Chapter 15
Ecology and Management of the Invasive Marine Macroalga *Caulerpa taxifolia*

Linda Walters

Abstract In coastal waters of Australia, the USA, and Europe, aquarium strains of the green macroalga *Caulerpa taxifolia* have invaded and caused ecological and economic disasters. As a result, this alga was placed on the International Union for the Conservation of Nature's list of 100 worst invasive species. Two things have promoted the invasions. First, *C. taxifolia* asexually reproduces by vegetative fragmentation. Fragments as small as 4 mm can survive and attach within 2 days. Second, this species has been and continues to be very popular with the aquarium industry, prized by both home hobbyists and public aquaria. Although regulations are now in place in many countries, retail shops and e-commerce continue to sell many species of feather *Caulerpa*, including *C. taxifolia*. "Aquarium dumping" is thought to be the reason for most, if not all, of the major invasions. Field eradication efforts have included manual and vacuum pump harvesting, covering colonies with opaque tarpaulins, subjecting *C. taxifolia* to a range of noxious chemicals, temperature, and salinity shocks, while outreach, monitoring, and modeling are promoted as ways to prevent future incursions. To date, only the USA and the West Lakes area of South Australia have eradicated *C. taxifolia*. Further research and outreach are needed to prevent future invasions of this noxious alga.

Keywords Marine Macroalga • *Caulerpa taxifolia* • Salinity tolerances • Competition • *Posidonia oceanica* • Aquarium Industry • Chlorophyta • vegetative fragmentation • secondary chemicals

15.1 Introduction

Caulerpa taxifolia (Vahl) C. Agardh (Caulerpales, Chlorophyta) is a brilliant green marine macroalga with multiple upright, feathery blades and a basal rhizome (stolon)

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that runs across the sandy or muddy bottom and is anchored to the substrate by bundles of colorless, filamentous, root-like rhizoids (Figs. 15.1 and 15.2). Growth is indeterminate (Collado-Vides and Robledo 1999), and *C. taxifolia* is native in subtidal waters in tropical and subtropical areas, including the Caribbean, Indonesia, Southeast Asia, Australia, and Hawaii (Phillips and Price 2002; Guiry and Dhonncha 2004). *Caulerpa taxifolia* can be found as isolated individuals on reef flats, sandy areas, or the undersides of floating docks (e.g., Coconut Island, Hawaii) or in a

Fig. 15.1 Two morphologies of invasive *Caulerpa taxifolia* from New South Wales, Australia. The more spiral morphology (individual on left) occurs in areas with higher levels of water motion

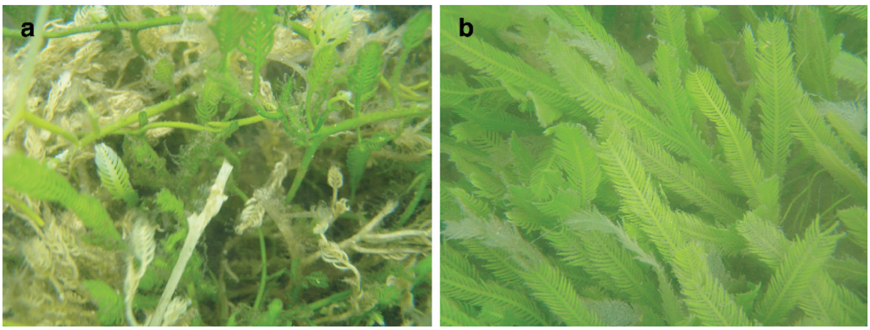

Fig. 15.2 *Caulerpa taxifolia* meadows. (**a**) A meadow of invasive *C. taxifolia* in early spring in Lake Conjola, NSW, Australia in which you can see new growth emerging from where the colonies had died back in the winter. (**b**) A lush meadow of native *C. taxifolia* from Moreton Bay, QLD, Australia

distinct, narrow band in soft sediments immediately seaward the low tide line (e.g., Moreton Bay, Australia) (personal observation). *Caulerpa taxifolia* is known by the aquarium industry as "feather *Caulerpa*" or "feather algae" and is lumped with a number of other species of *Caulerpa* with feathery blades (e.g., *C. sertularioides*, *C. ashmeadii*, *C. mexicana*), and this group has dominated the flora in both personal and public saltwater aquaria for many decades (Walters et al. 2006).

