MORPHOLOGICAL VARIABILITY IN A RED SEAWEED: CONFIRMATION OF CO-OCCURRING F. LESSONII AND F. CHAUVINII IN CHONDRACTHUS CHAMISSOI (RHODOPHYTA, GIGARTINALES)

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Variability in thallus morphology is common in red seaweeds. Two co-occurring forms have been described for Chondracanthus chamissoi based mainly on blade width. To determine whether two distinct forms or a range of intermediate morphologies occur in C. chamissoi, thalli were collected from three localities in southern Chile in autumn–winter, repeating the sampling in one locality in spring and in summer. In each occasion, individual sporophytic and male and female gametophytic clumps were collected, and the longest blade with intact apex from each clump was evaluated. Blade length, width, density of spines, axis curvature and thickness, and pinnule length and width were evaluated in each blade. Principal components analyses separated two groups of thalli, one group with narrow, thick, and curved (concavo-convex) blades, with few spines consistent with f. lessonii, and another with broad, thin, and flat blades, with many spines consistent with f. chauvinii. These variables also had bimodal frequency distributions. Pinnule measurements were mainly associated with differences among sporophytes and gametophytes. Age (length), phase of the life cycle, and sex were not related to the forms. Furthermore, thalli of both forms were collected side by side in the study sites and throughout the year so the occurrence of the two forms was not attributable to local environmental conditions. In this species, secondary basal disks are produced after attachment of apexes to the substratum. These disks may produce blades with a modified morphology in a way similar to proliferations and regenerations described for Schottera nicaeensis.

Key index words: carrageenophyte; edible seaweed; forms; Gigartinaceae; principal components analysis; secondary attachment; sympatry; variants

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Related species can exhibit great morphological similarity, making difficult to draw boundaries between them based only on morphological traits. This is more critical in groups of species with very simple morphologies, like many simple, bladed Gigartinaceae (Shaughnessy 1996, Ross et al. 2003). The use of molecular tools in such cases has clarified relations among taxa at the species and higher taxonomic levels (e.g., Hughey et al. 2001, Saunders 2005) and has often resulted in the identification of cryptic species (e.g., Ross et al. 2003, Hughey and Hommersand 2008, Montecinos et al. 2012, Saunders and Millar 2014, Yang and Kim 2016). Within a species, however, environmental factors may produce changes in morphology associated with large, geographical or smaller, local spatial scales, which may result in recognizable morphological entities such as ecotypes (e.g., Dring and West 1983, Faria et al. 2017) or morphotypes (e.g., Gutiérrez and Fernández 1992, Brodie et al. 1993, Shaughnessy 1996). Likewise, seasonal variation in environmental factors may also affect growth and development of thalli, having an effect on their morphology (Floc’h et al. 1987, Vega and Meneses 2001, Pratt and Johnson 2002).

Apart from the effect of environmental factors varying in space and time, differences in morphology can also be originated from factors related to the biology of the seaweeds themselves. Most red seaweeds have complex life cycles in which diploid individuals (i.e., the sporophytes) alternate with haploid individuals (i.e., the gametophytes), the latter further frequently occurring as separate male and female thalli. The third phase in this triphasic life cycle, the tiny diploid carposporophytes, develops after fertilization, and live parasitically on or inside the female gametophytes (Hommersand and Fredericq 1990). In some species, the thalli of gametophytes and sporophytes have remarkably different morphology (i.e., heteromorphic life cycles), although in most species the individuals of the two phases share the same morphology (i.e., isomorphic life cycles). Nonetheless, subtle differences between

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gametophytes and sporophytes have been described in some species with isomorphic life cycles (e.g., Brodie et al. 1993, Hommersand et al. 1993, Kain and Destombe 1995). Morphological differences can also be present between the female and male gametophytes (Van der Meer and Todd 1980, Shaugnessy 1996).

