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Factors that affect the re-attachment of *Chondracanthus chamissoi* (Rhodophyta, Gigartinales) thalli

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Abstract Vegetative reproduction of *Chondracanthus chamissoi* by means of fragmentation and re-attachment of thalli is considered an effective strategy for maintaining natural populations of this species. Here, we evaluate the effects of (1) time of drifting thallus, (2) type of substratum, and (3) photon flux density, on the re-attachment capacity of thallus fragments of *C. chamissoi*. The results show that re-attachment decreases with the time after detachment, and was higher at the lower photon flux densities tested (10 and 40 μmol photons $m^{-2}s^{-1}$), and on calcareous substratum. Secondary attachment discs are formed along the entire surface of the fragment.

Keywords *Chondracanthus chamissoi* · Chile · Seaweed · Vegetative reproduction

Thallus fragmentation is a common event in benthic red algae and can be caused by a variety of abiotic and biotic factors (Thomsen and Wernberg 2005). However, the success of fragmentation as a reproductive mechanism depends on the capacity of the fragments to re-attach to the substratum (Santelices and Varela 1994). The time required for propagules to develop holdfast structures is variable and depends on the hydrodynamic conditions as well as other factors, such as light and substratum, that may have different effects in different species (Floc'h et al. 1987; Santelices and Varela 1994). *Chondracanthus chamissoi* (C. Agardh) Kützing is a commercially important carragenophyte that can be found from Peru to southern Chile in wave protected sectors, from the low subtidal zone to depths of 15 m, on hard substrata of shells and rocks. González et al. (1997) suggested that the re-attachment of fragments of *C. chamissoi* is an important mechanism in the maintenance of populations of this species in northern Chile. This was quantitatively evaluated by Macchiavello et al. (2003), who demonstrated that this mechanism operates actively in the months of greatest biomass accumulation, combined with the recruitment of new individuals via spores. However, the biological details, as well the abiotic factors involved in the formation of secondary discs and re-attachment of *C. chamissoi* thalli, are still unknown.

This study evaluates the effect of factors such as time of drifting thallus fragments, type of substratum, and light intensity, on the capacity of *C. chamissoi* thalli to re-attach.

The fronds were obtained by autonomous diving at depths of 4–5 m, in a subtidal bed located south of Tongoy Bay (30° 8′ S, 71° 37′ W). Aquariums (5 L capacity) were partially filled with stones (smaller than 50 mm in diameter) or calcareous substratum (shell gravel) (15 aquariums for each substratum type) and 25 apical fragments (5 cm in length) were partially buried in the substratum of each aquarium. The substrata were obtained from the same place as the *C. chamissoi* samples and were washed with sea water and sifted through a 50 mm mesh. The aquariums were maintained with permanent aeration at 15°C; 12:12 h (L:D); 40 μmol photons $m^{-2}s^{-1}$, with water changes every 5 days. The duration of the experiment was 20 days. Every 5 days, the thalli from three aquariums with each type of substratum were removed for observation. The data were expressed as percentage of attached fragments in relation to

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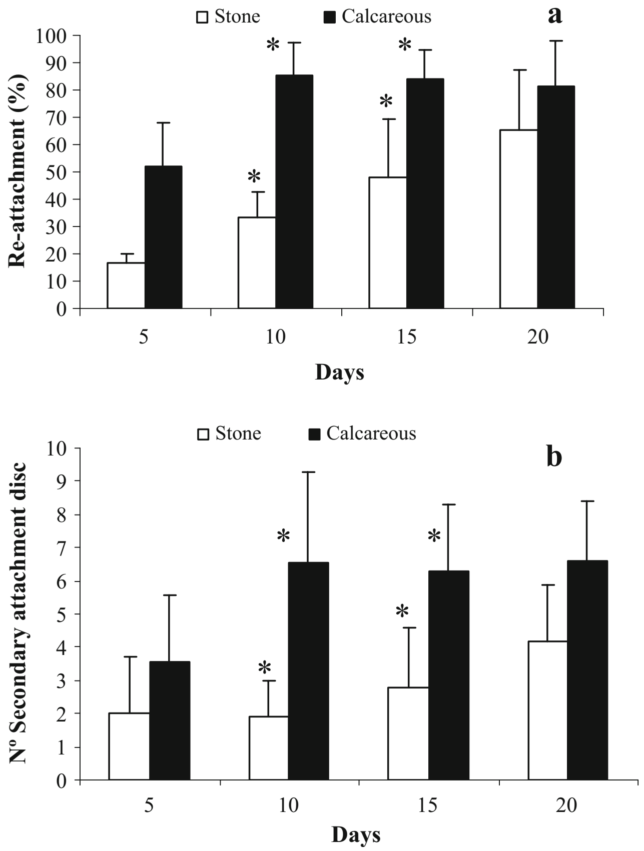