15.2 Invasion History of *Caulerpa taxifolia*

The aquarium strain of *C. taxifolia* has the distinction of being one of the world's 100 worst invasive species listed by the International Union for the Conservation of Nature (ICUN) and Europe's second worst macroalgal invasion on record (www.issg.org/database). The invasion history of the aquarium strain of *Caulerpa taxifolia* (*aka the killer alga) started with an accidental introduction into the Mediterranean Sea while cleaning tanks at the Monaco Oceanographic Museum in 1984 (Fig.15.3) (Meinesz and Hesse 1991, Meinesz 1999). Reports documented expansion from a small patch adjacent to the Museum to many areas in the Mediterranean at a rate of approximately 50 km per year, with boating activity, fishing nets, and water currents largely responsible for the spread (Meinesz et al. 1993, 2001; Sant et al. 1996). Dense populations of *C. taxifolia* are concentrated in zones with extensive development (Madl and Yip 2005). Monocultures of the aquarium strain of *C. taxifolia* now can be found at over 100 locations in Mediterranean waters extending for hundreds of kilometers (Madl and Yip 2005 for chronology). In the Mediterranean, *C. taxifolia* is found on steep slopes as well as flat bottom areas. Dense meadows are found at depths ranging from a few meters to over 40 m, while sparse meadows extend to 55 m and isolated individuals have been observed at 100 m (Meinesz and Hesse 1991; Belsher and Meinesz 1995). Through DNA forensics, the global origin of Mediterranean *C. taxifolia* was found to be Moreton Bay in Queensland, Australia (Wiedenmann et al. 2001). *Caulerpa taxifolia* was imported in the early 1970s by the Wilhelmina Zoologischbotanischer Garden in Stuttgart, Germany, which displayed the alga in its tropical aquarium (Jousson et al. 1998). Between 1980 and 1983, clones originating from Moreton Bay were given to the tropical aquarium of Nancy in northern France and subsequently to the Monaco Oceanographic Museum (Jousson et al. 1998). Clones were cultivated in various aquaria for 14 years prior to being found in Monaco waters.

In Japan, Komatsu et al. (2003) surveyed 65 public aquaria for *Caulerpa*. Sixteen of the 51 aquaria that responded to the survey cultured or exhibited *C. taxifolia*. Six purchased the alga from aquarium shops, one obtained *C. taxifolia* from another public aquarium (originally bought at a retail shop), and the rest were uncertain about origin but stated that the alga was from somewhere in Japan. The Notojima Aquarium staff reported temporary establishment of *C. taxifolia* in the Sea of Japan due to culturing practices. The aquarium initially received *C. taxifolia* when purchasing "foreign shrimp" of unknown taxonomy from an aquarium shop in Osaka. The aquarium staff grew the fragment in a tank. The fragment did well and was transferred to an open pool of 1,000 tons of seawater with an open-circuit

