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How different is Mediterranean *Caulerpa taxifolia* (Caulerpales: Chlorophyta) to other populations of the species?

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ABSTRACT: The green macroalgal species *Caulerpa taxifolia* is indigenous to tropical/subtropical Australia, ranging as far south as 28° and 29° 15′ S on the Australian mainland east and west coasts, respectively. The origin of disjunct populations of the species, discovered in 2000 on the Australian mainland east coast at localities to 35° S remains unknown, variously attributed to introduced exotic strains or range extensions from other eastern Australian populations. Some naturally occurring Australian populations of *C. taxifolia* are similar to Mediterranean *C. taxifolia*. In Australia, large broad forms of the species, which have been known in the region since 1860, grow luxuriantly in sheltered seagrass meadows, with some of these populations tolerating minimum surface seawater temperatures in winter of 12.5 to 14.5°C. Accordingly, the contention that the Mediterranean has been invaded by a genetically-modified, large, cold-adapted strain of *C. taxifolia* may be incorrect. It is crucial that genetic markers (DNA fingerprinting, microsatellites) sensitive at the population level are used to accurately determine the genetic relatedness of *C. taxifolia* populations.

KEY WORDS: Australia · *Caulerpa taxifolia* · Geographic distribution · Invasive species · Seaweed · Macroalga

INTRODUCTION

The marine green macroalga *Caulerpa taxifolia* (Vahl) C. Agardh has gained notoriety over the last two decades as an invasive species, most notably in the Mediterranean Sea, but more recently on other continents, including Australasia (Jousson et al. 2000). Since it was first discovered in 1984 near the Musée Océanographique, Monaco (Meinesz & Hesse 1991), *C. taxifolia* has spread to cover approximately 4700 ha of the Mediterranean seabed at more than 100 localities in Monaco, France, Italy, Spain and Croatia (Meinesz et al. 1998). Although the source population for the Mediterranean invasion has not been conclusively identified (Olsen et al. 1999), the presence of *C. taxifolia* in the region is currently attributed to either an aquarium escape or to a range extension by Lessepsian immigrant populations of the eastern Mediterranean. Meinesz & Hesse (1991), Meinesz & Boudouresque (1996) and Jousson et al. (1998) maintain that *C. taxifolia*, used as a decorative alga in public aquaria, was accidentally released into the sea near the Monaco Aquarium in the early 1980s. Alternatively, Chisholm et al. (1995) argued that *C. taxifolia*, possibly misidentified as a form of the morphologically somewhat similar *Caulerpa mexicana* Sonder ex Kützing, which has been present in the eastern Mediterranean as a Lessepsian immigrant from the Red Sea since the 1940s (Rayss 1941), had more recently dispersed to the western Mediterranean. The latter hypothesis has been challenged by studies of nuclear rDNA internal transcribed spacer (ITS) sequences (Olsen et al. 1998) and allozymes (Benzie et al. 2000), which have demon-

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strated that *C. taxifolia* and *C. mexicana* are separate entities. However, it remains possible that some populations of *C. mexicana* recorded from the Mediterranean, which were not investigated in above molecular studies, could be the misidentified *C. taxifolia* referred to by Chisholm et al. (1995) and Chisholm & Jaubert (1999).

Although *Caulerpa taxifolia* is reported to be widely distributed in the tropical Atlantic (Taylor 1960, Wynne 1986, 1998, Lawson & John 1987), Indian (Silva et al. 1996) and Pacific Oceans (Harvey 1860, Cribb 1958, Silva et al. 1987), the geographical range of the species in Australia has not previously been comprehensively documented in the literature. *C. taxifolia* has been reported from the eastern Australian coast (Harvey 1860, Lucas 1931, Cribb 1958, Price et al. 1976, Ngan & Price 1979, 1980a,b, Saenger 1979, Cribb 1996) and offshore in the South Pacific Ocean at Lord Howe Island, New South Wales (NSW) (Lucas 1935, Millar & Kraft 1994). Unfortunately, these records, some published decades ago in specialist phycological literature, are often overlooked. There is no comprehensive flora for Australian tropical macroalgae which would provide readily accessible distributional data for the species in Australia. It is therefore not surprising that comparisons of the similarities between Mediterranean and Moreton Bay populations of *C. taxifolia* (Pillen et al. 1998, Benzie et al. 2000) fuelled speculation of a recent introduction of the species into subtropical eastern Australia. Recent discoveries of disjunct populations of *C. taxifolia* on the NSW mainland coast, up to 800 km south of the species' southern distribution limit on the Australian continent, renewed the introduction debate and highlighted the need for detailed knowledge of the species in Australia for the purposes of developing management strategies for this potentially

