Vol. 314: 97–108, 2006 | MARINE ECOLOGY PROGRESS SERIES Mar Ecol Prog Ser | Published May 22

Taxonomic diversity and geographic distributions of aquarium-traded species of *Caulerpa* (Chlorophyta: Caulerpaceae) in southern California, USA

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ABSTRACT: We identified 14 taxa (10 species) of *Caulerpa* from retail aquarium outlets in southern California, USA, suggesting that the aquarium industry has the potential to be an important vector for transporting these non-native seaweeds into distant geographic regions. Seaweeds were sold in 58% and species of *Caulerpa* in 52% of the 50 stores visited between November 2000 and August 2001. *C. serrulata* var. *hummii* (18%), *C. taxifolia* (14%), *C. racemosa* (14%), and *C. racemosa* var. *lamourouxii* (14%) were the most commonly encountered taxa. The 14 aquarium-traded *Caulerpa* taxa were distributed from tropical to temperate waters. Only 3 (*C. ashmeadii*, *C. serrulata* var. *hummii* and *C. microphysa*) were confined to the tropics, whereas 12 had distributions extending into temperate seas. These temperate components to their distributions indicate that, if introduced, several other taxa of aquarium-traded *Caulerpa* besides *C. taxifolia* might be capable of establishing populations in southern Californian or other temperate waters.

KEY WORDS: Aquarium industry · *Caulerpa* spp. · Geographic distribution · Invasive seaweeds · Marine invasions

INTRODUCTION

Hundreds of non-indigenous species have established populations in aquatic habitats in North America (Ricciardi & Rasmussen 1998), and biological invasions are now recognized as a serious threat to marine biodiversity (Lubchenco et al. 1995). With few exceptions, seaweed introductions have received less attention compared to introduced species of marine invertebrates and salt-marsh plants. One such exception is the invasive strain of *Caulerpa taxifolia* (Vahl) C. Agardh, which first appeared in the Mediterranean Sea in 1984 (Meinesz & Hesse 1991), and since has received much scientific and public attention because of its prolific spread. *C. taxifolia* has been reported to have dramatic effects on native algal and seagrass communities (Verlaque & Fritayre 1994, Ceccherelli & Cinelli 1997, Relini et al. 1998, Piazzi et al. 2001, but see Francour et al. 1995 & Jaubert et al. 1999). In addition to establishing Mediterranean populations, the invasive strain of *C. taxifolia* was found in 2 small southern California lagoons in 2000 (Jousson et al. 2000) and also is believed to have established introduced populations in Australia (Grey 2001, Millar & Talbot 2002, Schaffelke et al. 2002, but see Murphy & Schaffelke 2003).

Most species of *Caulerpa* (Chlorophyta: Caulerpaceae) have tropical or subtropical distributions; however, at least 14 of the 80 recognized species occur exclusively in temperate seas and some, such as *C. taxifolia*, occur in tropical and subtropical waters but also extend their ranges along temperate coasts (Guiry & Nic Dhonncha 2002; available at: www.algaebase.org). The invasive populations of *C. taxifolia* in the Mediterranean Sea (Meinesz & Hesse 1991, Meinesz & Boudouresque 1996,

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Jousson et al. 1998), southern California (Dalton 2001, Frisch & Murray 2002), and perhaps New South Wales, Australia (PIRSA 2003; available at: www.pir.sa.gov.au/weeds) appear to have been introduced by release of algae from salt-water aquariums. These invasive populations differ from naturally occurring *C. taxifolia* by reaching larger size and growing in dense monospecific stands (Meinesz 1999, Millar & Talbot 2002, Williams & Grosholz 2002). Currently, all identified invasive strains of *C. taxifolia* are thought to have originated from Australian waters (Jousson et al. 2000, Meusnier et al. 2001, 2002, Weidenmann et al. 2001).

Caulerpa taxifolia is not the only species of *Caulerpa* to display invasive behavior (e.g. growing in dense monospecific stands) within or outside its natural range. For example, a variety of *C. racemosa*, known as *C. racemosa* var. *cylindracea* (Verlaque et al. 2003) has been introduced into the Mediterranean Sea, where it has significantly altered benthic communities (e.g. Verlaque 1994, Verlaque et al. 2000, Piazzi et al. 2001, Durand et al. 2002). This species now occurs in the coastal waters of 11 countries and all of the large islands in the Mediterranean and recently was reported from the Canary Islands (Verlaque et al. 2004). *C. racemosa* var. *cylindracea* (Sonder) Verlaque, Huisman & Boudouresque is endemic to SW Australia, where until 2003, it was known as *C. racemosa* var. *laetevirins* f. *cylindracea* (Sonder) Weber-van Bosse (Verlaque et al. 2003). Additionally, *C. brachypus* Harvey has been introduced into Florida (Jacoby et al. 2004; available at: http://www.flseagrant.org/library/publications/index.htm#subject_index; SGEF-156), *C. scalpelliformis* (R. Brown ex Turner) C. Agardh into the Mediterranean Sea (Verlaque 1994) and along the eastern Australian coast (Davis et al. 1997), and *C. verticillata* (R. Brown ex Turner) C. Agardh has overgrown coral reefs in its native Floridian waters (Raloff 2000, Jacoby et al. 2004; available at: http://www.flseagrant.org/library/publications/index.htm#subject_index; SGEF-156).