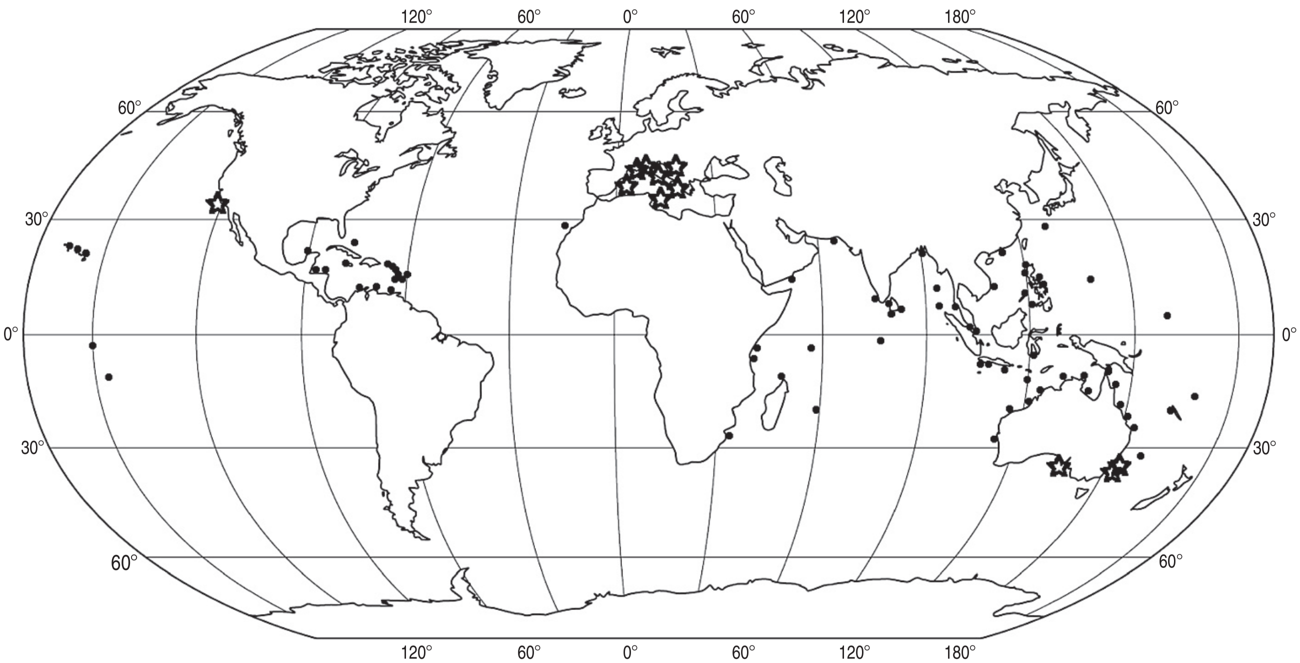

Fig. 15.3 Global distribution of *Caulerpa taxifolia*. Circles indicate native ranges and stars indicate known invasions (modified from Zaleski and Murray 2006)

water flow system. In August 1992, the aquarium staff observed two colonies of *C. taxifolia* (0.2 and 1.0 m diameter) in a coarse sand bed about 5 m from the pool's discharge pipe in the Sea of Japan (Komatsu et al. 2003). Both colonies disappeared in the winter of 1993. Two new colonies were observed in 1994; both disappeared in the winter (Komatsu et al. 2003). After that, the Notojima Aquarium began keeping their *C. taxifolia* cultures in a closed system. This Japanese aquarium strain genetically was identical to the Mediterranean aquarium strain (Komatsu et al. 2003). *C. taxifolia* did not become established in Japanese waters most likely because the water temperatures in the winter dropped below *C. taxifolia's* lower lethal limit (Komatsu et al. 2003). No *C. taxifolia* has been documented in Japanese waters since that time.

Populations of *C. taxifolia* were next discovered in April 2000 in Fisherman's Bay, Port Hacking along the southern outskirts of Sydney, Australia, more than 800 km south of its closest native distribution in the state of Queensland, where observational records date back to 1860 (Schaffelke et al. 2002). Also in April 2000, *C. taxifolia* was documented 200 km south of Sydney in Lake Conjola (Fig. 15.2). Researchers predict that the Port Hacking infestation started 2 years prior and the Lake Conjola infestation began 5–13 years earlier (Creese et al. 2004). In Australia, the number of invaded locations continues to increase with ten documented coastal lakes/estuary infestations in New South Wales (NSW), both north and south of Sydney, and two waterways in South Australia (Schaffelke et al. 2002; Millar 2004). Presently, Lake Conjola has the distinction of being the most severely infested location in NSW, and possibly Australia (West and West 2007). Here, *Caulerpa taxifolia* has replaced seagrass as the dominant macrophtye, covering approximately 30% of the lake floor (Creese et al. 2004). All invaded locations in Australia are relatively sheltered areas, are less than 10-m deep, and are soft sediment habitats that were either previously uncolonized or occupied by seagrasses (Creese et al. 2004; Davis et al. 2005).

Schaffelke et al. (2002) and Murphy and Schaffelke (2003) used molecular markers and determined that invasive *C. taxifolia* in Australia was not identical to the aquarium strain. Nor were NSW populations the result of a natural, southward range expansion along the eastern coastline (Phillips and Price 2002; Millar 2002). Most likely, the new infestations were the result of multiple domestic translocation(s), aided by boating, fishing, and the domestic aquarium trade (Schaffelke et al. 2002, 2006). Some areas, such as Port Hacking, have aquarium shops near shorelines, which stocked and sold *C. taxifolia* at the time the infestations were thought to have occurred (Creese et al. 2004). Other infested areas were much more remote, suggesting that boating and fishing activities were important for the transport of fragments (Relini et al. 2000). Indeed, many remote NSW infestations were popular fishing spots (Creese et al. 2004). Additionally, some areas where *C. taxifolia* currently is found were important commercial grounds prior to the lakes being closed to commercial fish netting in May 2002.

The year 2000 was a critical year for recognition of global infestations of *C. taxifolia*. In addition to the Australian invasions, populations of the aquarium strain of *C. taxifolia* were found in two lagoons in southern California: Agua

Hediona Lagoon and Huntington Harbor (Jousson et al. 2000; Anderson 2005). The source of both infestations was hypothesized to be personal aquaria, and the DNA forensics found that Californian *C. taxifolia* virtually was identical to the Mediterranean aquarium strain (Jousson et al. 2000). Already at high density, the Huntington Harbor invasion is thought to have started at least 2 years earlier, while the timing of the invasion in Agua Hediona Lagoon remains unknown (Williams and Grosholz 2002). Eradication efforts began immediately in both California locations and, to date, the USA is the only country with complete *C. taxifolia* eradication. A large celebration was held on12 July 2006 for this victory in spite of the price tag of over 7 million dollars and the necessary, but seemingly temporary, associated environmental harm (Anderson 2005; R. Woodfield, personal communication).