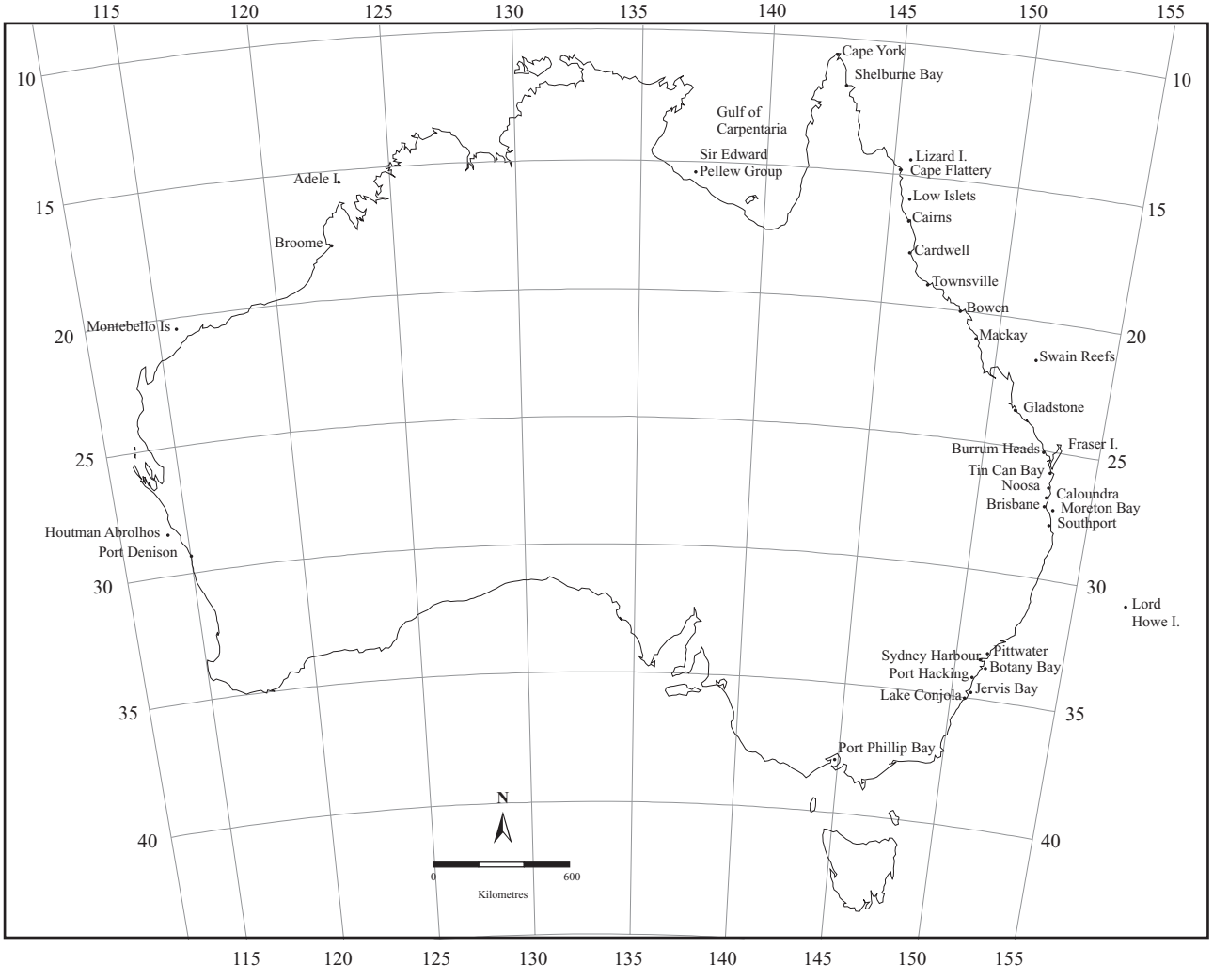

Fig 1. *Caulerpa taxifolia.* Geographic distribution in Australia

invasive alga. Despite the lack of published information, many specimens of Australian *C. taxifolia* are housed in Australian and European herbaria and many recent collections have been documented by one of us (I.R.P.) during a revision of the Australian representatives of the genus. This paper aims to clearly establish that *C. taxifolia* is indigenous to tropical/subtropical Australia, to document the geographical range of the species in Australia based on collections since 1855, to confirm determinations of herbarium specimens, to discuss intraspecific morphological variation and to provide an accurate scientific basis for further research on and management of the species in Australia. Furthermore, data on naturally occurring Australian and other tropical/subtropical populations of *C. taxifolia* may be useful in managing invasions of the species elsewhere, particularly in determining whether Mediterranean populations are markedly different to other populations of the species.

METHODS

Collections of *Caulerpa taxifolia* housed in most Australian and major European herbaria, as well as recent field collections and observations by various workers (including I.R.P.) were studied in order to confirm specimen identifications, to describe the morphological variability exhibited by the species and to fully document the geographical distribution of the species in Australia. Herbarium collections of *C. taxifolia* from Australia have been accrued over many decades, the result mostly of opportunistic collecting, less often from planned systematic ecological surveys or monitoring programs. In order to describe some of the important morphological variability of *C. taxifolia* in Australia, frond height and breadth measurements were recorded from herbarium specimens.