The ecological impacts of *Caulerpa taxifolia* and *C. racemosa* var. *cylindracea* invasions in the Mediterranean Sea highlight the need for improved understanding of the pathways for introducing *Caulerpa* spp. and other seaweeds into coastal waters. Ruiz et al. (2000) identified 8 vectors for introducing non-native species into marine communities, of which activities associated with shipping accounted for the most documented exotic seaweed introductions. A recent review of the hypothesized vectors for 184 nonindigenous species of marine plants (Ribera Siguan 2003) revealed that aquaculture activities (30 %) and ship-hull fouling (24 %) accounted for most seaweed introductions. Another pathway identified by Ribera Siguan (2003) was the aquarium trade. Although to date the only seaweed thought to have been introduced by this vector is *C. taxifolia* (Meinesz & Hesse 1991, Meinesz & Boudouresque 1996, Jousson et al. 1998, Dalton 2001), this invasive species poses a severe threat to colonized ecosystems. *C. taxifolia* was considered one of the world's 100 worst invasive species by the IUCN in 1999 (available at: http://www.issg.org/database/species/search.asp?st=100ss&fr=1&sts), and also was listed by the United States under the 1974 Federal Noxious Weed Act. Besides serving as a possible source of *C. taxifolia* introductions, the extent to which the aquarium trade might serve as a vector for other potentially invasive species of *Caulerpa* has not been previously addressed or incorporated into assessments of the risk of *Caulerpa* spp. introductions.

In this study, we used southern California as a model for examining the diversity of *Caulerpa* species available to salt-water aquarists in the United States. In recent years, there has been an increase in the shipping of ornamental species for personal use by hobbyists (Tlusty 2002, Padilla & Williams 2004), and southern California is recognized as a world hub for the transportation of goods and a common entry point for imported salt-water aquarium specimens. Therefore, southern California should provide a representative sample of *Caulerpa* species being sold to aquarists in the United States through retail stores. Our primary goals were to (1) identify *Caulerpa* taxa offered for sale in southern California and to determine the frequency with which these species were encountered in retail stores, and (2) compile information on the global distributions of these *Caulerpa* species in order to make predictions about which species might be able to tolerate marine habitats in southern California or other temperate seas. This study will contribute to risk assessment of *Caulerpa* spp. invasions in temperate waters.

MATERIALS AND METHODS

Retail aquarium-store sampling. We visited 50 salt-water aquarium outlets between November 2000 and August 2001 in southern California in San Diego, Orange and Los Angeles Counties. We attempted to visit all salt-water aquarium outlets listed in online and printed telephone directories in San Diego and Orange Counties, whereas we subsampled the more numerous stores in Los Angeles County (see Table 1). Preliminary visits were made to several large corporate/franchise pet stores, but seaweed was never found for sale. Hence, we focused our sampling efforts on independent, non-franchise stores that specialize in ornamental aquariums for hobbyists.

In Los Angeles County, stores were assigned to 1 of 15 geographic sections, and half of these were selected at random; 50% of the stores in each chosen section also were randomly selected and visits made to each of these stores. *Caulerpa* species available for sale were either identified *in situ* or purchased upon visitation and returned to the laboratory where they were identified and prepared as dried herbarium specimens. The frequencies of each species and of 'live rock' (e.g. hard rock or coral substratum colonized by multiple species, usually including soft corals, anemones, cryptic tubeworms and seaweeds) were then calculated for each southern California County based on their presence or absence within sampled stores. 'Live rock' was included in our surveys because of its potential to serve as a substratum for cryptic growths of *Caulerpa* spp. and other seaweeds.

Although *Caulerpa* species can be purchased electronically from Internet outlets, we restricted our sampling to retail stores where specimens could be observed and identified on site, and the availability of each species could be determined. We acknowledge that other *Caulerpa* species are being sold over the Internet (L. Walters pers. comm.). However, to our knowledge this study comprises the first account of the availability of *Caulerpa* species to salt-water aquarists, and is believed to be indicative of the diversity of *Caulerpa* species being transported and sold by the aquarium industry in the United States.

Geographic distributions. To formulate hypotheses about which aquarium-traded species of *Caulerpa* might be able to survive in southern California or other temperate waters, we constructed the geographic distribution of each taxon using specimen data obtained from the Smithsonian Institution Herbarium and the herbarium at the University of California, Berkeley, and distribution records reported in the published literature (a listing of all compiled records and sources is available upon request from the authors). The Smithsonian distribution information was acquired through collection-site data reported in the Smithsonian database, which contained 1278 *Caulerpa* specimens belonging to 13 of the 14 taxa identified in our collections. The Berkeley collection data were obtained by examining and confirming the identity of 415 herbarium specimens for 13 of the 14 identified aquarium taxa and noting the collection site for each specimen. The herbarium collection data recorded for each specimen from both the Smithsonian and Berkeley herbaria were used, along with published distributional records, to plot the site records for each encountered species on world maps. Neither herbaria contained specimens of *C. serrulata* var. *hummii* (Díaz-Piferrer) Farghaly, one of the identified aquarium specimens, so the distribution of this taxon was compiled solely from available literature records.