15.3 Why Is *Caulerpa* Such a Potent Invasive Species?

15.3.1 Reproductive Capacity

"Invasive success" refers to traits of a species that promote establishment, spread, and proliferation in the new range (Inderjit 2005). One hallmark trait of an invasive plant or macrophyte is its ability to rapidly spread to both close and distant locations. Short-range expansion occurs regularly via the basal rhizome in *C. taxifolia*. Long-range dispersal can occur via sexual or asexual reproduction. Sexual reproduction occurs in *C. taxifolia* with separate male and female individuals releasing gametes that are fertilized externally (Zuljevic and Antolic 2000). However, only male gametes, probably from a single clone that initially entered Monaco waters, have been documented in the Mediterranean (Zuljevic and Antolic 2000). No sexual reproduction has been described for any other invasive population either because only single sex clones entered the waterways or from the lack of site-specific research.

Many diverse genera of marine macroalgae excel at asexual reproduction via vegetative fragmentation (e.g., Fig. 15.4, Walters and Smith 1994; Herren et al. 2006). For this type of reproduction to be important, fragments must be generated regularly, have the ability to disperse widely, land safely, and then rapidly attach and grow under the new suite of biotic and abiotic conditions (Smith and Walters 1999; Walters 2003). With the genus *Caulerpa*, the capability is especially impressive as all members of the genus are siphonous, with no internal cell walls to reduce loss of cytoplasm when damage occurs that leads to fragmentation. Long before the genus *Caulerpa* became well known because of invasive characteristics, research was focused on understanding the underlying chemical properties that healed wounds in less than 1 min and kept fragments and the parent thallus from losing all the nucleus-rich cytoplasm (Dreher et al. 1978; Goddard and Dawes 1983).

Laboratory bioassays have confirmed that very small fragments of *C. taxifolia* can survive wounding and continue growing by producing new attachment rhizoids

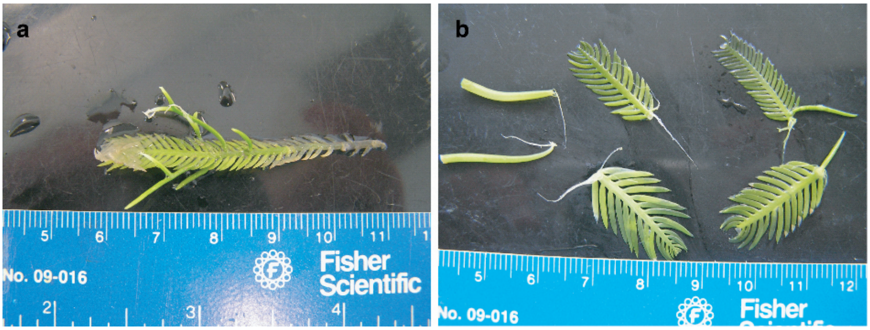

Fig. 15.4 Fragments of *Caulerpa taxifolia*. (**a**) New growth from a field-collected fragment. (**b**) New growth from laboratory trials

and new rhizomes from which new blades emerge. Much more robust than *C. verticillata* or *C. prolifera*, Smith and Walters (1999) found that native Hawaiian *C. taxifolia* fragments as small as 1 cm survived and produced new attachment rhizoids and rhizomes. To compare this to the success of native and invasive *C. taxifolia* from Australia, similar laboratory bioassays were run with invasive Lake Conjola and native Moreton Bay, Australia populations (L. Walters, P. Sacks, A. Davis and D. Burfiend, unpublished data). For both Australian populations, we found that blade fragments as small as 4 mm were successful and new growth was visible within 2–3 days. At 20-mm length, 100% of the blade fragments from Hawaii and both Australian populations survived and grew (Smith and Walters 1999; L. Walters, P. Sacks, A. Davis and D. Burfiend, unpublished data). Stolon-only fragments from Australia were only successful if they were at least 15 (Lake Conjola) or 20 mm in length (Moreton Bay) (L. Walters, P. Sacks, A. Davis and D. Burfiend, unpublished data). A small percentage of Hawaiian *C. taxifolia* stolons (10, 15, and 20-mm length) also survived (20%), but none attached (Smith and Walters 1999). For both Hawaiian and Australian *C. taxifolia*, new growth occurred at the wound sites, undamaged growing edges, and along branchlets. Unsuccessful fragments were obvious because all cytoplasm oozed out within 1 min and only the colorless cell walls remained. Finally, Smith and Walters (1999) determined the forces required to create fragments of *C. taxifolia* using a puncturometer (Pennings and Paul 1992). Forces needed were significantly less for fronds than that for stolons (Smith and Walters 1999).