RESULTS AND DISCUSSION

Caulerpa taxifolia is indigenous to tropical/subtropical Australia, evident from the many collections in the region (Figs. 1 & 2, Table 1), particularly those from the widely disparate localities of Cape York, Cardwell, Bowen and Caloundra on the eastern Australian coast, made 80 to 145 yr ago at the time of some of the earliest algal collections in subtropical/tropical Australia. This natural occurrence is also consistent with the observations that macroalgal species are generally not good dispersers across ocean basins (van den Hoek 1987) and that the biology of *C. taxifolia* hinders transoceanic, human-meditated dispersal of the species. *C. taxifolia* is not a fouling organism of ship hulls,

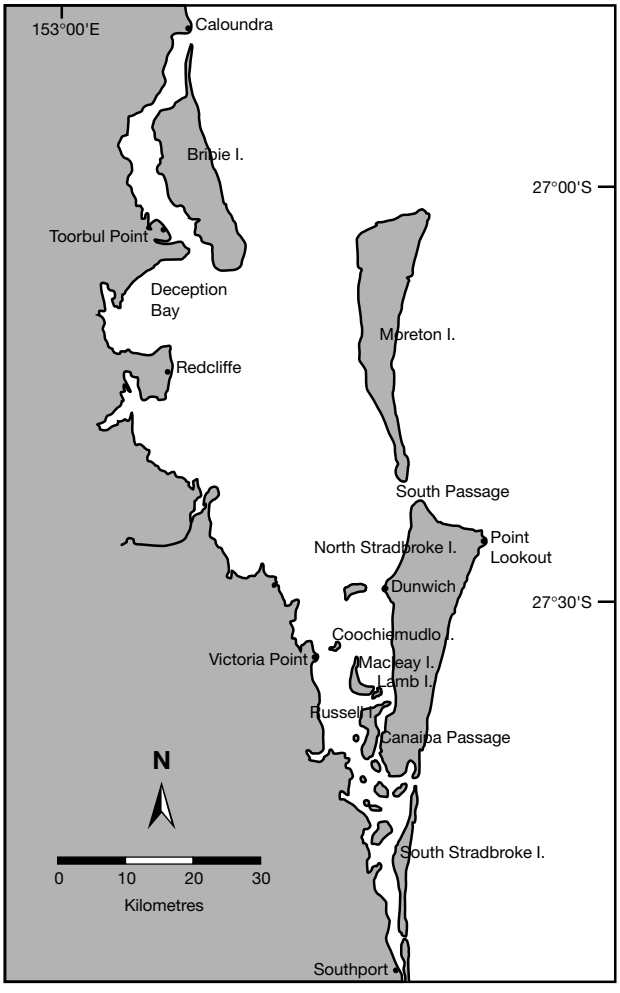

Fig. 2. *Caulerpa taxifolia.* Distribution of in subtropical Moreton Bay on the eastern Australian coast

a common method for the global transport of some exotic marine macroalgal species since the 19th century (Adams 1983, Nelson 1999), and there is little evidence to establish whether or not mature thalli, gametes, zygotes or the microscopic diploid stage would be viable after deballasting by ships following extended periods of darkness in ballast tanks. There is also no evidence for the accidental introduction of *C. taxifolia* when transporting invertebrate species to foreign mariculture facilities, a practise which has introduced many exotic macroalgal species to other continents since the early 1900s (Ribera & Boudouresque 1995). Rather, transport of living thalli by the aquarium trade seems to be the most probable method of dispersal, consistent with the first observation of *C. taxifolia* in the Mediterranean near the aquarium at Monaco in the early 1980s (Meinesz & Hesse 1991, Meinesz & Boudouresque 1996, Jousson et al. 1998).

Table 1. *Caulerpa taxifolia*. Selected herbarium specimens from Australia (nd: no data; herbarium abbreviations: AD, State Herbarium of South Australia; BM, Natural History Museum, London; BRI, Queensland Herbarium; HBG, Herbarium, Institut für Allgemeine Botanik, Hamburg; JCT, Herbarium, James Cook University, Townsville; LD, Botanical Museum, Lund; MEL, National Herbarium of Victoria; MURU, Herbarium, Murdoch University, Western Australia; NSW, National Herbarium of New South Wales; PERTH, West Australian Herbarium; TCD, Herbarium, Trinity College, Dublin)

