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Recent introduction of *Gracilaria parvispora* (Gracilariales, Rhodophyta) in Baja California, Mexico

Abstract: *Gracilaria parvispora* is reported for the first time as an invasive species in northwestern Mexico based on morphological, anatomical and molecular data. The species is widely distributed in the region, where it colonizes sandy and rocky habitats from intertidal areas down to a depth of 1.5 m. The morphological and anatomical data from the Mexican specimens matched the circumscription of the species in Hawaiian waters. Two molecular markers (*rbc*L and *cox*1) showed that the Mexican populations were closer to the Hawaiian populations than the Korean populations, which may relate to a similarity in seawater temperatures between Hawaii and Baja California. *Gracilaria parvispora* formed extensive mats together with *Gracilaria vermiculophylla*. It was found in stomach samples from a green turtle (*Chelonia mydas*) in the coastal lagoons of Baja California Sur. The ecological impacts of the two alien *Gracialria* species on other native species and communities have yet to be determined. This is the first demonstration of a second invasive *Gracilaria* species, following the introduction of *G. vermiculophylla* into the northwestern Mexico region.

Keywords: coastal lagoons; *Gracilaria parvispora*; *Gracilaria vermiculophylla*; invasive species; northwestern Mexico; rocky reefs.

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Introduction

Gracilaria is economically important as an agarophyte and is used for food in Asia, Hawaii and South America. It comprises more than 169 currently flagged species in AlgaeBase (Guiry and Guiry 2012) that are widely distributed from tropical to temperate waters. *Gracilaria* has been the focus of numerous systematic studies (e.g., Gurgel and Fredericq 2004); however, taxonomy of the species based on the morphological features is difficult. Two of the species, *Gracilaria salicornia* (C. Agardh) E.Y. Dawson and *Gracilaria vermiculophylla* (Ohmi) Papenfuss, are invasive in European and North American waters (Freshwater et al. 2006, Thomsen et al. 2007, Kim et al. 2010).

Gracilaria parvispora I.A. Abbott (Abbott 1985) was considered endemic to the Hawaiian waters until Kim et al. (2008) reported its occurrence in Korea and Japan, where it was known for a considerable period as *G. bursa-pastoris* (S.G. Gmelin) P.C. Silva. *Gracilaria parvispora* is distributed on flat reefs and sandy habitats in waters that have low to moderate turbulence and salinity and high nutrient levels (Abbott 1999). Over-harvesting for human consumption accounts for serious shortages in the natural populations; until the 1970s, it was the most "common limu" found in the Honolulu fish markets (Abbott 1996). Dreckmann (1999, 2006) recorded the occurrence of *G. parvispora* in coastal lagoons of the tropical Mexican Pacific based on extensive surveys in the Tehuantepec area, but without molecular identification.

As a part of a systematic evaluation of the family Gracilariaceae along the northwestern coast of Mexico (R. Riosmena-Rodriguez, L.D. García-Rodríguez and S.M. Boo, unpublished data), thalli of *G. parvispora* became available, and we confirmed its occurrence in the area based on molecular and morphological evidence. Here, we discuss the likely human-mediated distribution of *G. parvispora* in the Mexican Pacific region.

Table 1 Materials used in the present study.