15.3.2 Survival of Fragments in Field

Both storms and herbivory naturally create fragments, and these fragments add to fragmentation associated with recreational and commercial use of the waterways. Although normally negatively buoyant, fragments may float if covered with mucus or filamentous epiphytes (Chisholm et al. 2000). Lake Conjola (NSW, Australia) is very popular with recreational boaters, water skiers, jet skiers, and fishermen, especially during the summer holiday season. On ten dates between 17 December and 25 January 2007, 13.9 ± 2.3 boats per hour (mean ± S.E.) in Lake Conjola passed adjacent to *Caulerpa* meadows (L. Walters, P. Sacks, A. Davis, D. Burfiend, unpublished data). On the same dates and at the same locations, a mean of 34.0 ± 19.8 fragments (n = 10) were found in a 100 × 2 m band transect along the shoreline where *C. taxifolia* meadows were less than 2 m offshore. Boating traffic in Moreton Bay waterways in February 2007 was lower and consisted primarily of large sailboats, small fishing boats, and ferries (5.9 ± 1.0 boats/h), and we found about half as many fragments (19.7 ± 4.4) in similar transects in Moreton Bay waters (n = 14) (L. Walters, P. Sacks, A. Davis, D. Burfiend, unpublished data). Using Kruskal–Wallis nonparametric ANOVAs, there was significantly more boating activity in Lake Conjola (F = 19.17; p = 0.001) but no significant difference in the number of fragments (F = 0.19; p = 0.669). Ninety-eight percent and 99.9% of the fragments from Lake Conjola and Moreton Bay, respectively, were greater than 10 mm in length, allowing us to predict that the fragments will be successful. On the contrary, Wright (2005) found more asexual reproduction via fragmentation in Moreton Bay populations than at the invasive locations.

Fragments can be spread by anthropogenic activities related to boating and fishing (Sant et al. 1996; West 2003). In the Mediterranean, more fragments of *C. taxifolia* were found in locations where boats moored (Relini et al. 2000) and most new outbreaks appeared in areas of high boating activity (Meinesz et al. 1993). West et al. (2007) determined that fragments of Australian *C. taxifolia* created by all anchor types tested were of similar sizes. Eighty-two percent of anchors lowered into *C. taxifolia* beds fragmented individuals, and the biomass removed on a single anchor was as large as 49 g dry weight (West et al. 2007). Chains and ropes also generated fragments when lowered onto a meadow of *C. taxifolia* (96% chains, 4% ropes). Once removed from the water, fragment survivorship increased with clump size, protection from desiccation, and decreased exposure time (West et al. 2007). Likewise, Sant et al. (1996) found that fragments of aquarium *C. taxifolia* survived out of water in dark, humid conditions. Combined, the results suggest that multiple anchorings within a limited area can greatly promote dispersal of *C. taxifolia* while much longer dispersal (greater than hundreds of meters) is also possible when vessels travel long distances with fragments harbored inside anchor lockers, attached to ropes, or entangled on boat trailers (West et al. 2007). West et al. (2007) suggest that boaters may be more likely to discard larger, obvious clumps of *C. taxifolia* from anchors, rope, and chains while smaller fragments may be overlooked.

Fragment retention and attachment in *C. taxifolia* depends on season, hydrodynamics, and water depth. In Italy, aquarium-strain fragments (15-cm stolon with five fronds) survived best in summer months (Ceccherelli and Cinelli 1999a). Thibaut (2001) found that fragment survival on the French coast in the summer in 10-m water on sandy bottoms was as great as 98%, whereas only 50% establishment was found in shallower waters with more water motion. Many studies also have documented a positive correlation between fragment retention and structural complexity (e.g., A.R. Davis unpublished data). Wright and Davis (2006) determined experimentally that stolon growth and fragment success were linked in Australian *C. taxifolia*, and fragment recruitment was enhanced when stolons were present. Ceccherelli et al. (2002) found that dense, low-growing (turf) species promoted spread of aquarium *C. taxifolia*, while habitats with encrusting and erect macrophytes were less likely to be invaded.