Locality	Date of collection	Collector	Herbarium number	Morphological form	Habitat
Queensland					
Albany Is., Cape York	1855	F. Müller	TCD[a]	Broad	nd
Cape York	1866	E. Daemel	MEL 689701	Intermediate	nd
	1874	Moseley	BM[a]	Fragments only	nd
Bowen region					
Cape Gloucester	pre-1871	F. Kilner	BRI 701670	Broad	nd
Stone Is.	pre-1871	F. Kilner	MEL 677361	Intermediate	nd
Cape Upstart	pre-1871	nd	MEL 689703	Narrow	nd
Kings Beach	20 May 1962	A.B. Cribb	BRI 701129	Intermediate	nd
Fraser Is.	1885	A. McDonald	MEL 689705-9	Intermediate	nd
Caloundra	pre-1915	R.A. Bulcock	BRI 701666	Narrow	Wave exposed rocky coast
	1909	A.H.S. Lucas	NSW[a]	Narrow	Wave exposed rocky coast
	1916	T.H. Johnston	NSW[a]	Narrow	Wave exposed rocky coast
	10 Apr 1948	A.B. Cribb	BRI 701723	Narrow	Wave exposed rocky coast
	30 Apr 1949	G. McKeon	BRI 701128	Narrow	Drift
	19 May 1955	A.B. Cribb	BRI 701685	Narrow	Wave exposed rocky coast
	13 Apr 1957	A.B. Cribb	BRI 701680	Narrow	Wave exposed rocky coast
	5 Feb 1996	J. Phillips	BRI 716031	Narrow	Wave exposed rocky coast
Cardwell	Oct 1909	H. Newport	BRI 701668	Narrow	Sheltered passage
Southport-Nerang R	2 Jan 1946	A.B. Cribb	BRI 701676	Broad	Sheltered estuary
Lands End	11 May 1950	A.B. Cribb	BRI 701676	Broad	Sheltered estuary
Stradbroke Is.					
Point Lookout					
Frenchmans Beach	28 Dec 1948	G. McKeon	BRI 701683	Narrow	Drift
Deadmans Beach	13 Aug 1949	G. McKeon	BRI 701684	Narrow	Wave exposed rocky coast
Camel Rock	11 Aug 1949	G. McKeon	BRI 701682	Narrow	Wave exposed rocky coast
Cylinder Headland	10 Jul 1995	J. Phillips	BRI 705484	Narrow	Wave exposed rocky coast
Dunwich	May 1951	H.B.S. Womersley	AD A16313	Broad	Sheltered bay
	8 Jul 1995	J. Phillips	BRI 715494	Broad	Sheltered bay
	3 Jun 2000	J. Phillips	BRI 717424	Broad	Sheltered bay
Canaipa Passage,	16 May 1950	A.B. Cribb	BRI 701671	Broad	Sheltered bay
Moreton Bay	20 Oct 1961	J. Kearns	BRI 701126	Narrow	Sheltered bay
	5 Oct 2000	M. Davidson	BRI 717418	Broad	Sheltered bay
Noosa	23 May 1949	A.B. Cribb	BRI 700992	Narrow	Wave exposed rocky coast
	12 Apr 1954	A.B. Cribb	BRI 701679	Narrow	Wave exposed rocky coast
	4 Jun 1966	W.K. Smith	BRI 701127	Very narrow	Wave exposed rocky coast
Low Islets, northern Great Barrier Reef	15 Aug 1954	A.B. Cribb	BRI 701689	Narrow	In moat on reef flat
Tannan, near Gladstone	17 Aug 1955	A.B. Cribb	BRI 701681	Intermediate	Semi-sheltered coast
Ball Bay, near Mackay	22 May 1956	A.B. Cribb	BRI 711688	Intermediate	Sheltered bay
Shoal Point, north of Mackay	17 Aug 1970	I.R. Price	JCT A2141	Broad	Semi sheltered coast

Table 1 (continued)

Locality	Date of collection	Collector	Herbarium number	Morphological form	Habitat
Cape Flattery, Cooktown	1 May 1973	A.W.D. Larkum	JCT A2831	nd	nd
Lizard Is.	15 Nov 1973	I.R. Price	JCT A 8239	Broad	Sheltered site
Townsville	5 Dec 1978	I.R. Price	BRI 701675	Narrow	nd
	14 May 1994	I.R. Price	JCT A8252	Intermediate	nd
Victoria Point, Moreton Bay	28 Jan 1983	A.B. Cribb	BRI 701122	Broad	Sheltered bay
Toorbul Point	22 Sep 1983	A.B. Cribb	BRI 701121	Broad	Sheltered passage
Coolum	24 Apr 1986	A.B. Cribb	BRI 701120	Narrow	Wave exposed rocky coast
	16 Jun 2000	J. Wallis	BRI 717419	Narrow	Wave exposed rocky coast
Shellburne Bay	May 1992	T. Wassenberg	BRI 715310	Broad	Sheltered bay
Tin Can Bay	Sep 1992	J. Horrocks	BRI 715306	Intermediate	Sheltered bay
Burrum Heads	1 Oct 1997	J. Phillips	BRI 717420	Narrow	Sheltered estuary
Coochiemudlo Is., Moreton Bay	2 Jul 1997	J. Phillips	BRI 717421	Intermediate	Semi sheltered coast
Deception Bay, Moreton Bay	8 Mar 2001	L. Carseldine	BRI 740436	Broad	Sheltered bay
New South Wales					
Lord Howe Is.	May 1933	F Perrin & AHS Lucas	NSW A11413	Intermediate	Outer reef
Port Hacking	12 May 2000	B. Schaffelke	BRI 717423	Narrow	Sheltered estuary
Northern Territory					
Sir Edward Pellew Group	nd	E. Daemel	HBG	nd	nd
Western Australia					
Port Denison	14 Dec 1971	G.T. Kraft	AD A41168	Intermediate	Jetty pylons
North Is., Houtman Abrolhos	3 May 1960	R.D. Royce	PERTH 03985369	Intermediate	Subtidal, 40 m depth
Hermit Is., Montebello Is.	11 Jul 1992	J. Huisman	MURU A161	nd	nd
Broome	25 May 1967	J.R. Maconochie	AD A31896	Broad	Sublittoral pools
	nd	K.P. Foulkes	PERTH 02574268	Broad	Subtidal, 15 m depth
Adele Is.	8 Jul 1990	R.F. Kenneally	PERTH 01210084	Intermediate	Fringing reef