Species	Collection data	Voucher and reference	GenBank accession	
			*rbc*L	*cox*1
Gracilaria parvispora I.A.Abbott	Japan: Oki Island (May 7, 2003)	G280, Kim et al. 2008	EF434944[1]	KC113593
	Korea: Jongdal, Jeju (April 8, 2005)	Kim et al. 2008, Yang et al. 2008	EF434942[1]	EF434921[2]
	Korea: Shinyang Beach, Jeju (March 10, 2005)	G0435, Kim et al. 2008	EF434943[1]	KC113594
	USA: Hawaii (November 29, 2004)	Kim et al. 2008, Yang et al. 2008	EF434945[1]	EF434922[2]
	Korea: Kimnyeong, Jeju (May 14, 2007)	G0718	–	KC113595
	México: Huitussi, Bahía Navachiste. Sinaloa (April 18, 2008)	111	KC113596	KC113590
	México: San Juan, B.C. (February 27, 2008)	482	KC113599	KC113592
	México: Estero Sanbuto, Bahía Magdalena, BCS (November 8, 2008)	774	KC113598	KC113591
	México: Playa La Concha, La Paz, BCS (March 31, 2009)	1054	KC113597	–
Curdiea racovitzae Hariot	Antartica	Gurgel and Fredericq 2004	AY049426	–
Gracilaria apiculata P.L.Crouan *et* H.M.Crouan	Venezuela: La Encrujijada	Gurgel and Fredericq unpublished	AY049333	–
G. arcuata Zanardini	Philippines: Cebu	Gurgel and Fredericq 2004	AY049383	–
G. beckeri (J.Agardh) Papenfuss	South Africa	Gurgel and Fredericq 2004	AY049377	–
G. bursa-pastoris (S.G.Gmelin) P.C.Silva	Italy	Gurgel and Fredericq unpublished	AY049373	–
G. capensis (J. Agardh) Papenfuss	South Africa	Gurgel and Fredericq 2004	AY049378	–
G. cervicornis (Turner) J.Agardh	USA: Bahia Honda	Gurgel and Fredericq unpublished	AY049366	–
G. changii (B.M.Xia *et* I.A.Abbott) I.A.Abbott, J.Zhang *et* B.M.Xia	–	Gurgel and Fredericq unpublished	AY049388	–
G. chilensis C.J.Bird, McLachlan *et* E.C.Oliveira	Chile: De los Lagos	Kim et al. 2006	DQ095784	–
G. cuneifolia (Okamura) I.K.Lee *et* Kurogi	Korea: Jeju	Kim et al. 2006	DQ095787	–
G. curtissiae J.Agardh	–	Gurgel and Fredericq unpublished	AY049340	–
*G. damaecorni*s J. Agardh	USA: HBOI, Florida	Gurgel and Fredericq 2004	AY049326	–
G. domingensis (Kützing) Sonder ex Dickie	Brazil: Praia rasa, Buzios	Gurgel and Fredericq 2004	AY049371	–
G. galetensis C.F.D.Gurgel, S.Fredericq, *et* J.N.Norris	Panama	Gurgel and Fredericq 2004	AY049320	–
G. gracilis (Stackhouse) M.Steentoft, L.M.Irvine *et* W.F.Farnham	United Kingdom: England	Gurgel and Fredericq 2004	AY049400	–
G. hayi Gurgel, Fredericq *et* J.N.Norris	Panama	Gurgel and Fredericq 2004	AY049315	–
G. incurvata Okamura	Japan: Chiba	Kim et al. 2006	DQ095790	–
G. intermedia J.Agardh	Venezuela: Puerto Escondido	Gurgel and Fredericq 2004	AY049336	–
G. lacinulata (M.Vahl) M.A.Howe	Venezuela: Playa Barranquita	Gurgel and Fredericq 2004	AY049344	–
G. mammillaris (Montagne) M.A.Howe	USA: LA	Gurgel and Fredericq 2004	AY049323	–
G. occidentalis (Børgesen) M.Bodard	USA: LA	Gurgel and Fredericq 2004	AY049322	–
G. oliveirarum Gurgel, Fredericq *et* J.N.Norris	Venezuela: La Vela de Coro	Gurgel and Fredericq 2004	AY049330	–
G. ornata Areschoug	Panama	Gurgel and Fredericq 2004	AY049318	–
G. pacifica I.A.Abbott	USA: WA	Gurgel and Fredericq 2004	AY049397	–
G. punctata (Okamura) Yamada	Taiwan	Lin,S.-M. Unpublished	AY737447	–
G. salicornia (C.Agardh) E.Y.Dawson	Philippines	Gurgel and Fredericq 2004	AY049385	–
G. smithsoniensis Gurgel, Fredericq *et* J.N.Norris	Panama: Galeta Point	Gurgel and Fredericq 2004	AY049321	–
G. spinulosa (Okamura) Chang *et* Xia	Taiwan	Gurgel and Fredericq 2004	AY049395	–
G. tenuistipitata C.F.Chang *et* B.M.Xia	USA: Rhode Island	Gurgel and Fredericq unpublished	AY049314	–
G. textorii (Suringar) De Toni	Korea: Daechun	Kim et al. 2006	DQ095793	–
G. tikvahiae McLachlan	Mexico: San Agustin	Gurgel and Fredericq unpublished	AY049437	–

