination, 20 replicates were run, and all treatments were time-measured to determine the reaction time of individuals in each treatment. The aggressiveness of *A. alicemartinae*
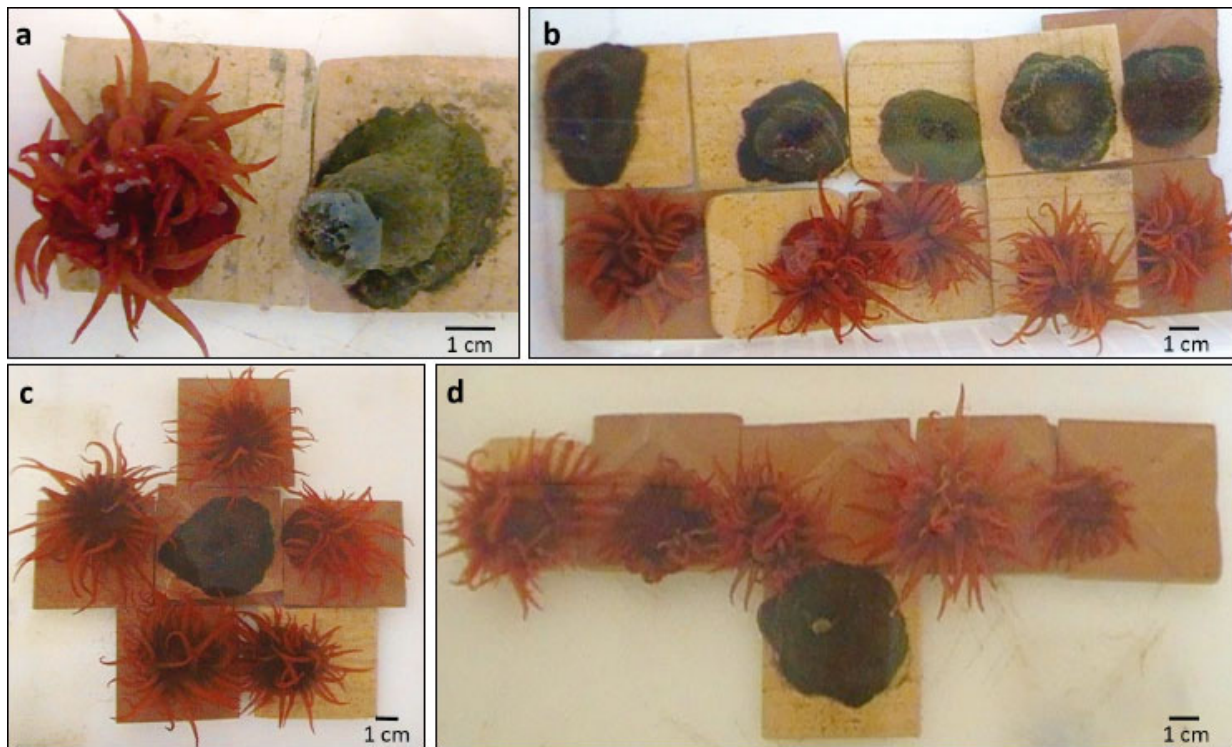
Fig. 1. Species' arrangements in treatments (or contests) designed to evaluate agonistic interactions between the native anemone *Phymactis papillosa* (green phenotype) and the non-native anemone *Anemonia alicemartinae*: (a) individual vs. individual, (b) aggregation vs. aggregation, (c) individual vs. surrounding aggregation, and (d) individual vs. lineal aggregation

was evaluated in each treatment, recording the escape behavior of individuals regardless of the species. Thus, the first individual that detached from the substrate after a direct attack was considered the losing species. A tie was considered when no aggressive behavior was observed between the species (interspecific interaction) or individuals of *A. alicemartinae* from different localities (intraspecific interaction). To avoid potential biases due to fatigue or acrorhagial responses after each contest, individuals were used for experiments only once and then returned to the field.