Fig. 1 Re-attachment of *Chondracanthus chamissoi* fragments in calcareous and stony substrata. **a** Percentage of re-attached fragments. **b** Number of secondary attachment discs (SADs) per fragment. Values are means (n=15) ± SE. *Asterisks* above bars indicate significant differences between calcareous and stony substrata

the total number of fragments contained in each aquarium. The number of the secondary attachment discs (SAD) formed by each fragment was also determined.

In another experiment, 500 apical fragments (5 cm in length) were maintained in simulated drift conditions in a 100 L capacity conical tank, with constant aeration and continuous water flow, at 15°C, 12:12 h (L:D) and 40 μmol photons $m^{-2}s^{-1}$. The fragments were cut at 10 day intervals to reduce them to their initial size. After 0 (control), 10, 20, 30, 40 and 50 days, 75 fragments were removed from the tank and partially buried in three 5 L aquariums with calcareous substratum (25 fragments in each aquarium). The percentage of fragments attached to the substratum and the number of SAD were determined after 10 days. These aquariums were maintained under the same conditions as above.

In a third experiment the effects of photon flux density (PFD) on fragment re-attachment and SAD formation were determined. For this experiment, 25 apical fragments (5 cm in length) were partially buried in calcareous substratum and subjected to three PFD treatments: 10, 40, or 120 μmol photons m^{-2} s^{-1}, at 15°C, 12:12 (L:D) and water changes every 5 days. Three 5 L aquariums were used as replicates for each treatment. After 10 days the re-attachment capacity of the fragments, as well as the number of SADs were evaluated.

A final experiment was designed to determine potential growth of erect axis from SAD. Three 5 L aquariums with calcareous substratum and conditions of 15°C, 40 μmol photons m^{-2} s^{-1}, 12:12 (L:D), permanent aeration and water change every 5 days were used; 25 apical fragments (5 cm length) were partially buried in the substratum. After 10 days the fragments that had not attached to the substratum were removed. The remaining fragments were observed weekly and the length (mm) of the most developed erect axis growing from each SAD was measured.

The homocedasticity and normality of all results were checked, followed by a one or two-way ANOVA. A Tukey´s test was utilized to ascertain differences among groups.

Chondracanthus chamissoi showed a high capacity for rapid re-attachment in all experiments. After 10 days of cultivation it was possible to observe fragments attached to substratum by several SAD, which were formed throughout the thallus surface.