[a]Herbarium specimens not numbered

This initial localised occurrence of *C. taxifolia* in the Mediterranean, followed by the relatively rapid spread by short-distance transport of thallus fragments entangled in boating gear and fishing nets (Meinesz 1992, Sant et al. 1996, Ceccherelli & Cinelli 1999, Smith & Walters 1999), fits the scenario of an invasion, contrasting markedly to the wide distribution pattern for Australian *C. taxifolia* documented over almost 150 yr. Although it is clear that indigenous populations of *C. taxifolia* are widespread in Australia, reports of similarities between some Australian and Mediterranean populations raise the possibility of recent introductions of exotic strains into Australia.

Caulerpa taxifolia is a common species in tropical/subtropical eastern Australia, occurring along the mainland coast, on the Great Barrier Reef (GBR) and on offshore islands, from Cape York (11° 54′ S, 142° 15′ E) to Southport (28° 00′ S, 153° 20′ E). The many collections of *C. taxifolia* made in Queensland during the late 19th and early 20th centuries, a period when the state was sparsely populated and when algal collections were usually made by foreign or amateur collectors, indicate that the species was relatively common at that time. Harvey (1860, Plate 178) was first to publish the occurrence of *C. taxifolia* for Australia, the record based on specimens collected at Albany Island, near Cape York in August, 1855 by the Victorian Government botanist Baron F. von Müller, during his participation on A. C. Gregory's North Australia Expedition (1855 to 1856) (Gregory 1884). Sonder (1871, 1881) and Lucas (1931) also cite specimens sampled by the plant collectors E. Daemel and F. Kilner from Cape York and the Bowen region, respectively, and early unpublished herbarium records locate the species at Cardwell in the tropics, at Fraser Island in the subtropics and even further south at Caloundra on the northern boundary of Moreton Bay (Figs. 1 & 2, Table 1). The Caloundra collections were made by A. H. S. Lucas, the first resident Australian phycologist in 1909 during an expedition

from Sydney and by the naturalist R. A. Bulcock. The label on the undated Bulcock specimen sheet was written by F. M. Bailey, the Colonist Botanist of Queensland (A. Bolin, Queensland Herbarium, pers. comm.), evidently before Bailey's death in 1915. Since the late 1940s, phycologists resident in Queensland have reported *C. taxifolia* from Noosa and Moreton Bay (Cribb 1958), Swain Reefs (southern GBR) (Saenger 1979), the Townsville region (Ngan & Price 1979, 1980a,b) and Lizard Island (northern GBR) (Price et al. 1976); these published records represent only a small proportion of the Queensland collections lodged in herbaria (Table 1). Many Queensland collections, including the 1951 collection from the Dunwich population that has been considered similar to Mediterranean populations (Pillen et al. 1998, Benzie et al. 2000, Chisholm et al. 2000), were made well before *C. taxifolia* was reported to be an invasive species in the Mediterranean.

In contrast to the Queensland coast, records of *Caulerpa taxifolia* from the tropical northern and western Australian coasts are limited to 1 published record from the Montebello Islands, Western Australia (WA) (Huisman 2000). Herbarium collections document the geographical range of *C. taxifolia* on the western Australian coast further south to Port Denison (29° 15′ S, 114° 56′ E), and provide 3 more records for WA and the only record, from the Sir Edward Pellew group (15° 33′ S, 114° 04′ E) in the southwestern Gulf of Carpentaria, for the Northern Territory (Fig. 1, Table 1). This apparent rare occurrence of the species on northern and western Australian coasts very likely reflects the paucity of algal collections in these remote regions, which still remain relatively thinly settled and poorly studied scientifically. Prior to a recent publication which reported some macroalgal collections from tropical WA (Huisman 2000), only 28 marine macroalgal species had been recorded from this coastline, which is several thousand kilometres in length and for which records of at least 300 species could be expected (Huisman et al. 1998). The wide distribution of *C. taxifolia* in tropical seas (Harvey 1860, Weber-van Bosse 1913, Silva et al. 1996), including in regions to Australia's immediate north such as Indonesia (Weber van Bosse 1898, 1913, Coppejans & Prud'Homme van Reine 1992), also suggests that *C. taxifolia* is probably more widespread on tropical northern and western Australian coasts than collections for the region presently indicate.