2.2. Data analysis

The results obtained from the treatments were analyzed by chi-squared tests, using a 2 × 2 contingency table for each treatment. In all cases, the response variable was the number of contests won (the species that remained on the substrate) by the anemone *A. alicemartinae* from Lirquén. The expected frequency was calculated considering that none of the evaluated species (*A. alicemartinae* and *P. papillosa*) would show competitive superiority, i.e. both species would win the same number of contests.

The time (seconds) that individuals took to initiate aggressive behavior was recorded. A 2-way analysis of variance (ANOVA) was conducted, with 2 factors: (1) content arrangement (fixed factor), i.e. individual vs. individual, individual vs. lineal aggregation and individual vs. surrounding aggregation; (2) species considering coloration patterns and location, i.e. Lirquén *A. alicemartinae* vs. green *P. papillosa*, Lirquén *A. alicemartinae* vs. red *P. papillosa*, Lirquén *A. alicemartinae* vs. Punta de Parra *A. alicemartinae*, and Lirquén *A. alicemartinae* vs. Lirquén *A. alicemartinae*. Finally, the aggressive behavior of *A. alicemartinae* was recorded by a video camera during the experiments and described afterwards.

3. RESULTS

3.1. Green *Phymactis papillosa* vs. *Anemonia alicemartinae*

Single individuals of *A. alicemartinae* showed significant losses (80%) in confrontations against single individuals of green *P. papillosa* ($\chi^2 = 8.89$, p = 0.02; Figs. 2 & 3A). A similar pattern was observed when lineal aggregations of *A. alicemartinae* interacted

Fig. 2. Sequence showing the aggressive behavior of single individuals of the native anemone *Phymactis papillosa's* green-phenotype against the non-native anemone *Anemonia alicemartinae*: (a) *P. papillosa* directed its tentacles towards the opponent, (b) raised its body, and (c) tilted its body towards *A. alicemartinae* to stick its tentacles onto its opponent's body, finally retracting in a pulling motion
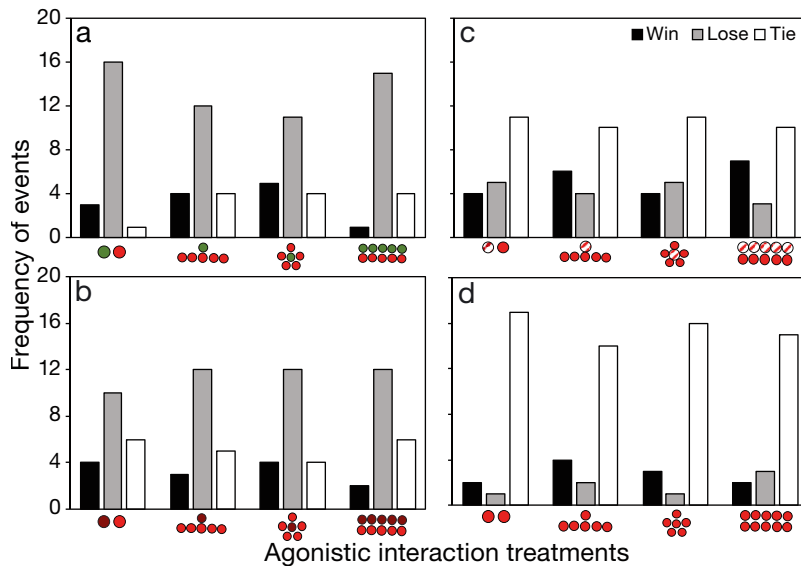

Fig. 3. Results of the agonistic interactions between the non-native anemone *Anemonia alicemartinae* and the native anemone *Phymactis papillosa*: interspecific, with (a) green and (b) red *P. papillosa* phenotypes; intraspecific, with *A. alicemartinae* from (c) both locations and (d) Lirquen only. Symbols on the *x*-axes refer to treatments described in Table 1

with single individuals of green *P. papillosa* (χ^2 = 4.00, p = 0.04), losing 60% of the total encounters (Figs. 3A & 4A). When *A. alicemartinae* aggregates were arranged in the surrounding configuration, no significant trends were observed in interactions with the other species (χ^2 = 2.25, p = 0.13; Figs. 3A & 4B).