*Chondracanthus chamissoi* (Rhodophyta, Gigarti-naceae) is a common red seaweed along the coasts of the southeastern Pacific Ocean, extending from Perú (5° S) to Ancud, Chile (42° S; Ramírez and Santelices 1991, Hoffmann and Santelices 1997), although recent molecular evidence indicates that this species is also present in Korea, Japan, and France (Yang et al. 2015). It has been used as a source for the extraction of the commercially important phycocolloid carrageenan (Hoffmann and Santelices 1997), but more recently, it has been exported as an edible seaweed to Asia (Bulboa and Macchiavello 2006). Locally, it can form large patches on rocky substrata to 15 m deep (Hoffmann and Santelices 1997), and it can also be found in intertidal pools on wave-swept as well as protected shores (Acleto 1986). It has a triphasic *Plocysiphonia*-type life cycle, with alternation of isomorphic gametophytic and sporophytic generations (Hommersand et al. 1993, Hoffmann and Santelices 1997, Ávila et al. 2010). Given that gametophytes are dioic, three types of free-living individuals can be found, the male and female gametophytes and the sporophytes.

In his work about the algae of Perú, Howe (1914) identified three separate species, *Gigartina chamissoi*, *G. lessonii*, and *G. chawinii*, indicating that their extreme forms were recognizable, but that it was difficult to draw lines clearly to separate them from each other. He also mentioned that all three species could be collected further south, in Chile. Dawson et al. (1964) discussed the descriptions made by Howe (1914) and preferred to consider them as a single species, *G. chamissoi*, but acknowledging that two morphological groups could be recognized, the *lessonii* form with slender blades up to 3–5 mm in width, and the *chawinii* form with blades up to 25 mm in width or more. They also indicated that the narrowest forms had no superficial outgrowths on the blades, while thalli of intermediate width (<5 mm) had “sparse, short, denteate outgrowths scattered along the central area of the blade”, and “coarser thalli” were “provided with more or less abundant superficial, spinous outgrowths” (Dawson et al. 1964). Acleto (1986) maintained the interpretation of two forms within the species. Ramírez and Santelices (1991) acknowledged the morphological variability, and preferred to maintain the distinction of three species. The two forms have not been mentioned directly in recent descriptions (Santelices 1989, Hoffmann and Santelices 1997), although morphological variability in this species is highlighted. Hommersand et al. (1993) transferred this species to the genus *Chondracanthus*.


The aim of this study was to analyze quantitatively some morphological characters of blades of *Chondracanthus chamissoi* to determine whether two distinct forms occur or, alternatively, whether the two forms described represent the extremes in a morphological gradient.

Sporophytes, and male and female gametophytic thalli were included to assess whether slight heteromorphy or sexual dimorphism occurred. Thalli of different morphology had been noted to grow in close proximity. Sampling was done in different localities to evaluate whether co-occurrence of blades with different characteristics was common. Also, samples were obtained in different seasons to include a wider suite of environmental conditions and developmental stages of the thalli.

**MATERIALS AND METHODS**

Thalli were collected at three localities in the Biobío Region, southern Chile: Ramuntcho, located on the southern side of San Vicente Bay (36°45′06″ S 75°11′04″ W), Cocholgue, located on the eastern side of Concepción Bay (36°35′15″ S 72°58′00″ W), and Punta Lavapié (37°08′55″ S 73°35′13″ W) located at an exposed point, but where tiers of rocky outcrops reduced direct wave impact (Fig. 1). The three localities have moderate to well-developed patches of *Chondracanthus chamissoi*. For the morphological descriptions, a single site was sampled in autumn–winter in each of these three localities. These were done in June 2017 for Ramuntcho and July 2017 for Punta Lavapié and Cocholgue (winter site 1). In spring (September 2017), a different site (spring site 2) was sampled in Cocholgue. This new site was located 1.5 km north from the first one in this locality. In January, 2018 (austal summer), both sites (summer sites 1 and 2) of Cocholgue were sampled again on the same day. Thus, six samples were analyzed in all, including three localities and spanning from late autumn to early summer.

Each sampling site was chosen on flat or gently sloping, shallow, subtidal rocky platforms with boulders occurring only occasionally. Clumps of *Chondracanthus chamissoi* (groups of blades arising from a single basal disk) generally occurred in patches, usually ranging from 0.5 to over 1.5 m in diameter, although more continuous or sparse distributions could also be found, forming beds that could extend for several tens of meters. The deepest sampling site was the one at Ramuntcho, at a depth of 3 m, which was sampled by scuba diving, while those at Punta Lavapié and both sites 1 and 2 at Cocholgue were shallower, located no deeper than 1.0 m below sea level. Sampling in the latter two localities was done...