The discovery in 2000 of disjunct populations of *Caulerpa taxifolia* in the Pittwater (33° 38′ S, 151° 18′ E), in Port Hacking (34° 06′ S, 151° 10′ E) and in Lake Conjola (35° 16′ S, 150° 30′ S) on the central mainland coast of NSW, locates the species up to 800 km further south than its previous southern distributional limit on the Australian mainland east coast, at Southport (28° 00′ S, 153° 20′ E) and thus represents a significant range extension for *C. taxifolia* on the Australian mainland east coast. It is unlikely that *C. taxifolia* had been overlooked on the NSW coast, which has been relatively well studied phycologically since the early 1900s, particularly since southern outlier populations of the species had been previously reported from the oceanic Lord Howe Island (31° 33′ S, 159° 05′ E) (Lucas 1935, Millar & Kraft 1994), which is remote from, but politically part of NSW. Lord Howe Island is more strongly influenced by the warm East Australian Current than the mainland coast, which results in warmer (17 to 25°C annually) surface seawater temperatures (SSTs) (Allen & Paxton 1974) than would normally be experienced at such a high latitude, including the warm temperate mainland coast of NSW (see Womersley 1984), where the new populations of *C. taxifolia* have been discovered. Lord Howe Island is regarded as a tropical outpost in the South Pacific Ocean, supporting probably the world's southernmost coral reef (Allen & Paxton 1974), many tropical macroalgal species (Millar & Kraft 1994) and hermatypic corals (Harriott et al. 1995).

The occurrence of *Caulerpa taxifolia* at regular intervals along the eastern Australian coast from tropical Cape York to subtropical Southport and also as far south as subtropical Port Denison on the western Australian coast indicates that it is not a strictly tropical species as has often been stated (Meinesz & Boudouresque 1996, Komatsu et al. 1997, Jousson et al. 2000), but rather belongs to a large group of macroalgal species that have a tropical to warm temperate distribution pattern. *C. taxifolia* has previously been reported from warm temperate Bermuda (32° N) (Taylor 1960) and the Gulf of Suez (28 to 30° N) (Chisholm et al. 2000). Furthermore, the genus *Caulerpa* is not a strictly tropical genus, with 8 of the 12 species (forms and varieties not considered) recorded for Queensland, ranging from the tropics to subtropical Moreton Bay (Phillips 1997). Three of these species (*Caulerpa brachypus* Harvey, *C. lentillifera* J. Agardh and *C. peltata* Lamouroux) have a similar distribution in the Indian Ocean, where they range as far south as South Africa (Silva et al. 1996).

Strictly tropical macroalgal species are stenothermal, having a lower temperature tolerance limit of 18 to 20°C, which corresponds to the 20°C winter seawater isotherm (Pakker et al. 1995, 1996). This isotherm occurs on the Australian east coast near 23° S latitude (Middleton 1995), approximately 550 km north of Southport, the pre-2000 southern distribution limit of *Caulerpa taxifolia* on this coast. On the Australian west coast, the 20°C winter seawater isotherm appears on SST maps (see Middleton 1995) to be located at 29° S,

but this reflects the warming effect of the offshore winter southward-flowing Leeuwin Current, a phenomenon also responsible for the higher SSTs offshore Houtman Abrolhos (28° 43′ S). Inshore waters at the same latitude, which are not influenced by this current, have SSTs 4 to 7°C lower (Dakin 1919), and consequently the extent of truly tropical waters inshore is even further north, at 22° S (Morgan & Wells 1991). Macroalgal species with tropical to warm temperate distribution patterns have a lower temperature tolerance limit of 10 to 15°C (Cambridge et al. 1987, 1990a,b, Breeman 1988, Lüning 1990, Pakker et al. 1996), and these temperature limits correlate well with the distributional limits of *C. taxifolia* in the Moreton Bay region on the east coast and Port Denison on the west coast. Moreton Bay experiences an annual SST variation of 14.5 to 27.5°C (Endean et al. 1956), although a greater annual SST variation (12.5 to 32°C) was reported during a coral study in shallow eastern bay waters (Johnson & Neil 1998) where *C. taxifolia* is common (J. Phillips pers. obs). Winter minimum SSTs in Moreton Bay are similar to winter temperatures reported for the Mediterranean Sea, and these temperatures are also consistent with the lower lethal temperature limit of 10 to 13°C for Mediterranean *C. taxifolia* (Meinesz & Hesse 1991, Komatsu et al. 1997) and of 9 to 11°C for *C. taxifolia* from Moreton Bay (Chisholm et al. 2000). These observations further support the challenge by Chisholm et al. (2000) contesting the assertion that Mediterranean populations of *C. taxifolia* are composed of genetically modified, cold-adapted strains (Meinesz & Hesse 1991, Komatsu et al. 1997, Jousson et al. 2000).