When aggregations of both species interacted, *A. alicemartinae* showed significantly lower aggressiveness, losing 75% of the confrontations (χ^2 = 12.25, p = 0.004; Figs. 3A & 5).

3.2. Red *P. papillosa* vs. *A. alicemartinae*

No consistent trends were found when single individuals of *A. alicemartinae* confronted single individuals of red *P. papillosa* (χ^2 = 2.57, p = 0.11; Fig. 3B).

However, significant differences were observed when lineal aggregations of *A. alicemartinae* interacted with single individuals of red *P. papillosa* (χ^2 = 5.40, p = 0.02), with the former losing 60% of the trials (Fig. 3B). Similar results were also found when *A. alicemartinae* were set in the surrounding configuration to face single individuals of red *P. papillosa* (χ^2 = 4.00, p = 0.04; Fig. 3B). When aggregations of both species interacted, *A. alicemartinae* lost most of the encounters (60%) (χ^2 = 7.14, p = 0.007; Fig. 3B).

3.3. Intraspecific agonistic behavior in *A. alicemartinae*

Intraspecific confrontations between individuals of *A. alicemartinae* from Lirquén (within the locality) and between individuals from the 2 localities finished mostly as ties (Fig. 3C,D). No significant differences were found in any of these contest treatments (Table 2).

3.4. Response time of the agonistic interaction between both anemone species

Interaction response time depended upon the identity of the confronting species (*A. alicemartinae* or *P. papillosa*) and not on the spatial arrangement of the opponents (lineal aggregation, surrounding aggregation or single individuals) (Table 3). The *a posteriori* test showed that the longest response time was observed within conspecific individuals of *A. alicemartinae*, regardless of their location of origin (mean ± SD: 34.4 ± 3.6 min). The shortest response time was

Table 2. Chi-squared analyses carried out on the different intraspecific interactions between individuals of *A. alicemartinae* from Lirquén and Punta de Parra. Symbols refer to treatments described in Table 1

Intraspecific interactions	χ^2	P
(○ ●)	0.11	0.74
(● ●)	0.33	0.56
(cluster with ○)	0.11	0.74
(line with ○)	0.40	0.53
(cross cluster)	1.00	0.32
(line with top ●)	0.66	0.41
(block of ●)	0.20	0.65
(block with ○ row)	1.60	0.21

Table 3. A 2-way analysis of variance on the aggressive response times of the non-native *Anemonia alicemartinae* and the native anemone *Phymactis papillosa* in different contests. Factors consisted of a spatial arrangement of opponents (individual/individual, individual/lineal aggregations, individual/ surrounding aggregations and lineal aggregations/lineal aggregations). Combination of species treatments were Lirquén *A. alicemartinae* vs. green *P. papillosa*, Lirquén *A. alicemartinae* vs. red *P. papillosa*, Lirquén *A. alicemartinae* vs. Punta de Parra *A. alicemartinae*, and Lirquén *A. alicemartinae* vs. Lirquén *A. alicemartinae*. df: degree of freedom, MS: mean square. Significant differences in **bold**

Factors	df	MS	*F*	p
Spatial arrangement (SA)	3	121.6	0.79	0.50
Species combination (S)	3	1137.5	7.38	**>0.001**
SA × S	9	46.7	0.30	0.97
Error	166	154.1		

registered in contests between individuals of *A. alicemartinae* from Lirquén and green phenotype individuals of *P. papillosa* (23.6 ± 2.2 min; Table 4).

