REVISTA CHILENA DE HISTORIA NATURAL

Revista Chilena de Historia Natural 86: 369-372, 2013

NATURAL HISTORY NOTE

Potential dispersal mechanisms of the cryptogenic anemone, *Anemonia alicemartinae*

Potenciales mecanismos de dispersión de la anémona criptogénica, *Anemonia alicemartinae*

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Anemonia alicemartinae Häussermann & Försterra 2001 is a cryptogenic species (*sensu* Carlton 1996, i.e. of unknown origin), meaning that there is not enough evidence to discriminate whether it is native or introduced. Since its first record in northern Chile by Sebens & Paine (1979) as *Actinia* sp., its range of distribution has greatly expanded towards southern Chile during the last 50 years, currently covering over 1900 km of coastline (Häussermann & Försterra 2001, Castilla et al. 2005). Fission seems to be *A. alicemartinae*'s main mechanism of reproduction, likely compensating for the low abundance, or even absence, of fertile males in populations (Häussermann & Försterra 2001, Chen et al. 2008). Furthermore, this species has low substrata selectivity (Thiel & Gutow 2005) and a high capacity to detach and re-adhere to substrate (Häussermann & Försterra 2001). These traits, together with the possibility of individuals rafting while attached to floating substrates, could explain the rapid spread of *A. alicemartinae* by facilitating large scale movements, and ultimately the colonization of new sites.

In the field individuals are commonly found in lower intertidal and shallow subtidal zones, attached to rocks, algae and even semi-buried in sand. Drifting individuals have been recorded during moments of low tides and intense heat, suggesting that temperature and desiccation may trigger detachment in these organisms. Additionally, adhesion strength may also be an important factor, varying with different types of substrata, with hard substrata being more stable and allowing greater resistance to water flow.

In order to determine whether detachment of individuals varies with substrate type and temperature, we collected approximately 100 individuals from Lirquén (36°43'8.10" S; 72° 59'6.59" W) in January 2010. Anemones were acclimated in the lab for one week and allowed to attach either to rocks or algae (*Ulva* sp.). We designed an experiment to evaluate the effects of temperature, substrate and desiccation on attachment strength, by subjecting individuals to a three-way, factorial design. Groups of three anemones were attached to either rocks or algae and placed in aquaria with different temperature and water exposure conditions (n = 4 replicates of anemone groups). Temperature treatments corresponded to: 10 °C (the average water temperature for summer during high tides) or 30 °C (the maximum average recorded in tidepools during low tide). Desiccation treatments corresponded to complete immersion under water (submerged) or complete exposure to air (emerged). After two hours of treatment, we attempted to detach individuals by squirting seawater directly at the pedal disc at the point where it meets the substratum, using a manual pump sprayer 15 times. We recorded the number of anemones which detached and calculated frequencies per replicate. The results were analyzed using a three-way ANOVA. Assumptions of normality, homogeneity of variances and correlation between means and variances were tested using Shapiro-Wilk's test, Cochran's C test and Pearson's correlation, respectively. Significant differences were analyzed using Tukey's test. Following experimental treatments, 58 % of the anemones detached from their substrate, and 64 % of those which detached dislodged themselves spontaneously (i.e. without being squirted). Each factor was significant; however there were no significant interactions between the factors temperature, substrata or exposure. Anemones on algae detached more frequently than on rocks ($F_{1,24}$ = 10.35, P = 0.0036), more frequently while emerged than submerged ($F_{1,24}$ = 10.35, P = 0.0036) and more frequently at high temperature than at low temperature ($F_{1,24}$ = 22.10, P = 0.000089) (Table 1). Some anemone species respond to high temperatures by diminishing their locomotive activity (Wahl 1985) and increasing their metabolic rate through increased oxygen consumption (Shumway 1978). If this were the case, then for *A. alicemartinae*, detaching would be a more effective escape strategy, similar to *Metridium senile* which detaches to escape oxygen fluctuations (Shumway 1978).

To assess intra habitat movement dynamics we tagged 51 individuals of *A. alicemartinae* in the field. Using needles and colored threads, individuals were pierced through the tentacle crown and the individual's geographic position was recorded using GPS coordinates (the marking procedure was previously tested in the lab and showed no detrimental effects on the survival or performance of the organisms; D López & P Arancibia, unpublished data). We marked 30 individuals on a boulder beach in the intertidal zone, 18 of which were at a wave exposed site and 12 at a protected site. Within each intertidal category approximately half of the anemones marked were attached to rocks and half to seaweed. The same marking procedure was used on 21 individuals in 18 tidepools, all of which were attached to rocks. After a period of 24 h we recorded the presence or absence of each individual at the site where it had been initially marked. We recaptured 86 % of individuals from tidepools, whereas on the boulder beach no more than 42 % of marked individuals were recovered. In the case of the exposed site, only 28 % of the tagged organisms were found. Regardless of the exposure, anemones attached to rocks were more prone to remain at the same spot after a tidal cycle, whereas anemones on seaweeds tended to disappear (Table 2). In tidepools, the retention of individuals was definitely higher, but intra habitat movements were recorded, with new individuals (i.e. untagged individuals) appearing in pools. To estimate small scale movements of anemones, 20 previously acclimated individuals were followed for 24 h. In pairs, they were placed in ten aquaria with seawater and

TABLE 1

ANOVA results for effects of Temperature, Substrate and Water Exposure on the frequency of detachment of *Anemonia alicemartinae* individuals. SS: sum of squares; df: degrees of freedom; MS: mean squares; F: Fisher's statistic; P: probability level.