For the purposes of this study, temperate waters were defined as those cooler than 18°C because stenothermic tropical seaweeds are believed to have lower temperature survival limits of 18 to 20°C (Pakker et al. 1995). To employ a conservative approach in identifying *Caulerpa* species with temperate distributions, we used a 15°C average sea-surface temperature (SST) line, modeled after Verlaque et al. (2000), as well as the 30° N and 30° S latitude lines as markers for temperate waters. The 30° N and 30° S latitude lines are considered to be temperate-zone boundaries because these markers are in close proximity to the 15°C average SST line.

RESULTS

Species availability and diversity

We identified 66 specimens belonging to 10 *Caulerpa* species and 14 separate taxa from retail aquarium outlets (Table 1). Seaweeds were sold in 58% and species of *Caulerpa* in 52% of the 50 visited stores indicating that, where seaweeds were offered for sale, species of *Caulerpa* were usually being sold (Table 1). Seaweeds in general, and *Caulerpa* spp. in particular, were sold at similar frequencies in the 3 southern California counties; however, the availability of each *Caulerpa* taxon varied greatly among stores and among the 3 counties (Table 1). *Caulerpa serrulata* var. *hummii* (18%), *C. taxifolia* (14%), *C. racemosa* (14%), and *C. racemosa* var. *lamourouxii* (Turner) Weber-van Bosse (14%) were the most commonly sold taxa, whereas *C. ashmeadii* Harvey (2%), *C. brachypus* (2%), and *C. webbiana* Montagne (2%) were rarely encountered.

Seaweeds were mostly sold as unattached thallus clumps, but also were found affixed to 'live rock'. 'Live rock' was offered for sale in 94% of all visited stores and was available at similar frequencies in the 3 southern California counties (Table 1). Of the 'live rock' found in the aquarium outlets, 18% supported visible growths of *Caulerpa* spp. The presence of *Caulerpa* spp. on 'live rock', however, was probably much greater, since cryptic thalli could not be detected by direct observation and we did not routinely hold 'live rock' in aquariums and later inspect this substratum for new *Caulerpa* spp. growths.

Geographic distributions

Aquarium-traded *Caulerpa* species sampled during our study are distributed worldwide, from temperate to tropical waters, and fall within 9 geographic regions as defined by the Smithsonian database: Carolinian, Gulf of California, Indian Ocean, Indo-West Pacific, Japan, Mediterranean, NE Atlantic, tropical East Pacific, and

Table 1. Availability of 'live rock', species of *Caulerpa*, and other seaweeds in retail aquarium outlets in 3 counties of southern California, USA, showing number of stores selling listed aquarium specimens (n = number of visited stores)

	County			All counties	
	Orange (n = 20)	San Diego (n = 11)	Los Angeles (n = 19)	Total (n = 50)	% of visited stores
'Live rock':	19	10	18	47	94
(with visible *Caulerpa* spp.)	(4)	(4)	(1)	(19)	(18)
Seaweeds					
Caulerpa (all species)	12	6	8	26	52
C. serrulata var. *hummii*	1	6	2	9	18
C. taxifolia	2	1	4	7	14
C. racemosa	3	1	3	7	14
C. racemosa var. *lamourouxii*	4	1	2	7	14
C. microphysa	2	4	0	6	12
C. sertularioides	3	2	1	6	12
C. peltata	1	1	3	5	10
C. prolifera	2	0	1	3	6
C. racemosa var. *macrophysa*	1	0	2	3	6
C. serrulata	2	0	1	3	6
C. racemosa var. *peltata*	1	0	1	2	4
C. ashmeadii	1	0	0	1	2
C. brachypus	1	0	0	1	2
C. webbiana	0	1	0	1	2
Other species	1	0	2	3	6
Total	13	6	10	29	58

tropical West Atlantic. All 14 taxa reside in the tropical West Atlantic, whereas 12 of our sampled varieties occur in the Indo-West Pacific, and 10 are found in both the Indian Ocean and in Japan; 4 taxa occur in the NE Atlantic, 4 in the Mediterranean and Carolinian regions, and 2 in both the tropical East Pacific and Gulf of California. Members of the morphologically complex *C. racemosa* assemblage occurred within all 9 regions, whereas *C. taxifolia* and *C. sertularioides* (S. Gmelin) M. Howe were recorded for 6 of the 9 regions. The other 8 *Caulerpa* taxa were found in 5 or fewer of the Smithsonian geographic regions.

Only 3 of the species we recorded from aquarium stores, *Caulerpa ashmeadii*, *C. serrulata* var. *hummii* and *C. microphysa* (Weber-van Bosse) Feldmann, were limited to tropical waters; the other 11 taxa have geographic distributions that extend into temperate seas (Fig. 1). Based on our distributional records, all *Caulerpa* taxa with temperate extensions to their distributions naturally occur poleward of the 15°C isotherm or 30° N or 30° S latitude in at least 1 of the 9 geographic regions.

DISCUSSION

At the time of our study, multiple species of *Caulerpa* were widely sold throughout southern California, appearing in more than half of the visited retail aquarium stores. The common occurrence of *Caulerpa* species, together with the high diversity of taxa we encountered, indicate that the aquarium industry is a potentially significant vector for transporting non-native *Caulerpa* species into southern California and other coastal regions.