3.5. Description of the agonistic behavior between the native and non-native anemones

Given that aggressiveness was observed mainly in *P. papillosa*, we focused the description of the agonis-

Table 4. Results of the *a posteriori* Tukey test for the comparison of the agonistic behavior response times of the non-native anemone *Anemonia alicemartinae* and the native anemone *Phymactis papillosa* in different treatments. T1: Lirquén *A. alicemartinae* vs. green *P. papillosa*, T2: Lirquén *A. alicemartinae* vs. red *P. papillosa*, T3: Lirquén *A. alicemartinae* vs. Punta de Parra *A. alicemartinae*, T4: Lirquén *A. alicemartinae* vs. Lirquén *A. alicemartinae*. Values in the first row correspond to the mean response times (min). Significant differences in **bold** (p < 0.05)

	T1 23.62	T 29.7	T3 34.4	T4 32.6
T1		**0.0296**	**0.0001**	**0.0316**
T2	**0.0296**		0.2668	0.8217
T3	**0.0001**	0.2668		0.9585
T4	**0.0168**	0.8217	0.9585	

tic behaviors on this species. When *P. papillosa* was first confronted with physical contact, it retracted its tentacles to its mouth. If *A. alicemartinae* made contact again, *P. papillosa* directed its tentacles to the opponent, raising its body and shifting from a circular to an enlarged shape (Fig. 2). *P. papillosa* then tilted its body towards *A. alicemartinae* and stuck its tentacles onto the opponent's body, then proceeding to retract in a pulling motion. This caused the removal of a few of *A. alicemartinae*'s tentacles, and on some occasions, a complete detachment of the body from the surface. This phenomenon caused the displacement of *A. alicemartinae*, which fled from the aggressive behavior of *P. papillosa*. Lastly, *P. papillosa* remained in the same place, with fully retracted tentacles, returning to its initial shape and position.

In treatments where single individuals of *P. papillosa* were confronted with a group of *A. alicemartinae*, despite their numerical disadvantage, they won most of the trials. During the frontal line confrontations, *P. papillosa* only attacked its closest *A. alicemartinae* opponent (Fig. 4A). However, when an aggregation of *A. alicemartinae* surrounded a single individual of *P. papillosa*, *P. papillosa* responded by attacking all of the individuals in the aggregation, one by one, in order to displace them all (Fig. 4B). In treatments where aggregations of both species were in confrontation, group attacks were not observed; only individuals attacked their closest opponents (Fig. 5).