Resultados del análisis de varianza para los efectos de Temperatura, Sustrato y Exposición al agua, y el desprendimiento de individuos de *Anemonia alicemartinae*, SS: Suma de cuadrados; df: grados de libertad; MS: cuadrados medios; F: estadígrafo de Fisher; P: nivel de probabilidad.

Source of variation	SS	df	MS	F	P
Temperature	12534.7	1	12534.7	22.10	< 0.001
Substrate	5868.1	1	5868.1	10.35	0.004
Exposure	5868.1	1	5868.1	10.35	0.004
Temperature*Substrate	34.7	1	34.7	0.06	0.807
Temperature*Exposure	312.5	1	312.5	0.55	0.465
Substrate*Exposure	34.7	1	34.7	0.06	0.807
Temperature*Substrate*Exposure	34.7	1	34.7	0.06	0.807
Error	13611.1	24	567.1		

TABLE 2

Percent of anemones marked and recovered (i.e., recorded at the same position after 24 h) from different areas of the intertidal zone of Lirquén.

Porcentaje de anémonas marcadas y recapturadas (i.e. registradas en la misma posición después de 24 h) en distintas áreas de la zona intermareal de Lirquén.

Intertidal zone category	Substrate	Number of marked individuals	Number of recovered individuals	% Individuals recovered
Exposed	Rock	9	5	55.56
	Seaweed	9	0	0
Protected	Rock	7	4	57.14
	Seaweed	5	1	20.00
Tide pools	Rock	21	18	85.71

aeration. Once they attached to the walls of the aquarium, their initial position was marked. After 24 h the linear distance from the starting point was estimated using a ruler. Movement recordings in the lab showed that only in one of the ten aquaria, anemones maintained their initial position, while in six aquaria only one of the individuals moved. The average distance covered was 2.64 ± 2.12 cm (mean ± SD) per day. This corresponds well with the observations of Rivadeneira & Oliva (2001) who described anemones as semi-sessile organisms that can only move relatively short distances.

The establishment of individuals at new sites depends on several factors, including genetic variability, body size, abundance, local adaptation abilities and physical tolerance (Arim et al. 2006). According to our findings, the behavior of *Anemonia alicemartinae* may be a dispersal strategy which could explain its establishment success on the coast of Chile. These results demonstrate that even at sites with low disturbance regimes, such as tidepools, there is still movement of individuals on a small and larger scale. Systems with higher water exchange were more dynamic, exhibiting a high turnover of individuals. The evidence gathered here suggests that *A. alicemartinae* individuals use at least two dispersal mechanisms: short distance displacement (intra habitat), which allows them to select among local conditions, and long distance movement (inter habitat), which

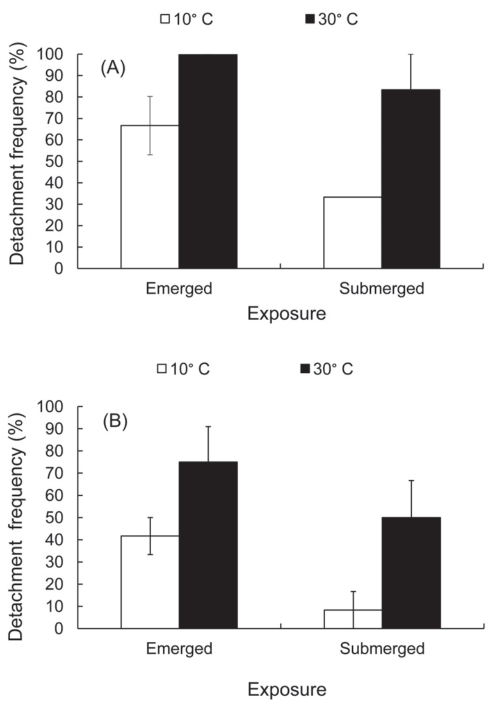

Fig. 1: Frequency of detachment by anemones on (A) seaweed and (B) rocky substrata (n = 4), subjected to two different temperatures and two water exposure conditions (emerged or submerged), under laboratory conditions. Vertical bars on the columns are standard errors.

Frecuencia de desprendimiento de anémonas en (A) alga y (B) roca (n = 4), sometidos a dos condiciones distintas de temperatura y dos condiciones de exposición al agua, bajo condiciones de laboratorio. Las barras verticales sobre las columnas son errores estándares.

could facilitate the colonization of new sites and may be an important large scale dispersal mechanism, as has been shown for other coastal anemones who migrate seasonally or annually in response to abiotic stress (e.g., temperature, oxygen, wind, waves, desiccation) or biotic factors (e.g., predators, competitors) where detachment and passive migration seem to be part of their life-history strategies (Riemann-Zürneck 1998). More studies are needed to assess whether individuals of *A. alicemartinae* are able to travel long distances by themselves or if these movements are facilitated by the use of other floating substrata.

ACKNOWLEDGEMENTS: The information compiled in this article was gathered as part of the Invasion Ecology class of the Master's Program in Marine Ecology at UCSC DNL and PAA thank Tuition Remission, Stipend and Teaching Assistance Fellowships granted by the Master Program and Facultad de Ciencias, UCSC. All authors thank Heraldo Álvarez for his valuable support in the field.

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Editorial responsibility: Álvaro T. Palma
Received March 25, 2013; accepted July 3, 2013

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