The mainly sporadic collecting of macroalgae along much of the tropical/subtropical Australian coast has resulted in the limited published data on the abundance of *Caulerpa taxifolia* in tropical/subtropical Australia. In tropical northern Queensland, *C. taxifolia* is locally abundant in winter and spring, usually occurring in the lower intertidal zone on wave-exposed rocky shores along the mainland coast in the Townsville region as well as on hard substrata on reef flats of the GBR (Ngan & Price 1980a,b, I. R. Price pers. obs.). In southern Queensland, at the wave exposed localities of Coolum, Caloundra and Point Lookout, *C. taxifolia* is not common, growing in the sublittoral fringe and subtidally attached to rocks covered by an algal turf (J. Phillips pers. obs.). The abundance of *C. taxifolia* in sheltered Moreton Bay is variable, the species appearing to be more abundant in the eastern bay, where it has been noted during seagrass surveys. On Macleay, Lamb and Russell Islands, *C. taxifolia* forms a monospecific narrow band, slightly deeper than the adjacent intertidal *Zostera*/*Halophila* seagrass community (FRC Coastal Resource and Environmental 1996). On channel edges near Moreton Island, on the Aldershot Banks, off South Stradbroke Island (as *Caulerpa mexicana*, Young & Kirkman 1975) and at Dunwich, North Stradbroke Island (Pillen et al. 1998), the species grows subtidally with the seagrass *Halophila spinulosa* (R. Br.) Aschers. The density of the erect fronds of *C. taxifolia* in dense stands at Dunwich is slightly less at 4183 ± 1370 fronds m^{-2} (Pillen et al. 1998), than the density (5100 to 13 920 primary fronds m^{-2}) reported for Mediterranean populations of the species (Meinesz et al. 1995).

Thalli of the western Mediterranean *Caulerpa taxifolia* have been considered to be much larger than those of tropical strains of the species (Meinesz & Hesse 1991, Meinesz et al. 1995). However, large broad forms of this morphologically variable species are not of recent origin, having long ago been reported by Harvey (1860) from Albany Island, Australia, and from abundant collections in Ceylon (Sri Lanka) and the Friendly Islands (Tonga). Fronds of the Albany Island specimens reported by Harvey are 13 to 14.5 cm long and 1.7 to 2 cm broad. Sonder (1871) reported specimens from Cape York, Albany Island and Bowen as *C. taxifolia* var. *asplenioides* Harvey, the 'var. *asplenioides*' used during the 19th century to denote the broad form of the species. Børgesen (1907) reported erect fronds of *C. taxifolia* from St Jan, West Indies, growing at 30 m depth to be '16 cm or more' long and 1.5 cm broad.

The broad form of *Caulerpa taxifolia* is found at many localities in Queensland (Table 1) and is only 1 morphotype expressed by the species in this geographical region. Although there is some variation within any given population, broad forms of *C. taxifolia* generally occur on unconsolidated substrates in sheltered bays and estuaries along the whole coastline, intermediate forms occur in habitats exposed to moderate wave action, as on the mainland coast bordering the GBR lagoon, and narrow forms inhabit the shallow sublittoral zone on wave-exposed coasts in southern Queensland and on the outer reef edges in the GBR system. Harvey (1860), Børgesen (1907) and Cribb (1958) also described similar correlation between thallus size and habitat for *C. taxifolia* from Tonga, West Indies, and southern Queensland, respectively. Although various different morphological forms of *C. taxifolia* (e.g. narrow and broad) can be recognised, variation in frond size is continuous, grading from one form to another. Australian specimens of *C. taxifolia* we examined varied from 1.5 to 20 cm in frond length and from 2 to 20 mm in frond breadth, although Cribb (1996) reported frond lengths up to 30 cm for broad forms growing in Moreton Bay. Generally, narrow Australian forms have fronds 2 to 10 cm long and 2 to

5 mm broad, fronds of intermediate forms are 2 to 10 cm long and 6 to 9 mm broad and fronds of broad forms are 5 to 20 cm long and 10 to 20 mm broad. Tropical Queensland specimens tended to be typically smaller than southern Queensland plants, usually attaining a maximum length and breadth of 15 cm and 15 mm, respectively.

The recent discovery of *Caulerpa taxifolia* in New South Wales, well outside of the documented pre-2000 geographical range of the species in Australia, caused considerable concern among phycologists and government departments responsible for managing the marine environment. Although it is now evident that *C. taxifolia* is indigenous to tropical/subtropical Australia, it has not yet been possible to determine whether the populations from mainland NSW represent an introduction from outside Australia, possibly released into the wild by aquarium hobbyists, or a significant range extension sourced from Queensland populations either via intermittent incursions inshore of East Australian Current waters or by human-mediated dispersal. Distinguishing between indigenous and exotic populations of the same species is difficult. In such circumstances, proof of an introduction of exotic populations of *C. taxifolia* cannot be based solely on large or increasing population size since *Caulerpa* species are known to exhibit marked fluctuations in population size, both in the Mediterranean (*C. prolifera* [Forskål] Lamouroux and *C. racemosa* [Forskål] J. Agardh; Meinesz et al. 1995, Chisholm & Jaubert 1999 and references therein) and in Australia.