15.3.3 Temperature and Salinity Tolerances of C. Taxifolia

Tolerance of a wide range of temperatures is another attribute of a successful invasive species. *Caulerpa* is endemic in tropical and subtropical regions around the world (Fig. 15.3), and latitude is a significant predictor of native occurrences (Creese et al. 2004; Glardon et al. 2008). Silva (2003) stated that members of the genus *Caulerpa* also can grow in locations up to 34°N along the southeastern US coastline, where the Gulf Stream typically warms the water. From known historical temperatures, Keppner (2002) suggested that the potential thermal distribution for *C. taxifolia* in the USA is (1) just south of Virginia Beach, VA on Atlantic coast, (2) Stonewall Bank, OR on the Pacific Coast, (3) throughout the Gulf of Mexico, (4) Hawaii, (5) Puerto Rico, (6) the US Virgin islands, (7) American Samoa, (8) Guam, and (9) the Northern Mariana Islands. In Europe, Ivesa et al. (2006) reported that invasive *C. taxifolia* was first recorded in Malinska (Island of Krk), Croatia in 1994, the highest northern latitude (45°7′30′) documented for *C. taxifolia*. However, only a few thalli were present in 2004 surveys, and low temperatures (9.5–10.5°C) in the previous winter were the suspected cause of the decline.

Many lab and field studies have determined experimentally the thermal tolerance range for *C. taxifolia*. Komatsu et al. (1997) determined that the upper temperature limit was 31.5–32.5°C, allowing *C. taxifolia* to thrive in tropical waters around the globe. The lower lethal temperature is much more important for understanding the potential range of *C. taxifolia*, and Komatsu et al. (1997) found the lower threshold to be between 9 and 10°C for fragments of the Mediterranean *C. taxifolia*. Additionally, Komatsu et al. (1997) found that minimum temperatures of 15 and 17.5°C were required for new growth of blades and stolons, respectively, for aquarium *C. taxifolia*. At the Monaco Oceanographic Museum, winter daily seawater temperatures from 1978 to 1991 were only below 11°C for 3 days (Meinesz and Hesse 1991). Minimum water temperatures in Moreton Bay, Australia are similar to minimum temperatures in the Mediterranean Sea (12°C) (Wright and Davis 2006). Chisholm et al. (2000) reported that *C. taxifolia* from Moreton Bay had a lower lethal temperature between 9 and 11°C. The lower limit for Lake Conjola was 11°C while it was 14°C for Port Hacking (Phillips and Price 2002; Wright and Davis 2006). Fragments did not grow at temperatures less than 20°C and had 100% mortality at 15°C or less in NSW trials (West 2003). When introduced into the Sea of Japan, *C. taxifolia* failed to establish where the mean surface water temperature averaged 9°C for 2 months (Komatsu et al. 2003). In Croatia, the biomass of *C. taxifolia* was reduced after cold winters (9.5–10.5°C). In addition to suggesting a sharp lower limit for survival, the results suggest that *C. taxifolia* naturally has a wide temperature tolerance. These results, in turn, refute early suggestions that the Mediterranean clone had become increasingly cold-adapted while propagated and dispersed through the aquarium industry.

In the Mediterranean and NSW, *C. taxifolia* is considered pseudoperennial because individuals dieback in winter months (Fig. 15.2). In both locations, researchers have documented that *C. taxifolia* reached maximal size at the end of the summer months and then decreased in dimensions, especially blade height, during cold weather (Meinesz et al. 1995; Ceccherelli and Cinelli 1999b; Glasby et al. 2005a). Temporary diebacks in shallow areas with only knots of stolons and a few bleached blades were often observed during winter when temperatures reached as low as 11°C (Wright and Davis 2006). In Italian waters, percent cover went from 2.7% in April to 100% in October (Balata et al. 2004). Williams and Schroeder (2004) found that chloroplasts were translocated to buried portions of tissue when fragments were either heat or cold-shocked.

West and West (2007) simultaneously compared the impact of six salinities (range: 15–30 ppt) and four temperatures (15–30°C) on *C. taxifolia* from Lake Conjola, NSW. Blades, rhizomes, and thalli (= rhizome plus one blade) had similar responses in the lab trial. Some fragments in all morphological categories doubled in size over the week-long trial by producing new stolons and fronds; the maximum growth rate was 174 mm/week (West and West 2007). Fragments grew well at salinities ≥ 22.5 ppt and temperatures ≥ 20°C, while mortality approached 100% at lower salinities and temperatures. The result was especially interesting in light of the changes to some NSW waterways. In 2001, the entrance to Lake Conjola was manipulated to keep the lake permanently open to the sea (West and West 2007). The current salinity in Lake Conjola is always above 30 ppt. Prior to 2001, Lake Conjola often was less than 17 ppt for extended periods of time. Entrance manipulation may have improved the success of invasive *C. taxifolia*.