Lastly, the aggressive behavior observed in individuals of *A. alicemartinae* was quite different than that of *P. papillosa*. This anemone did not retract its tentacles but kept them open towards the outside. *A. alicemartinae* made the first contact with its tentacles when confronting the native anemone. Once the contact occurred, *A. alicemartinae's* escape behavior
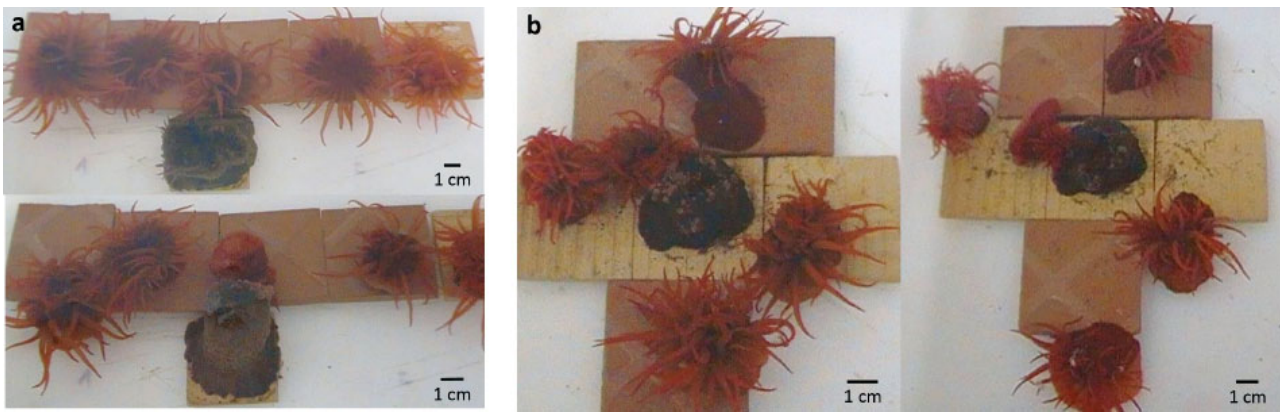
Fig. 4. Sequence showing the aggressive behavior of single individuals of the native anemone *Phymactis papillosa's* green-phenotype against aggregations of the non-native anemone *Anemonia alicemartinae* in (a) lineal aggregations and (b) surrounding aggregations
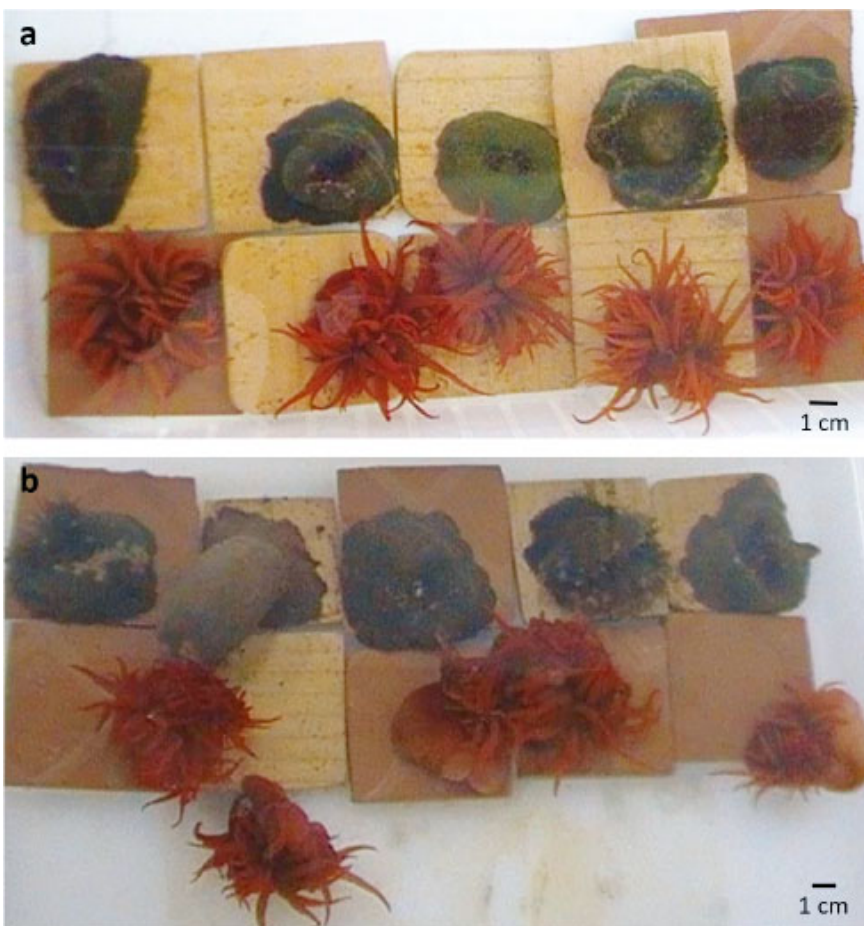

Fig. 5. Sequence showing the aggressive behavior of individuals of the native anemone *Phymactis papillosa's* green-phenotype against the non-native anemone *Anemonia alicemartinae* when confronted in lineal aggregations: (a) initial position when both species confronted one another and (b) attack position and dislodgement of *A. alicemartinae*

started; it detached its pedal disk, crawled away with its tentacles, and then inflated its body to finally float away and escape (Fig. 6).