There is ample evidence that several of the more than 20 species of *Caulerpa* recorded for Australia can be locally abundant, particularly in bays and estuaries close to large population centres. The southern Australian endemic species, *C. remotifolia* Sonder and *C. longifolia* C. Agardh, which are common at many localities in the Port Phillip Bay, Victoria (King et al. 1971), were, together with the cosmopolitan *Ulva lactuca* L., community dominants in the upper subtidal zone near the then major sewage outfall for Melbourne at Werribee (Axelrad et al. 1981). Unlike many other algal species, such as the kelp *Ecklonia radiata* (C. Agardh) J. Agardh, *C. remotifolia* and *C. longifolia* did not disappear from, but flourished in habitats near the outfall. The Indian Ocean *C. scalpelliformis* (R. Brown ex Turner) C. Agardh, which in Australia ranged from Perth on the western Australian coast along the south coast to Jervis Bay on the Australian east coast (Womersley 1984), has recently extended its geographical range by approximately 150 km to become locally abundant in Botany Bay (Davis et al. 1997). *C. filiformis* (Suhr) Hering, which was first reported for Australia in 1927 from a single locality in Botany Bay and as drift in Sydney Harbour (Lucas 1927, as *C. ligulata* Harvey), had originally been described from South Africa almost a century earlier (Suhr 1834). Subsequently, May (1976) reported the species as locally dominant at numerous other locations in the Sydney region and attributed the increase in abundance to either acclimation and spread of an introduced species or to an increasing volume of sewage discharged in the area over the previous 20 years. The likelihood of the former hypothesis appeared to be diminished by a study of nuclear ITS sequences, which demonstrated that Australian and African populations of *C. filiformis* were sufficiently different to be regarded as 2 distinct species (Pillmann et al. 1997). However, the introduction hypothesis cannot be totally discounted, because the few African populations of *C. filiformis* sampled may not have included the source population of any putative introduction (Dr G. Zuccarello pers. comm.). A dense population of *C. taxifolia* at Dunwich, Moreton Bay, has been reported as expanding (Pillen et al. 1998), but as no prior quantitative data exist and the population apparently was only sampled once, the claimed increase in population size cannot be substantiated, particularly since dense populations of *C. taxifolia* were observed during seagrass surveys in eastern Moreton Bay 3 decades ago (Young & Kirkman 1975).

Molecular genetics may provide the means to determine whether exotic populations of *Caulerpa taxifolia* occur in Australia, and if they coexist and can hybridise with Australian indigenous populations of the species. Molecular genetic markers such as allozymes (Benzie et al. 1997) and sequences of the rDNA ITS region (Pillmann et al. 1997, Olsen et al. 1998) have been used successfully to distinguish different species of *Caulerpa*, but these markers lack the resolution necessary to differentiate populations of a species, providing only inconclusive results when applied to population level studies of *C. taxifolia* (Jousson et al. 1998, 2000, Benzie et al. 2000). Macroalgal species generally have low levels of electrophoretically detectable genetic variation at the population level (Sosa & Lindstrom 1999), a feature which also applies to *C. taxifolia* (Benzie et al. 1997, 2000). Limited intraspecific variability of the rDNA ITS region has normally been detected using DNA sequence information, indicating that this type of information is inadequate for determining population structure and for distinguishing different *C. taxifolia* populations (Hillis et al. 1996, Olsen et al. 1998, 1999).

Developing management protocols for Australian *Caulerpa taxifolia* relies on establishing if exotic strains have been introduced and then differentiating indigenous from exotic populations of the species. No systematic studies have been undertaken to determine the population structure of *C. taxifolia* anywhere in the world, although these data are an essential prerequi-

site before conclusive statements can be made about migration and introduction of *C. taxifolia* strains outside their natural geographical range. High-resolution genetic markers (DNA fingerprints, microsatellites), which would enable detailed analysis of polymorphism in macroalgae at the intraspecific level, have not as yet been applied to *C. taxifolia* populations, even though these techniques have been used on populations of other macroalgal species. The use of such molecular genetic markers becomes especially powerful in combination with a well thought-out and rigorous field-sampling program of various populations aimed at describing the full extent of genotypic diversity in a species, vital information that previous molecular studies on *C. taxifolia* have failed to establish. It is only after these criteria have been incorporated into molecular studies that possible relationships between eastern Australian and Mediterranean populations (Pillen et al. 1998, Benzie et al. 2000, Jousson et al. 2000) can be conclusively evaluated.

The present paper clearly demonstrates the need to undertake studies on naturally occurring populations of invasive species, in order to gain an accurate perspective on the biology of the species. We have shown that Mediterranean populations of *Caulerpa taxifolia* are not markedly different to some Australian tropical/subtropical populations of the species. Natural populations of *C. taxifolia* generally exhibit considerable size variation, including a broad form which has been reported from tropical oceans for nearly 150 yr and which is comparable in its morphology to the Mediterranean form. From its geographic distribution on Australian coasts, it is obvious that *C. taxifolia* is not a strictly tropical species, but ranges south into the subtropics, the southernmost populations experiencing similar SSTs to those in the Mediterranean Sea. Furthermore, the broad form of *C. taxifolia* is abundant in seagrass meadows in Moreton Bay, similar to the niche that the invasive alga now occupies in the Mediterranean. In view of these findings and in the absence of definitive population-level genetic studies, there is still insufficient evidence to support the assertion that the Mediterranean is being invaded by an exceptionally vigorous, cold-tolerant, genetically modified strain of *C. taxifolia* (Komatsu et al. 1997, Jousson et al. 1998, 2000).

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