15.3.4 Blade Lengths, Depths, and Densities

The ability to vary photosynthetic capacity (e.g., blade length, pigment concentration) when spatial competition occurs and along a depth gradient promotes invasiveness of marine macrophytes. Dumay et al. (2002) found an increase in blade length in response to competition between *C. taxifolia* and the seagrass *Posidonia oceanica*. In Mediterranean waters, blades of aquarium strain *C. taxifolia* as long as 60 cm were recorded in water up to 100-m deep (Meinesz et al. 1995; Belsher and Meinesz 1995), while the average range in shallower waters was 4–20 cm (Ceccherelli and Cinelli 1997, 1998). In Croatia, frond lengths ranged from 10 to 18 cm (Ivesa et al. 2006). In California, the maximum frond length was 24.6 cm, with a mean of 10.4 cm (Williams and Grosholz 2002). In Australia, Wright and

Davis (2006) found that the fronds of invasive populations of *C. taxifolia* were significantly shorter than native individuals when populations from 1 to 3 m of water were compared. In Moreton Bay, fronds ranged from 7.8 to 11 cm, while at Lake Conjola the range was 3.5 to 6.5 cm and the Port Hacking range was 1.6 to 5.5 cm (Wright and Davis 2006). Combined, the data suggest that large fronds are possible but only occur if required for survival in deeper waters or when competing for space.

Huge densities of *C. taxifolia* have been documented in invaded habitats. Average densities at invaded sites in Australia are currently the highest recorded globally, with 4,700 stolons and 9,000 blades/m^2 (Wright and Davis 2006). Mediterranean populations follow closely behind with 8,000 blades/m^2 and fresh weights of 11.5 kg/m^2 (de Villele and Verlaque 1995). Thibaut et al. (2004) found colonies to be denser at 5-m depths than 20-m depths in French waters; the former ranged from 203 to 518 g dry wt/m^2 and the latter was 62–466 g dry wt/m^2. Williams and Grosholz (2002) examined *C. taxifolia* that invaded Huntington Harbor in CA and found that the mean number of stolon meristems (horizontal shoots/runners) was 555 ± 182/m^2 ($\pm$SE) and the mean number of blades/m^2 = 1,478.

15.3.5 Competition

Seagrass habitat is an excellent predictor for finding species in *Caulerpa* (Glardon et al. 2008). In Florida, Glardon et al. (2008) surveyed 132 sites and of the 31 where *Caulerpa* was found, 24 were in seagrass beds. Native *Caulerpa* species are known to grow adjacent to seagrass beds or to be the first colonizers of areas that later are colonized by seagrasses (Williams 1984, 1990; Magalhaes et al. 2003). The interaction differs from invasive *C. taxifolia* and seagrasses in the Mediterranean. In the Mediterranean, *C. taxifolia* is especially adept at establishing on the edges of seagrass beds in the warmer months (Ceccherelli and Cinelli 1999b) and then outcompeting the seagrass *Posidonia oceanica* (Chisholm and Jaubert 1997; de Villele and Verlaque 1994; Montefalcone et al. 2007), but not always *Cymodocea nodosa* (Ceccherelli and Sechi 2002). Both live and dead rhizomes of *P. oceanica* proved to be suitable substrate for retention of fragments of invasive *C. taxifolia* (Cuny et al. 1995). Researchers additionally have found that *Caulerpa* fragments were more likely to recruit in *Posidonia* beds in deeper waters because the seagrass blades moved more by wave motion in shallower waters and fragments were dislodged or abraded (Cecherelli and Cinelli 1999b).

Posidonia oceanica meadows cover large areas of the Mediterranean seabed and are an important primary producer, providing food, shelter, spawning ground, and nursery for a huge variety of fishes and invertebrates (e.g., Madl and Yip 2005). Phenolic compounds in *Posidonia* that are known to increase if damaged were not allelopathic to *C. taxfolia* (Agostini et al. 1998), while competition with aquarium *C. taxifolia* caused *Posidonia* to decrease leaf longevity, possibly due to *Caulerpa's* allelopathic compounds (Dumay et al. 2002). Other authors have suggested that

Posidonia may be able to effectively compete with *C. taxifolia* in areas with limited urban pollution, but *C. taxifolia* will win in polluted areas (Jaubert et al. 1999). Williams and Grosholz (2002) found that in California, biomass of the seagrass *Ruppia maritima* was 20 times lower if mixed with *C. taxifolia* than alone.