The aquarium industry sells an extensive assortment of marine organisms, and the introductions into freshwaters of exotic fishes from the aquarium trade (Courtenay & Stauffer 1990, Padilla & Williams 2004) and the collection of ornamentals from the wild (Tlusty 2002) have long been recognized as significant ecological problems. For example, 40 reproducing populations of exotic fishes were established in fresh and coastal waters in the United States in 1984 (Taylor et al. 1984), and this number had risen to 46 by 1990, with 65% having been introduced by the aquarium-fish trade (Courtenay & Stauffer 1990). Moreover, all 16 non-native fishes recorded from the western Atlantic were imported by the aquarium trade (Semmens et al. 2004), including the lionfish *Pterois volitans*, which is believed to have established a self-sustaining population in the region (Whitfield et al. 2002). The extensive history of aquarium-fish introductions underscores the potential importance of the aquarium trade as a vector for invasive aquatic species, including seaweeds.

Of the 14 *Caulerpa* taxa found in our aquarium-store surveys, 11 occur as natives in temperate waters, a finding contrary to the belief that species of *Caulerpa* have strictly tropical to subtropical distributions (e.g. Fama et al. 2002). For example, Phillips & Price (2002) indicated that *C. taxifolia* occurs in subtropical habitats on the east coast of Australia (Moreton Bay, 27° 00′ S), but this region experiences SSTs as cold as 14.5°C, a temperature similar to winter minimum SSTs in areas of the Mediterranean and Adriatic Seas now occupied by the invasive strain of *C. taxifolia* (Komatsu et al. 1997).

The natural geographic distribution of an introduced species is linked to its likelihood of successfully establishing populations because of its tolerance of environmental conditions, especially temperature (Ruiz et al. 2000, Boudouresque & Verlaque 2002, Phillips & Price 2002). Perhaps both *Caulerpa taxifolia* (e.g. Meinesz & Hesse 1991, Verlaque 1994, Meinesz & Boudouresque 1996, Jousson et al. 1998) and *C. racemosa* var. *cylindracea* (e.g. Verlaque 1994, Verlaque et al. 2000, 2003, 2004) have successfully established invasive populations in temperate waters outside their natural geographic range because these species also have temperate components to their native distributions. If so, based on temperature conditions encountered across their native geographic distributions, 11 of the *Caulerpa* taxa recorded for sale in southern California aquarium stores hypothetically have the ability to colonize local and other temperate waters.

Species within the genus *Caulerpa* are morphologically plastic and often difficult to identify because of intraspecific form variation resulting from responses to environmental conditions such as light (Peterson 1972, Calvert 1976, Collado-Vides & Robledo 1999) and temperature (Enomoto & Ohba 1987, Ohba et al. 1992). Nevertheless, measurements of anatomical characters of *Caulerpa* species obtained from aquarium stores matched up well with values listed in published identification keys, suggesting that collected specimens were recently imported or did not change in key morphological characters under aquarium conditions (Frisch 2003). Although *C. taxifolia* has been listed under the United States Federal Noxious Weed Act, and the California Fish and Game Code 2300 (available at: www.leginfo.ca.gov) bans the importation, possession and sale of 9 species of *Caulerpa* in the state of California, enforcement is extremely difficult because of problems in distinguishing *C. taxifolia* and other banned *Caulerpa* species from non-restricted species.

Even within morphologically delimited species, invasive varieties or strains of *Caulerpa* can be difficult to distinguish without molecular data. For example, 3 *C. racemosa* varieties have been identified in the Mediterranean Sea using both morphological (Verlaque et al. 2000) and genetic (Durand et al. 2002) criteria. Because these varieties are difficult to distinguish on morphological grounds alone, most of the published literature on *C. racemosa* invasions in the Mediterranean Sea (Verlaque 1994, Ceccherelli et al. 2000, Piazzi et al. 2001, Ceccherelli & Campo 2002, Piazzi & Ceccherelli 2002) fails to identify the invasive variety,

