Blades and papillae as likely dispersing propagules in Chilean populations of *Mastocarpus* sp. (Rhodophyta, Gigartinales)

Láminas y papilas como posibles propágulos de dispersión en poblaciones chilenas de *Mastocarpus* sp. (Rhodophyta, Gigartinales)

Mauricio H. Oróstica¹,², Ricardo D. Otaíza³ and Paula E. Neill³

¹Centro Regional de Investigación y Desarrollo Sustentable de Atacama (CRIDESAT) CONICYT-REGIONAL R0611003, Avda. Copayapu 485, Copiapó, Chile
²Programa de Magíster Ciencias del Mar, Facultad de Ciencias del Mar, Universidad Católica del Norte, Avda. Larrondo 1281, Coquimbo, Chile
³Departamento de Ecología, Facultad de Ciencias, Universidad Católica de la Santísima Concepción, Concepción, Chile.
rotaiza@ucsc.cl

Resumen.- *Mastocarpus* sp. es un alga roja nativa a la costa del Pacífico de Norteamérica, y también presente en Concepción, Chile (ca. 37°S), donde se ha propuesto como especie no indígena. Su establecimiento y expansión podrían verse favorecidos si láminas y papilas constituyeran propágulos. Las características de desprendimiento de estas dos estructuras apoyan esta interpretación. Láminas de *Mastocarpus* sp. requirieron menos fuerza para ser desprendidas desde las rocas que láminas de otras algas rojas comunes. Asimismo, un estimado mensual de 14,9% de las papilas con cistocarpos maduros se desprenden de láminas sometidas a turbulencia en laboratorio. Además, es común encontrar láminas y papilas a la deriva, y liberan esporas de pigmentación normal. La distribución de papilas a lo largo de las láminas, considerando su madurez, sugiere un patrón de desprendimiento predecible. Papilas nuevas fueron más abundantes en segmentos distales de láminas, y papilas viejas en segmentos centrales. La abundancia de cicatrices dejadas por papilas desprendidas fue mayor en segmentos basales, sugiriendo que las papilas que dejaron esas cicatrices portaban cistocarpos maduros. Concluimos que los puntos de adhesión de láminas y papilas se tornarían relativamente más débiles a medida que crecen, facilitando su desprendimiento. Esto no representa la abscisión de estructuras senescentes ya que en su interior crecen carpoesporofitos con esporas que pueden ser liberadas. Esto facilitaría el establecimiento de nuevos individuos a distancias y lugares diferentes de los que alcanzarían las esporas, pudiendo ser consideradas como estructuras alternativas de dispersión. Como tales, podrían afectar la dinámica poblacional y expansión de rango de *Mastocarpus* sp. en Chile.

Palabras clave: Desprendimiento, especie no indígena, estrategia de dispersión, fragmentos a la deriva, Phyllophoraceae

Abstract.- *Mastocarpus* sp. is a red macroalga native to the Pacific coast of North America, and present around Concepción, Chile (ca. 37°S), where it has been suggested as a non-indigenous species. Its establishment and expansion could be favored if blades and papillae function as propagules. The characteristics of the detachment of these two structures support this interpretation. Blades of *Mastocarpus* sp. become detached from rocks more readily than other common, bladed red seaweeds. In turn, a monthly estimate of up to 14.9% of papillae carrying mature cystocarps easily broke off from blades when experimentally subjected to turbulence in the laboratory. Additionally, blades and papillae are commonly found drifting, and release normally pigmented spores. The distribution of papillae along the blades, considering their maturity, suggests a predictable detachment pattern. New papillae were more abundant on distal segments, old papillae on middle segments, and scars of shed papillae on basal segments, suggesting that shed papillae carried mature cystocarps. We conclude that blades and papillae have attachment points that become relatively weaker as they grow and mature, facilitating their detachment. This does not represent abscission of empty or senescent structures because carposporophytes growing inside these structures still carry spores that can be released. Thus, blades and papillae may be important in facilitating the establishment of new individuals at distances and places different from what is achieved by spores and, hence, could be considered as alternative dispersing entities. As such, they could affect the population dynamics and range expansion of *Mastocarpus* sp. in Chile.

Key words: Detachment, dislodgment, dispersal strategy, drifting fragments, non-indigenous species, Phyllophoraceae
INTRODUCTION

For seaweeds, and other benthic organisms, dispersal is a fundamental process in maintaining and restoring local populations, and in the colonization of new environments (Santelices 1990, Reed et al. 2000, Kinlan & Gaines 2003, Shanks et al. 2003). In seaweeds, propagules are structures that become detached from the parental thallus, drift away and produce new established individuals (Hoffmann 1987, Macchiavello et al. 2003, Hernández-Carmona et al. 2006, Stewart 2006, Sussmann & DeWreede 2007, McKenzie & Bellgrove 2008).