(**Table 1** Continued)

Species	Collection data	Voucher and reference	GenBank accession	
			*rbc*L	*cox*1
G. venezuelensis W.R.Taylor	USA: Florida	Gurgel and Fredericq 2004	AF539603	–
G. vermiculophylla (Ohmi) Papenfuss	France: Belon estuary	Rueness 2005	AY725172	–
G. vieillardii P.C.Silva	Taiwan	Gurgel and Fredericq 2004	AY049394	–
G. yoneshigueana Gurgel, Fredericq *et* J.N.Norris	Brazil	Gurgel and Fredericq 2004	AY049372	–
Gracilariopsis chorda (Holmes) Ohmi	Korea: Jindo	Kim et al. 2006	DQ095785	–
Gracilariopsis longissima (S.G.Gmelin) M.Steentoft, L.M.Irvine *et* W.F.Farnham	Namibia	Gurgel et al. 2003	AY049410	–
Hydropuntia cornea (J.Agardh) M.J.Wynne	Venezuela	Gurgel and Fredericq 2004	AY049338	–
H. crassissima (P.L.Crouan *et* H.M.Crouan) M.J.Wynne	Panama	Gurgel and Fredericq 2004	AY049351	–
H. edulis (S.G.Gmelin) Gurgel *et* Fredericq	Philippines: Little Santa Cruz	Gurgel and Fredericq 2004	AY049387	–
H. eucheumatoides (Harvey) Gurgel *et* Fredericq	Philippines: Cebu	Gurgel and Fredericq 2004	AY049389	–
H. preissiana (Sonder) Gurgel *et* Fredericq	Australia	Gurgel and Fredericq 2004	AY049403	–
H. rangiferina (Kützing) Gurgel *et* Fredericq	Ghana	Gurgel and Fredericq 2004	AY049379	–
H. secunda Gurgel *et* Fredericq	USA: Florida	Gurgel and Fredericq unpublished	AY049361	–
H. urvillei Montagne	Australia	Gurgel and Fredericq 2004	AY049402	–
H. usneoides (C.Agardh) Gurgel *et* Fredericq	Mexico: Campeche Bay	Gurgel and Fredericq 2004	AY049346	–
Melanthalia abscissa (Turner) J.D.Hooker *et* Harvey	New Zealand	Gurgel and Fredericq 2004	AY049428	–

Materials and methods

Morphological analysis

Gracilaria parvispora was collected in northwestern Mexico (Table 1) from a range of localities where at least three sites at each were visited. It occurred at depths from the intertidal down to 1.5 m on both rocky and sandy substrata. At least three thalli were collected from each site from June 2008 to July 2010 and preserved wet in a 4% seawater-formalin solution for anatomical analysis, and at least another three thalli were preserved fresh/dry in silica gel for molecular analysis. Morphological and anatomical analyses were based on the diagnostic features provided by Abbott (1999) using a compound microscope. Thin sections were processed by histological techniques following Riosmena-Rodríguez et al. (1999).