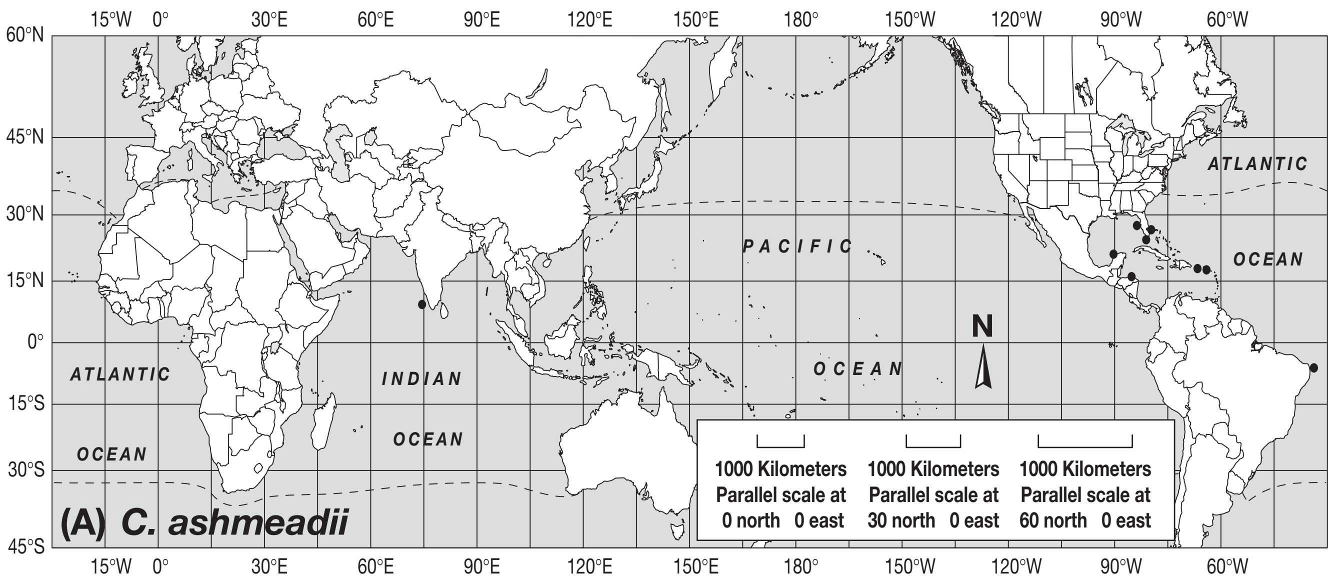
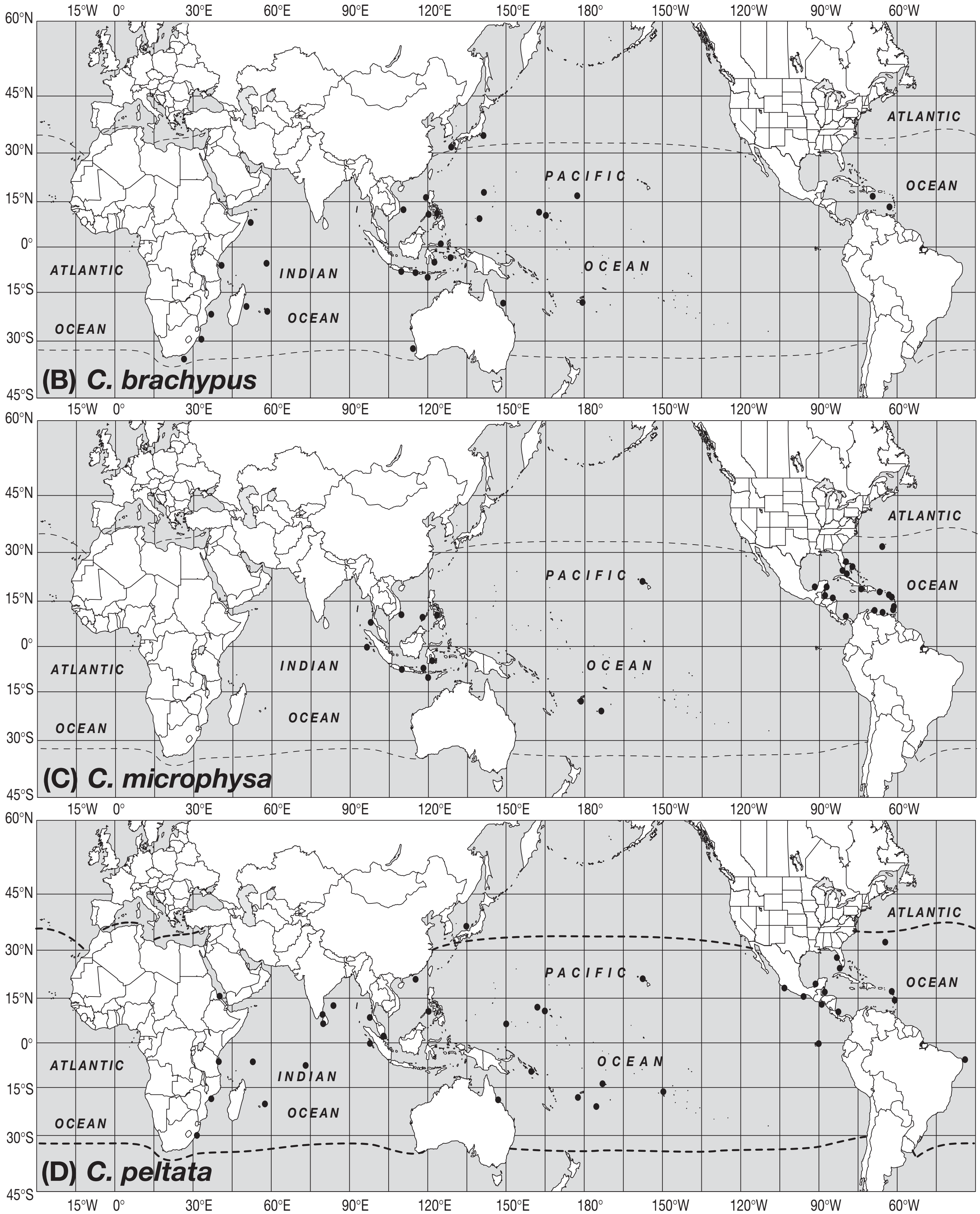


Fig. 1. *Caulerpa* spp. Global distributions of aquarium-purchased species of *Caulerpa*. Dashed line: 15°C average winter sea surface temperature (modeled after Verlaque et al. 2000). (A) *C. ashmeadii*; (B) *C. brachypus*; (C) *C. microphysa*; (D) *C. peltata*; (E) *C. prolifera*; (F) invasive *C. racemosa* populations now known as *C. racemosa* var. *cylindracea*; (G) *C. racemosa* var. *lamourouxii*; (H) *C. racemosa* var. *macrophysa*; (I) *C. racemosa* var. *peltata*; (J) *C. serrulata*; (K) *C. sertularioides*; (L) *C. taxifolia*; (M) *C. webbiana*. For (F) and (L), invasion sites are also shown (●) native range; (○) known invasions. In (F), (★) represents endemic *C. racemosa* var. *cylindracea*. In (J), (X) represents *C. serrulata* var. *hummii*