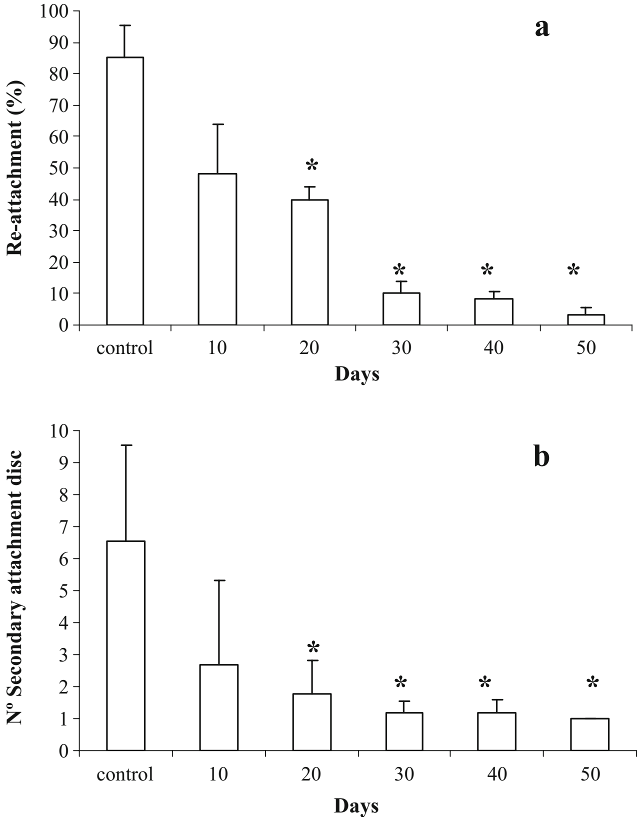

Fig. 2 Re-attachment of *C. chamissoi* fragments after different drifting times. **a** Percent of re-attached fragments. **b** Number of SADs per fragment. Values are means (n=3) ± SE. *Asterisks* above bars indicate significant differences from the control

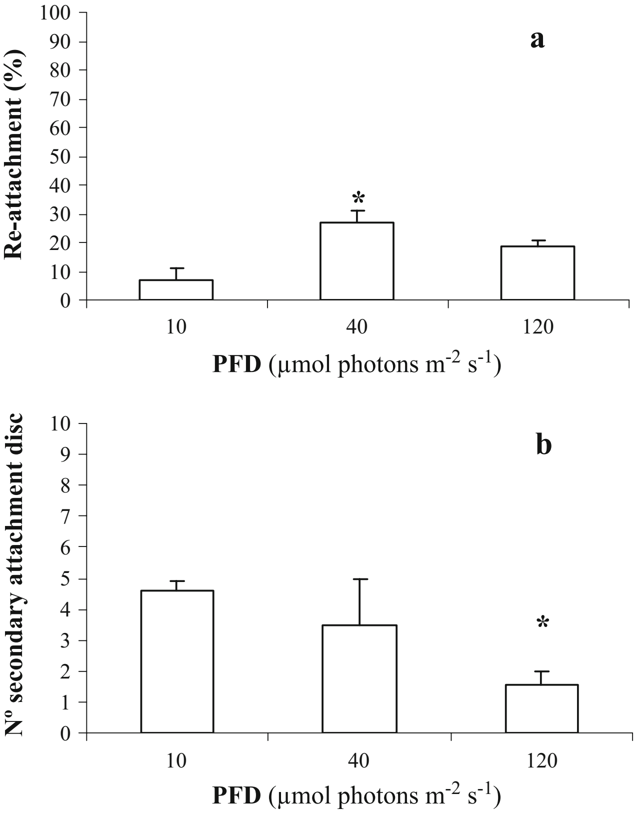

Fig. 3 Re-attachment of *C. chamissoi* fragments submitted to different photon flux density (PFD) (10, 40 or 120 μmol photons m^{-2} s^{-1}). **a** Number of re-attached fragments. **b** Number of secondary attachment discs per fragment. Values are means (n=3) ± SE. *Asterisks* above bars indicate significant differences between PFD treatments

The number of fragments attached to calcareous substratum was greater than that attached to stony substratum, but the differences were significant (P<0.05) only at 5 and 10 days (Fig. 1a). The fragments formed more SAD on calcareous than on stony substratum in all of the studied periods; however, these differences were significant only for 10 and 15 days of cultivation (P<0.05) (Fig. 1b).

After 20 days of simulated drift conditions, a significant decrease (P<0.05) in the re-attachment capacity of the fragments was observed in all subsequent drift times (Fig. 2a), compared to controls. Figure 2a shows a decrease in the number of SAD formed per fragment (P<0.05) with the increase in drifting time.

The results show that both re-attachment and the formation of SAD presented differences among the PFD treatments (P<0.05), with the highest percentage of re-attachment occurring with 40 μmol photons m^{-2} s^{-1} (Fig. 3a) and the highest number of SAD per fragment being registered at 10 and 40 μmol photons m^{-2} s^{-1} (Fig. 3b).