Molecular analysis

Total genomic DNA in our samples was extracted from silica-gel-dried specimens using a LaboPass™ Tissue Mini kit (Hokkaido System Science, Hokkaido, Japan) following the manufacturer's instructions. Extracts were dissolved in 200 μl of distilled water. The extracted DNA was stored at -20°C and used for PCR amplification. Specific primer pairs were used for the amplification and sequencing reactions of each gene as follows. For the plastid *rbc*L, *rbc*LF145-*rbc*LR898 and *rbc*LF762-*rbc*LR1442 primers (Kim et al. 2010) were used. For the mitochondrial *cox*1, COXI43F and COXI1549R (Geraldino et al. 2006) were used. PCR amplifications were performed using a TaKaRa Ex Taq reaction kit (Takara Shuzo, Shiga, Japan). PCR amplifications were performed in a total volume of 25 μl containing the components reported by Yang et al. (2008). The PCR products were purified with the LaboPass™ PCR (Hokkaido System Science) and then sequenced commercially (Genoteck Co., Daejeon, Korea). Both electropherogram outputs from each sample were edited using Chromas software, version 1.45 (http://www.technelysium.com.au/chromas.html). The alignments of newly analyzed and previously registered sequences in GenBank were performed manually using Se-Al software, version 2.0a11 (Andrew Rambaut, http://evolve.200.ox.ac.uk/). Maximum likelihood (ML) phylogenetic analysis was performed using the GTR + Γ model implemented in RAxML software (Stamatakis 2006). Statistical support for each branch was obtained from 1000 bootstrap replications using the same substitution model and RAxML program settings. A statistical parsimony network was created using TCS software, version 1.21 (Clement et al. 2000). All of the sequences obtained have been deposited in GenBank (Table 1).

Results

Morphological analysis

Most *Gracilaria parvispora* collections came from a mixture of sand and rocky substrata. Thalli are red to brownish, and sometimes green, and have a single dominant axis, usually with three orders of branching. Axes are solid, compressed with age and are often half the thickness of the main branches (Figure 1). Branches are irregularly alternate, furcate and mixed with unilateral or secondary branching in whole or in part.

In transverse section, medullary cells are large and have thick cell walls. The medulla is surrounded by two layers of cortical cells, which are small, roundish and pigmented in the outermost layer; the transition from the cortex to the medulla is abrupt (Figure 2).

Tetrasporophytes, gametophytes and carposporophytes were found in all sites sampled. Cystocarps have a distinctively acute apex and consist of small pericarp cells with star-shaped contents and large gonimoblast cells; cystocarps are 2–5 mm in diameter (Figure 3).

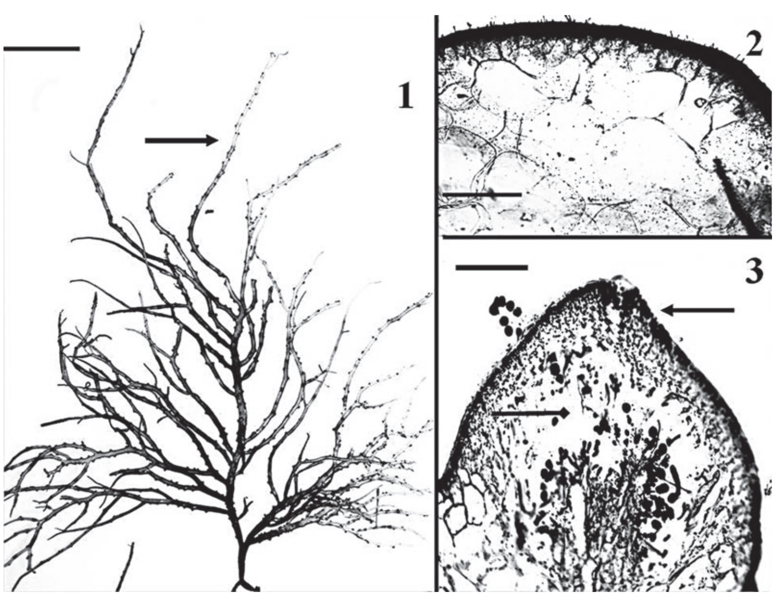
Molecular analysis

In ML analyses, four *rbc*L sequences from different locations in Baja California formed a clade with other sequences of *Gracilaria parvispora* from Hawaii, Korea and Japan (Figure 4). This was also true for three *cox*1 sequences from Baja California (tree not shown). We found three haplotypes in the *rbc*L data. One haplotype was identical between the Hawaiian and Mexican populations, although it was connected with the other Mexican haplotype (voucher 111, Huitussi, Bahía Navachiste, Sinaloa, México; April 18, 2008) by three missing haplotypes (Figure 5). We found four haplotypes with more missing haplotypes in *cox*1.