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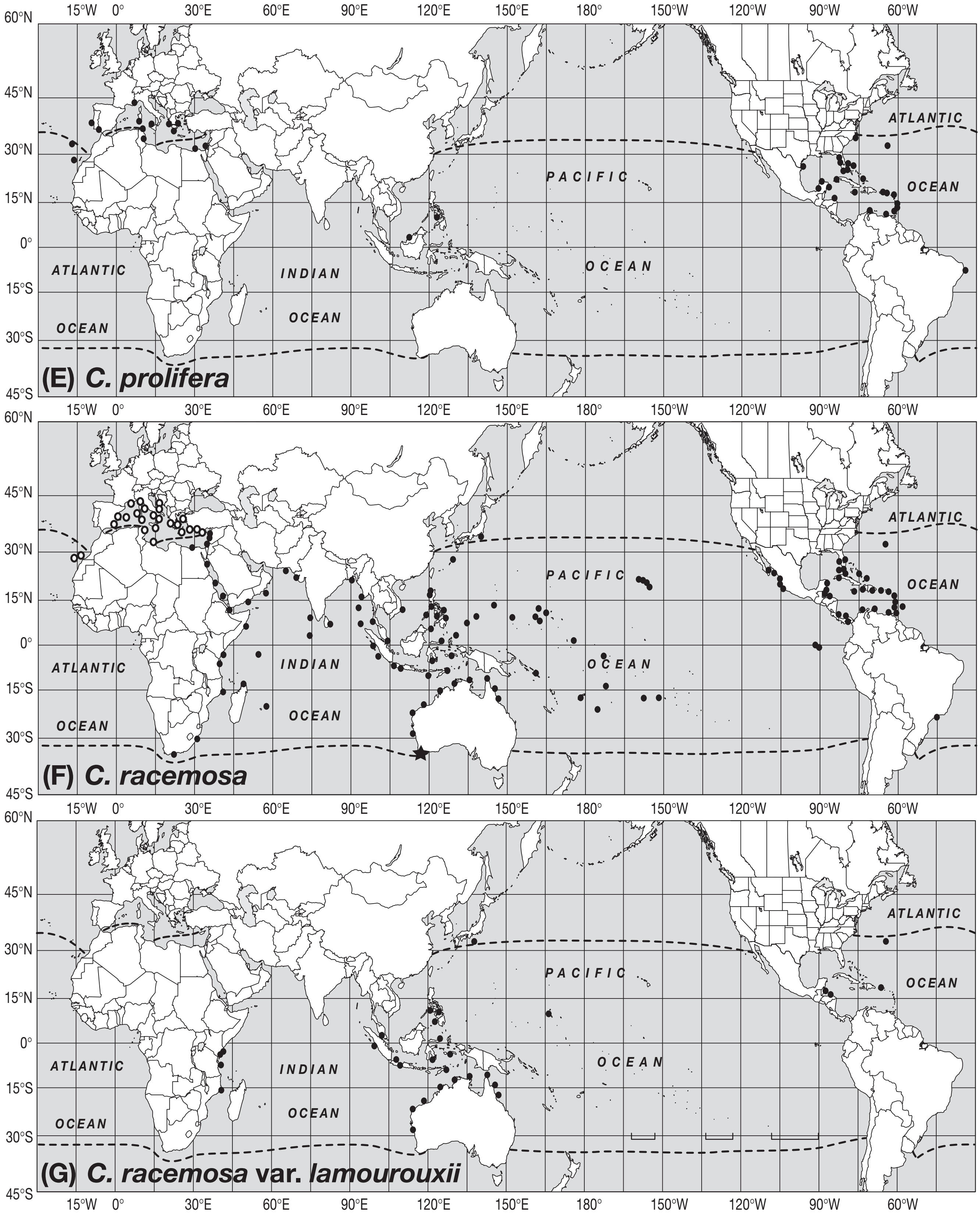