Every secondary attachment disc developed by the *C. chamissoi* fragments formed erect axes. These showed exponential growth (R^2=0.9689), reaching 12.68 mm after 4 weeks with a growth rate of 7.4±2 (% day^{-1}) (Fig. 4).

The present study shows that thallus fragments of *C. chamissoi* are capable of re-attaching to the substratum by means of the formation of SAD, from which new thalli can be generated. This reproductive mechanism can be separated into four consecutive phases: (1) thallus fragmentation, (2) entrapment of the fragment in the substratum, (3) SAD formation, and (4) new frond generation.

For *C. chamissoi* fragments, a longer time in the water column means fewer possibilities for re-attachment once they come into contact with the substratum, avoiding the rapid formation of secondary attachment structures. This could be related to morphological changes during free-floating in which the frond becomes globular and ramified (unpublished observation) due to the thinning and multidirectional elongation and curvature of the pinules. Fronds with these globular thalli are not easily trapped by the sediment whereas recently detached *C. chamissoi* branches have a higher probability of penetrating and being trapped by gravel.

Although *C. chamissoi* is a species that inhabits both calcareous and non-calcareous gravel substrata, the results showed that re-attachment of fragments and development of SAD structures were higher in calcareous than in stony substratum. Calcareous substratum is rougher, which we believe helps in the retention of fragments of *C. chamissoi* as well as in SAD formation. Apart from this attachment, calcareous substratum may be chemically inducing, as observed in *Gelidium chilense* (Santelices and Varela 1994) and for zygotes of the brown alga *Pelvetia sp.* (Robinson and Cone 1980). These results are of interest for management of natural populations and for repopulation of bare areas. Recently, Bulboa et al. (2005) reported that the ability to form attachment discs rapidly and abundantly is also observed on artificial substrata such as polypropylene ropes, which prevents the loss of thalli in culture.

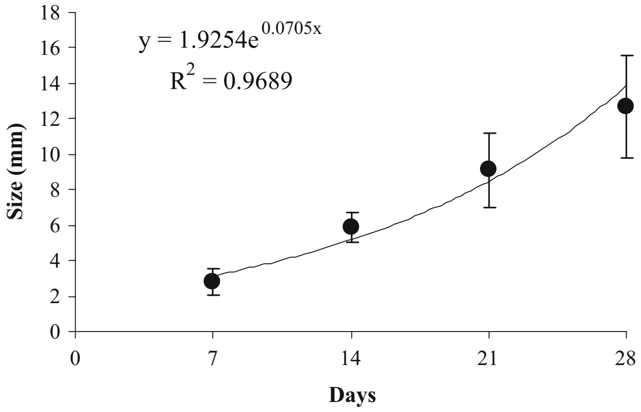

Fig. 4 Increase in the length (mm) of the erect axis formed from SADs of *C. chamissoi* on calcareous substratum, in a period of 4 weeks. Values are means and (n=3)±SE

The attachment structures of macroalgae are known to exhibit negative phototropism (Buggeln 1981), which directs their formation towards the substratum, thereby creating an effective anchoring structure (Norton and Mathieson 1983). Low irradiances favor this process, because higher light levels bring about positive phototropism, preventing the thalli from attaching to the substratum (Salinas 1991). Our results corroborate this tendency, showing that re-attachment and SAD formation in *C. chamissoi* occur preferably at low or medium PFDs. Similar results were reported by D'Antonio and Gibor (1985) for *Gelidium robustum*, where the formation of rhizoids in plantlets was higher when cultivated at lower PFDs (40 μmol photons m^{-2} s^{-1}). Carmona and Santos (2006) remark on a similar situation for *Gelidium sesquipedale*, in which the re-attachment process in the field occurs at lower PFDs, under the canopy of frond tufts.

Formation of SAD occurs throughout the surface of the thallus fragment. This demonstrates the high capacity of the species to re-attach itself from practically any part of its surface. On the other hand, abundant erect axes arise from SAD, and grow rapidly (7.4±2 % day^{-1}). These results are good news for the development of cultivation techniques for this species based on vegetative reproduction, which are beginning to be evaluated (Bulboa et al. 2005), where the birth of new fronds from SAD can be an advantage for subsequent growth after harvesting.

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