Discussion

Our *rbc*L and *cox*1 analysis clearly demonstrated the occurrence of *Gracilaria parvispora* in the northwestern Mexico region. The morphology of Mexican plants was consistent with those of Hawaiian and Korean plants, having compressed thalli with prominent unilateral branching, and small and star-shaped cells in the pericarp.

The widespread distribution of *G. parvispora* from northwestern Mexico, Hawaii, Korea and Japan is interesting. *Gracilaria parvispora* was for a long time reported



Figures 1–3 (1) *Gracilaria parvispora*: Morphology showing the tapering of the branches and the carposporangia (arrow indicates dark dots of thallus surface). Scale bar, 5 cm. (2) *Gracilaria parvispora*: Transverse section showing the abrupt transition between the medulla and cortex. Scale bar, 500 µm. (3) *Gracilaria parvispora*: Longitudinal section of the carposporphyte with acute apex (arrow) and abundant auxiliary filaments (arrow with diamond-shaped head). Scale bar, 500 µm.

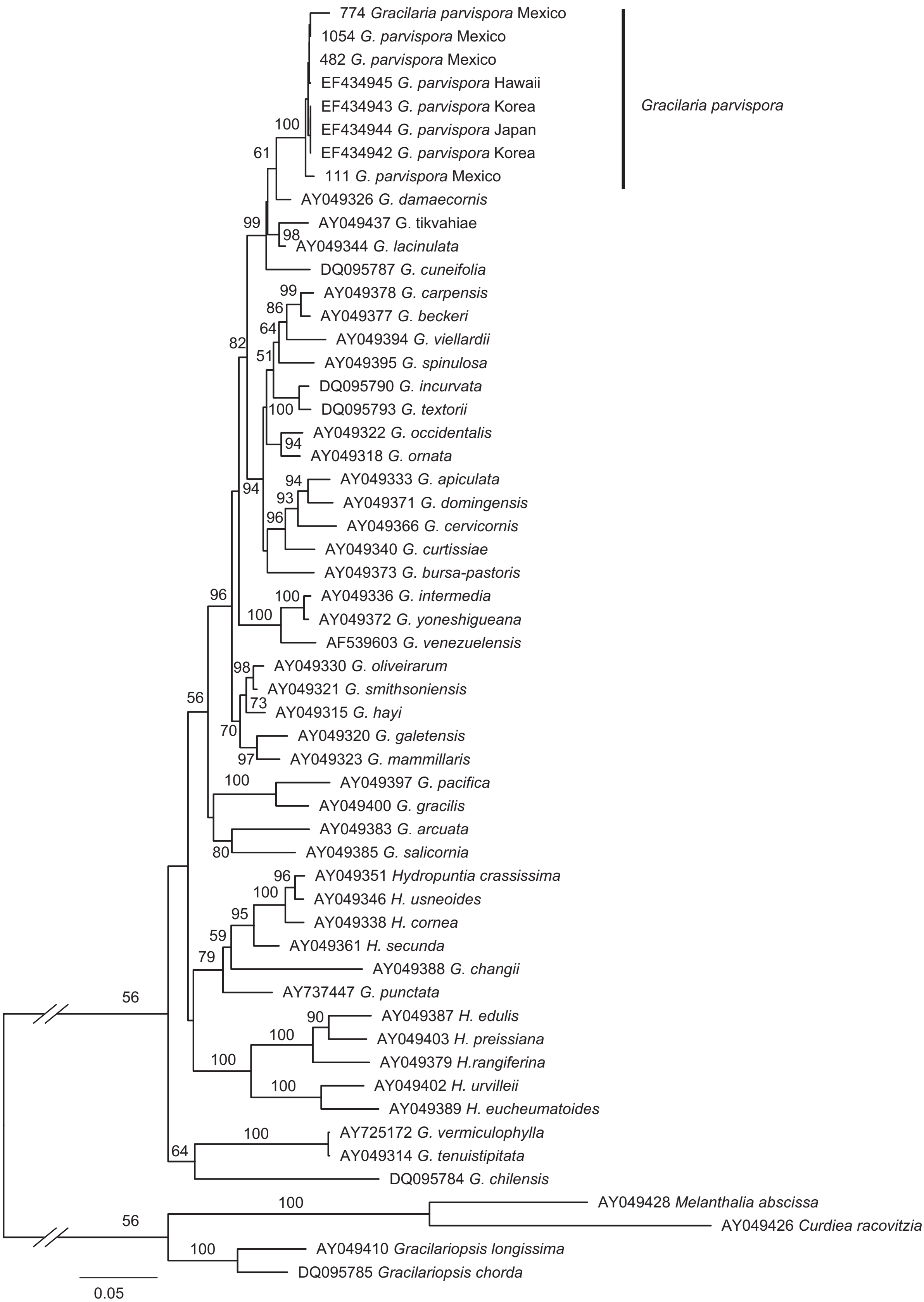


Figure 4 *Gracilaria parvispora*: ML tree of the *rbc*L from México produced by RaXML software. Bootstrap values were estimated using 1000 replicates.

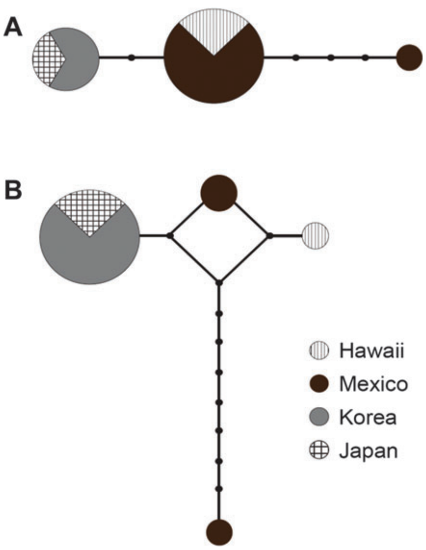


Figure 5 *Gracilaria parvispora*: Statistical parsimony networks. (A) *rbc*L network; (B) *cox*1 network. Small black dots indicate missing haplotypes (either extinct or not sampled).