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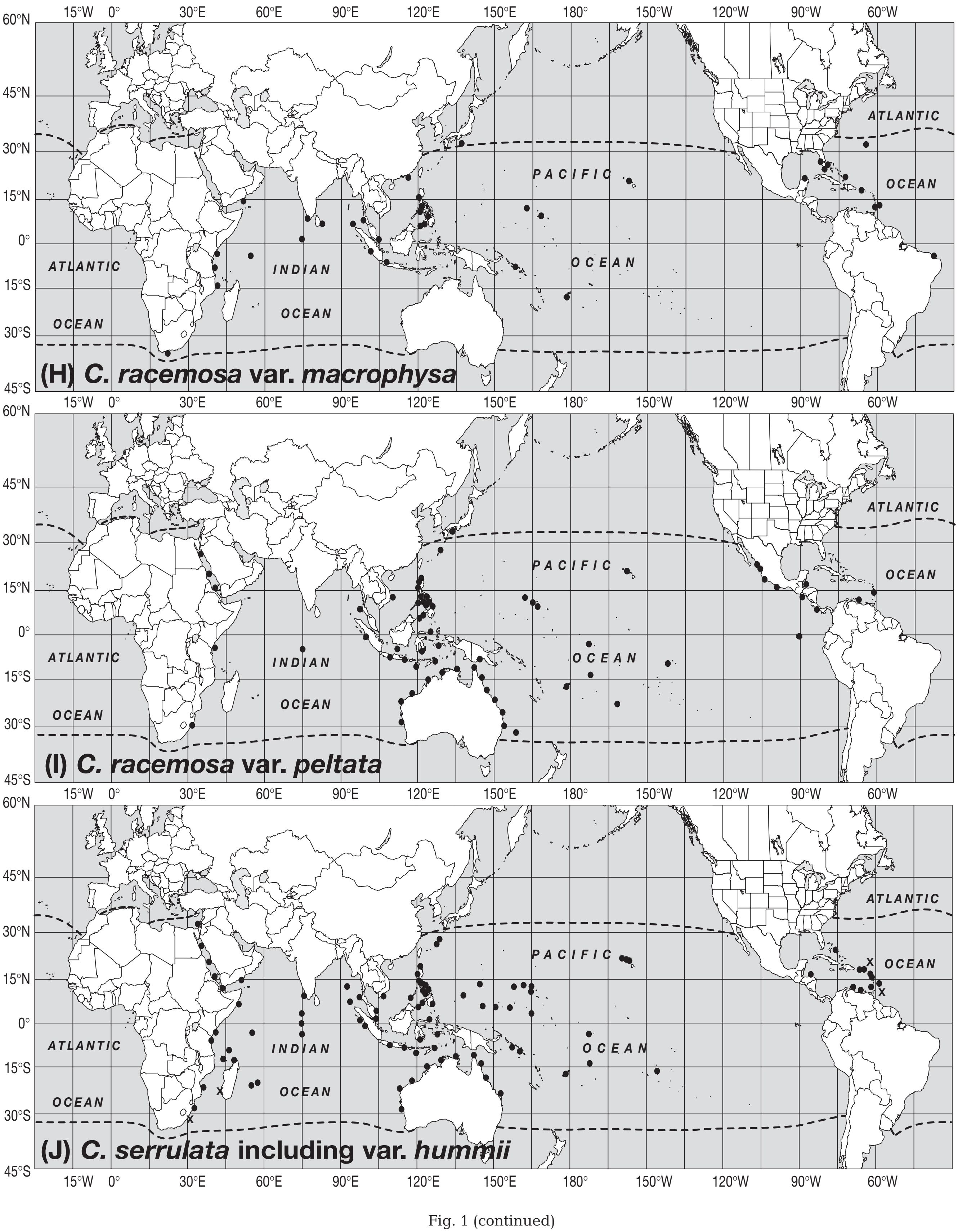

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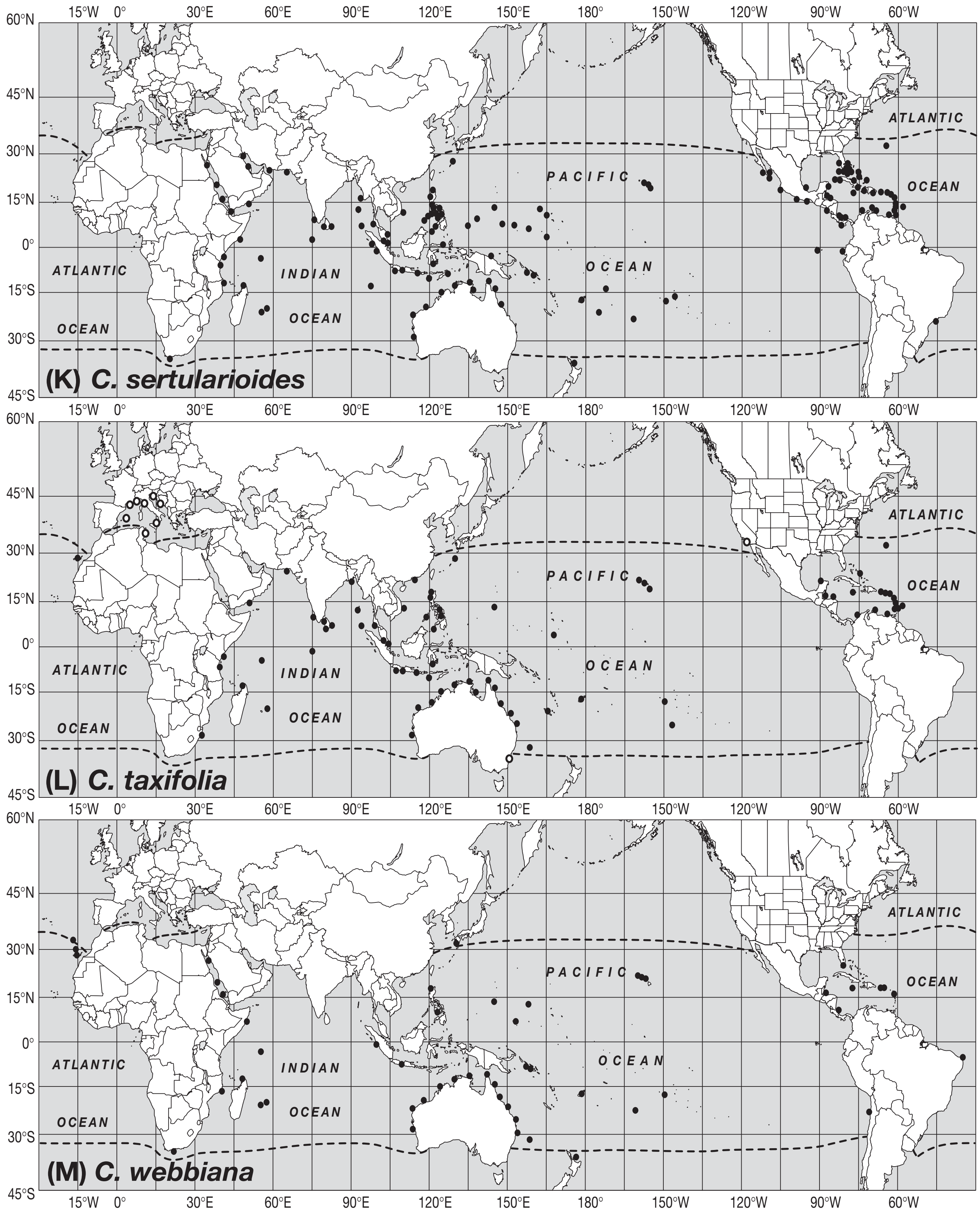