Unicellular entities (e.g., spores, gametes and zygotes) are the most common types of propagules in seaweeds, and have received considerable attention in the literature (e.g., Hoffmann 1987, Santelices 1990, Clayton 1992, Norton 1992, Reed et al. 1992, Kendrick & Walker 1995, Gaylord et al. 2002, Opazo & Otaíza 2007). In contrast, the importance of multicellular structures associated with vegetative reproduction is less frequently considered, despite the fact that breakage and drifting of thallus fragments may be a common dispersal mechanism for many seaweeds. Moreover, unicellular propagules have the capacity for primary attachment via the evacuation of adhesive vesicle contents, whereas drifting fragments may have different secondary attachment mechanisms, e.g., rhizoids (Pueschel 1990, Salinas 1991) or other secondary attachment structures (e.g., Otaíza & Fonseca 2011).

Detachment and drifting of large fragments (e.g., sporophylls in some Laminariales) or even whole thalli carrying mature reproductive structures is frequent in macroalgae (Vásquez & Tala 1995, Mathieson et al. 2003, Macaya et al. 2005, Hernández-Carmona et al. 2006, McKenzie & Bellgrove 2008). While drifting, or once in contact with the substratum, these fragments may release spores or gametes, which are able to generate new individuals.

The release and dispersal of vegetative fragments can have important demographic effects. For example, fragments of Gracilaria chilensis are the main propagation structures for this species (Santelices & Doty 1989, Buschmann et al. 1995). Drifting can also have important biogeographic effects. Floating kelp contribute to the connectivity of their populations and of associated organisms (Smith 2002, Hinojosa et al. 2010). Furthermore, fragmentation has favored the expansion of some non-indigenous algal invaders (Mags & Stegenga 1999) like Caulerpa taxifolia in Mediterranean and Australian waters (Ceccherelli & Cinelli 1999, Smith & Walters 1999, Ceccherelli & Piazzii 2001, Wright & Davis 2006, Khou et al. 2007) and Codium fragile on Atlantic and Pacific coasts (Garbary et al. 2004). Indeed, invading species increase their chances of becoming established and expanding their populations when they have multiple types of propagules.

The genus Mastocarpus (Rhodophyta, Gigartinales) has several species on the northeastern Pacific coasts (Lindstrom et al. 2011). In contrast, a single species has been cited for the Chilean coasts (southeastern Pacific). Initially identified as Mastocarpus papillatus (C. Agardh) Kützing, the species present in Chile has been recently reassigned to Mastocarpus latissimus (Harvey) (see Lindstrom et al. 2011). This species is distributed from Alaska to southern California (Lindstrom et al. 2011) and is also very common around Concepción, south-central Chile (36°45’S; 73°03’W; Santelices 1989, Hoffmann & Santelices 1997, cited in both references as M. papillatus). This disjunct geographic distribution, together with a lack of congenerics in Chile and multiple congenerics present in Europe and Asia, occurrence in regions with potential vectors (e.g., international and national ports), and biological characteristics common in successful algal invaders like crustose growth form and ability for asexual reproduction (Hewitt et al. 2007, Carlton 2009), has lead to the proposal that this species is introduced on Chilean coasts (Castilla et al. 2005).

Species in the genus Mastocarpus have heteromorphic life-cycles in which crustose tetrasporophytes alternate with bladed gametophytes (Zupan & West 1988, Lindstrom et al. 2011), although direct development of female gametophytes also occurs (Zupan & West 1988, Fierst et al. 2010, Lindstrom et al. 2011). In the Mastocarpus populations present in Chile, blades grow from a perennial, crustose base to which they are attached by a narrow stipe (Hoffmann & Santelices 1997). Reproductive, female gametophytic blades produce papillae which harbor the carposporophytes (Lindstrom et al. 2011). Unlike M. latissimus, male gametophytes are smooth, without papillae; given this discrepancy with the description given by Lindstrom et al. (2011), the species studied in this work will be referred to as Mastocarpus sp. For Mastocarpus species, only unicellular propagules (tetraspores and carpospores) have been described (e.g., West 1972, Polanshek & West 1977, Zupan & West 1988), although the possibility of detached blades playing a role in dispersal has been suggested (e.g., Carrington 1990).

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