as *Gracilaria bursa-pastoris* or *Gracilaria compressa* (C. Agardh) Gmelin *sensu* Yamamoto in Japan and Korea (Okamura 1915, Yamamoto 1978, Kim et al. 2008). This history of *G. parvispora* in East Asia contradicts Abbott's (1999) suggestion that *G. parvispora* is endemic to Hawaii. According to Nelson et al. (2009), the earliest herbarium specimen at the Bishop Museum was collected in 1908, and there was no Hawaiian name for this species. It has been available in Hawaiian fish markets since about 1945, and its Hawaiian name, "Long Ogo", comes from its Japanese name "Ogo Nori". Nelson et al. (2009) reported that it was likely introduced to Hawaii, starting in 1885, by Japanese contract workers brought in to tend sugarcane fields. Here, we propose the possible human-mediated introduction of *G. parvispora* in northwest Mexico because *G. parvispora* was not reported at Oaxaca-Chiapas in the south-central Mexican Pacific before 1999 (Dreckmann 1999), and there were no heterotypic synonyms for this species in Mexico (Dreckmann and Sentiés 2009). The identical *rbc*L haplotype between Hawaii and Mexico implies that the origin of the Mexican populations is likely Hawaii. However, two different haplotypes in the Mexican populations may indicate possible multiple introductions from Hawaii and/or East Asian waters. The plants collected in Baja California occurred in sandy and rocky habitats from intertidal areas down to a depth of 1.5 m, as in Hawaii (Abbott 1999).

Gracilaria parvispora is the second invasive species of the genus reported in the northwestern Mexico after *Gracilaria vermiculophylla*. Both have been found forming extensive mats and were found in stomach samples of green turtles (*Chelonia mydas* Linnaeus) in the coastal