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which is now known to be *C. racemosa* var. *cylindracea* (Verlaque et al. 2003). The invasive strain of *C. taxifolia* is also difficult to distinguish from non-invasive strains based solely on morphological criteria. This invasive strain was linked with inshore Australian populations (Meusnier et al. 2002), and Meusnier et al. (2004) recently provided evidence confirming 2 incipient species of *C. taxifolia*, i.e. the invasive inshore/mainland form that grows in Australia in turbid sheltered bays and estuaries, which experience cold (12.5 to 14.5°C) winter temperatures (Phillips & Price 2002), and the offshore form that is associated with coral reefs and clear oligotrophic water. Genetic examination of aquarium-purchased species of *Caulerpa* is needed to determine whether *C. racemosa* var. *cylindracea* or the invasive strain of *C. taxifolia* were among our specimens.

Once established, invasive species are very difficult to control or eradicate in open marine environments (Kuris & Culver 1999), resulting in the need to prevent initial introductions (Ruiz & Crooks 2001). As pointed out by Ruiz & Carlton (2003), emphasis should be placed on preventing the introduction of species with a high probability of invasion or impact. Management of a *Caulerpa* spp. invasion poses particularly severe challenges. For example, invasive populations of *C. taxifolia* exhibit fast growth rates and form large, dense meadows. Although sexual reproduction is known to occur in the genus (Enomoto & Ohba 1987, Ohba et al. 1992), all invasive populations of *C. taxifolia* appear to be clonal and to spread easily by fragmentation and vegetative propagation (Ceccherelli & Cinelli 1999, Williams & Schroeder 2004). Even very small *Caulerpa* spp. fragments (≥10 mm) are able to produce new stolons (rhizomes) and rhizoids (root-like structures) that can grow into new individuals (Smith & Walters 1999). Given its rapid growth and high rate of dispersal, the eradication of *C. taxifolia* from 2 small southern California lagoons was most probably an anomaly resulting from early detection of small spatially confined colonies and the rapid response of coastal managers. Even in this case, however, eradication was labor-intensive and costly—US $4.1 million from July 2000 to 2002, with more funds spent through spring 2005 (Padilla & Williams 2004).

The rise in demand for marine organisms by aquarium hobbyists (Tlusty 2002, Padilla & Williams 2004) indicates that introductions of aquarium species, including possible introductions of *Caulerpa* spp., are likely wherever this hobby is prevalent. The popularity and wide availability of species of *Caulerpa* and 'live rock', which can harbor cryptic *Caulerpa* thalli, increase the likelihood of accidental introductions, particularly in warm subtropical or tropical waters where most *Caulerpa* species occur naturally. Nevertheless, many *Caulerpa* taxa, including most of those sold in southern California aquarium stores, have temperate components to their native distributions, suggesting that other species of *Caulerpa* besides the invasive *C. taxifolia* and *C. racemosa* var. *cylindracea* might be able to establish populations in previously unoccupied temperate waters. Prevention of future *Caulerpa* spp. introductions is essential, because managers are unable to predict the ecological impacts of introduced *Caulerpa* species on marine habitats and control/eradication programs will be costly—and unlikely to succeed.

Acknowledgements. We thank J. Norris and B. Sims, from the Smithsonian Institution, for their help with arranging logistics for visiting, laboratory space, and accessing herbarium specimens. Furthermore, we thank J. Norris for his discussions and help with species identifications. We also thank P. Silva for giving us access to the specimens at the University of California, Berkeley Herbarium and, K. Donovan for assistance with the illustrations. In addition, we thank S. Ellis for providing the needed permits for obtaining and working with specimens of *Caulerpa* in California. This study was supported by the National Sea Grant College Program of the US Department of Commerce's National Oceanic and Atmospheric Administration under NOAA Grant #NA66RG0477, project number R/CZ-63PD, and Grant #NA16RG2256 to S. N. M. through the California Sea Grant College Program. We are grateful to L. Duguay and P. Grifman of the University of Southern California Sea Grant Program for their administrative assistance and encouragement in completing this study. Funding also was provided by the California State University, Fullerton Department of Biological Science and Departmental Associations Council.

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Editorial responsibility: Lisa Levin (Contributing Editor), La Jolla, California, USA

Submitted: March 16, 2005; Accepted: September 2, 2005
Proofs received from author(s): April 24, 2006