4. DISCUSSION

In the present study, we confirmed interspecific agonistic interactions between the native anemone *Phymactis papillosa* and the cryptogenic anemone *Anemonia alicemartinae*. These results show that the latter proved to be a weaker competitor in comparison to the native species. *A. alicemartinae* lost most agonistic encounters, regardless of how many individuals confronted *P. papillosa*. Intraspecific interactions in *A. alicemartinae* showed that, although relatively higher frequencies of ties were observed between individuals from the same locality compared to contests between conspecifics from different sites, no significant aggressiveness was evidenced among *A. alicemartinae*. The low level of aggressiveness observed in *A. alicemartinae*
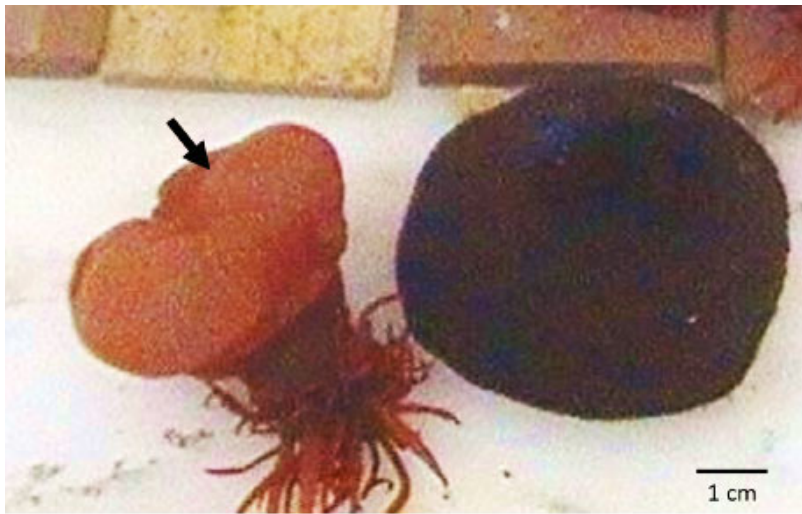
Fig. 6. *A. alicemartinae* demonstrating its escape behavior from confrontation with the native anemone *Phymactis papillosa*. Arrow indicates the floating mechanism for dispersal

could be compensated for with other behavioral and biological mechanisms, such as escape behavior and clonal reproduction, which could explain its successful range expansion along the SE Pacific coast.

The 3 key stages of aggressive behavior detailed by Brace (1981) using the anemone *P. clematis* were observed in the present experiments: (1) initial approach between the 2 species, *A. alicemartinae* and *P. papillosa*, where tentacles of both species tended to enlarge; (2) tentacle extension and flexion, mostly by the native species whose tentacles approached the other species with an apparent nematocyst discharge that triggered a contraction and, in most cases, displacement of *A. alicemartinae*; (3) once the displaced species moved away, the native species returned to its resting position. The aggressive structures of anemone species are acrorhagi (Daly 2003). These structures consist of dense batteries of large cnidocysts used for aggressive behavior. Contact with the acrorhagi may produce an escape response or even death in extreme cases. Individuals of *P. clematis* participating in intraspecific aggression have shown extreme contraction and stretching of the column towards the opponent, resulting in the discharge of nematocysts from the acrorhagi. In this species, the victim has usually been observed to move away and detach from the substratum. In our experiments, attacks of *P. papillosa* did not trigger any necrosis or death of *A. alicemartinae* individuals, at least in a short time period (2 d).