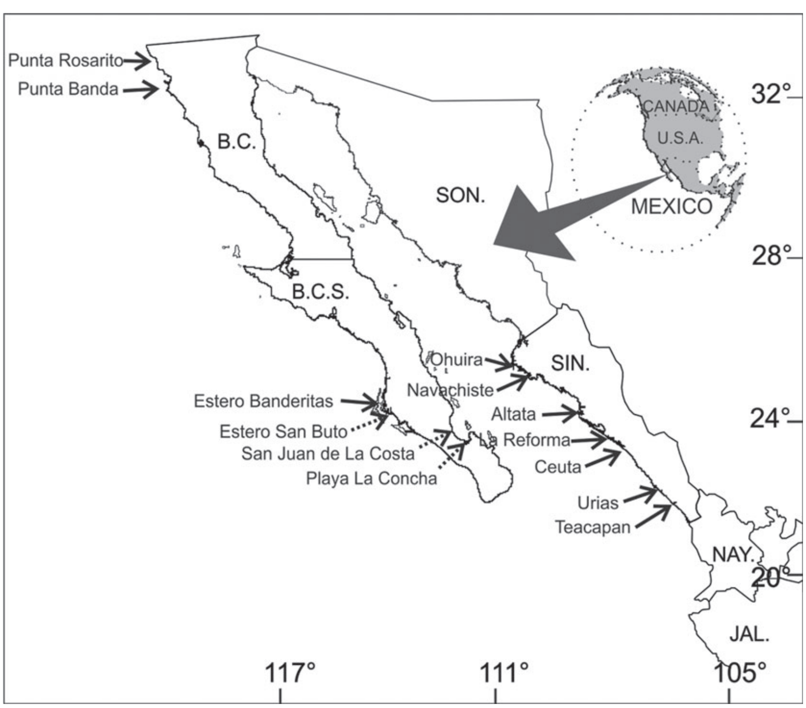


Figure 6 Geographical distributions of *Gracilaria parvispora* (dashed arrow shafts) and *Gracilaria vermicullophylla* (solid arrows) on the northwestern Mexico coastline (Pacheco-Ruíz and Aguilar-Rosas 1984, Ochoa-Izaguirre et al. 2002, Bellorin et al. 2004, Talavera-Sáenz et al. 2007, Riosmena-Rodríguez et al. 2010, Miller et al. 2011).

lagoons of Baja California, as described by López-Mendilaharsu et al. (2008), which suggests that the species are distributed in deeper areas. The geographical distribution of *G. parvispora* is patchy (Figure 6); it occurs only in certain coastal lagoons with high monthly nutrient concentrations and located near high-density human populations. This is true for Hawaiian populations that are only found in areas of local nitrogen enrichment from anthropogenic sources in Hawaii (Nelson et al. 2009).

A similar trend is present in the known records of *G. vermiculophylla* (Figure 6). Although collections were made in many coastal lagoons, e.g., Bahia Magdalena, San Ignacio on the Pacific Coast of Baja California and Sinaloa and Baja California Sur in the Gulf of California (Ochoa-Izaguirre et al. 2007), the molecular identification of *G. vermiculophylla* is not yet available for the southern Mexican populations. It will be necessary to perform further studies to confirm records of *G. vermiculophylla* because its habit is similar to that of *G. parvispora*.

Two molecular markers (*rbc*L and *cox*1) showed that the Mexican populations are close to the Hawaiian populations and distant from the Korean populations. This result likely relates to the similarity in environmental conditions, such as seawater temperatures between Hawaii and Baja California. However, there are many missing haplotypes within the Mexican populations. More extensive sampling will highlight the genetic structure of *G. parvispora* in the eastern North Pacific region.

Gracilaria parvispora is the 13th seaweed species introduced to Baja California (see table 1 in Miller et al. 2011), and this is the first demonstration of a second invasive *Gracilaria* species based on molecular and morphological data (the other being *G. vermiculophylla*) from the Baja California region. Because it is one of the most popular edible seaweeds in Hawaii and a popular species for marine aquaria (Glen et al. 1996, Abbott 1999, http://marineplantbook.com/marinebookgracilaria-parvis.htm), *G. parvispora* may be transported by people for seaweed salads, marine aquaria or tests for mass cultivation in Baja California. Because of climate change, including the frequency and severity of El Niño/Southern Oscillation events that may increase habitat suitability for non-native species (Williams and Smith 2007), ecological monitoring of introduced seaweeds in Baja California is consistently needed for maintenance and conservation of healthy shore communities (Riosmena-Rodríguez et al. 2012).

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