A high variability was observed in aggressive behaviors among the treatments, in terms of frequency and response time. However, as a general pattern, *A.*

alicemartinae was a weak competitor when confronted with *P. papillosa* and lost more frequently than initially expected. When the 2 color phenotypes of *P. papillosa* were compared, *A. alicemartinae* showed highly aggressive behavior in the presence of the red phenotype and a faster escape response compared to its reaction to green *P. papillosa*. Brace (1981), when working with *P. papillosa*, did not differentiate between red and brown colors, observing this combined phenotype to be significantly more aggressive than the green phenotype. However, we herein observed that the green phenotype showed higher competitive success relative to the red phenotype. This discrepancy in respect to Brace (1981) may be explained by potential differences in the aggressiveness level between the red and brown colors of *P. papillosa*, which was not compared in either Brace's work or in the present work. It is clear that additional experiments considering both morphotypes separately are needed.

The total subordination of the cryptogenic anemone *A. alicemartinae* to the native species contrasts with an extensive number of studies in which species that successfully colonize and establish in new habitats overwhelm and displace native species (Molnar et al. 2008). Nonetheless, weak competitors could use alternative strategies to increase their survival and establishment success. A species may occupy habitats where its main competitor is not present to try to avoid direct interactions (Edwards & Connell 2012). According to previous studies, the anemone *A. alicemartinae* is rather efficient regarding its escape response, with a high capacity to detach from the substrate, drift in the water column and reattach in a new area and substrate, facilitating dispersion and colonization of more suitable habitats (López et al. 2013). This dispersal strategy has been commonly observed in other anemone species, which may facilitate the colonization of new sites on both small and large spatial scales (Riemann-Zurneck 1998). According to several works, escape behavior in coastal anemones may respond to abiotic stress (e.g. temperature, oxygen, wave strength, desiccation) or biotic factors (e.g. predators, competitors), where detachment and passive migration appear to be part of their life-history strategies (Riemann-Zürneck 1998).

Additionally, the success of *A. alicemartinae* in extending its distributional range may also be ex-

plained by its high reproductive potential, mainly asexual by fission (Häussermann & Försterra 2001). This reproductive strategy is rather advantageous during the first stages of expansion, due to founder effect limitations where the encounter of gametes is highly unlikely (Taylor & Hastings 2005). In the well-known case of the alga *Caulerpa taxifolia* invading the Mediterranean Sea, vegetative dissemination could promote its rapid and exponential spread throughout Europe (Sant et al. 1996, Jousson et al. 2000). Among marine invertebrates, the invasive coral species *Tubastraea coccinea* and *T. tagusensis* have high frequency of clones in introduced populations along Brazilian coasts, with asexual reproduction dominating in the invasive range and contributing to the invasive success of these species (Capel et al. 2017).

Regarding the non-aggressive interactions of conspecific aggregations of *A. alicemartinae*, this behavior may suggest weak intraspecific competition, regardless of where individuals originate. A plausible explanation could be related to the fact that asexual reproduction is the main strategy in *A. alicemartinae.* This may produce a high proportion of clonal individuals; therefore, when physical contact occurs, they could histologically recognize each other in terms of compatibility. Former studies using the anemone *Actinia equina* have shown that the level of aggressiveness is correlated with genetic divergence, showing intra- and interspecific aggression (Turner et al. 2003). Intraspecific aggressiveness in the anemone *Anthopleura elegantissima* greatly depends on a combination of behavioral and morphological attributes of competing clones (Ayre & Grosberg 1995). Future genetic studies would help to estimate the proportion of clones within populations of *A. alicemartinae.*

5. CONCLUSIONS

We herein have provided evidence that the cryptogenic anemone *Anemonia alicemartinae* does not have the capacity to displace competitors with agonistic interactions in order to successfully spread along the Chilean coast. Thus, in species with weak competitive ability, as was observed here when *A. alicemartinae* confronted the native anemone *Phymactis papillosa*, mechanisms to reduce direct interaction are important in order to increase the probability of establishment. Escape behavior, asexual reproduction and high dispersal potential, all of which have been reported in *A. alicemartinae*, could explain this species'

successful expansion along the Chilean coast. Our findings highlight the importance of understanding the role of interspecific interactions in the context of marine bio-invasion ecology.

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