15.3.6 Secondary Chemistry and Predation

Many marine algae are defended from herbivory by a wide diversity of secondary metabolites (e.g., Paul et al. 2001). Some green algae, including *C. taxifolia*, use an activated defense system whereby damage from feeding or abrasion results in the conversion of a stored secondary metabolite with minimal to moderate biological activity into a product with greater bioactivity (Paul and Van Alstyne 1992). If damaged, caulerpenyne, the dominant toxin in *C. taxifolia*, is transformed into a more toxic and deterrent cytotoxic sesquiterpene, which has greater antifeedant, antibiotic, and antifouling properties (Paul and Fenical 1986; Paul et al. 1987; Jung and Pohnert 2001). Reactive chemicals that are present within seconds after tissue damage act locally as defensive metabolites during the relatively slow feeding process by urchins or slugs (Sureda et al. 2006). *Caulerpa taxifolia* also has 10, 11-epoxy-caulerpenyne and caulerpenynol, two minor sesquiterpenoids, taxifolials, and other terpenes (Raffaelli et al. 1997; Paul 2002).

Caulerpenyne helps with wound response (Adolph et al. 2005) and is very unstable in seawater (Amade and Lemee 1998). Samples degraded by 50% in 4h and 95% in 24h (Amade and Lemee 1998). More caulerpenyne was found in blades than stolons in *C. taxifolia* (Dumay et al. 2002) and content varied seasonally in the Mediterranean (Amade and Lemee 1998), with the lowest concentrations in the winter followed by a sharp increase in summer (Dumay et al. 2002). Additionally, caulerpenyne content decreased with depth (Amade and Lemee 1998). Caulerpenyne levels were greater in the aquarium strain than native strains (Guerriero et al. 1992) and accounted for up to 1.3% of algal fresh weight or 2% + of algal dry mass (Paul 2002). Caulerpenyne was lethal in tropical waters to the sea urchin *Lytechinus pictus* (fertilized eggs, sperm, larvae) and toxic to the damselfish *Pomacentrus coruleus* and *Dascyllus aruanus* (Paul and Fenical 1986). Lemee et al. (1993) found that aquarium *C. taxifolia* whole extracts were toxic to mammals and eggs of the sea urchin *Paracentrotus lividus*. However, *Oxynoe olivacea*, a Mediterranean sacoglossan opisthobranch, expands its diet to consume *C. taxifolia* after the alga invades an area and uses caulerpenyne for self-protection by transforming caulerpenyne into oxytoxin-2, the mollusc's main defensive metabolite (Cutignano et al. 2004; Gianguzza et al. 2007).

Foraging behaviors and population structures of vertebrates and invertebrates were negatively impacted by *C. taxifolia* in numerous studies (e.g., Boudouresque et al. 1996; Relini et al. 1998; Davis et al. 2005). Densities and biomasses of fish assemblages were significantly lower in *Caulerpa*-invaded Mediterranean *Posidonia* beds (Francour et al. 1995; Harmelin-Vivien et al. 1999; Levi and Francour 2004;

Galil 2007). In southeastern Australia, total numbers of fishes were similar when *Caulerpa* and native seagrass beds were observed (York et al. 2006). However, species richness was significantly reduced in *Caulerpa* patches with high proportions of gobiid fishes and limited numbers of syngnathid and monacanthid fish species (York et al. 2006). In NSW, Gollan and Wright (2006) found that there were only four herbivores that co-occurred with *C. taxifolia*. The fish *Girella tricuspidata*, the sea hare *Aplysia dactylomela,* and two mesograzers, the amphipod *Cymadusa setosa* and the polychaete *Platynereis dumerilii antipoda,* all preferentially fed on other food sources in lab and field trials. Pinnegar and Polunin (2000) examined *C. taxifolia* impacts on the labrid fish *Coris julis*, which has limited migration and dispersal. Oxidative stress was examined for foraging *C. julis* in three habitat types: meadows of *C. taxifolia*, *C. prolifera*, and *P. oceanica* in waters surrounding Mallorca Island, Spain. Increased activity of liver antioxidant enzymes in *Caulerpa* meadows suggested ongoing detoxification of caulerpenyne by *C. julis* if algal blades or organisms that previously have consumed *Caulerpa* blades were ingested (Pinnegar and Polunin 2000). Even humans have suffered ill effects from caulerpenyne. Patients have been diagnosed with food poisoning after consuming *Sarpa salpa*, a fish that consumes *C. taxifolia* in the Mediterranean; doctors also documented neurological disorders such as amnesia, vertigo, and hallucinations associated with caulerpenyne consumption (DeHaro et al. 1993).

Predators have been documented to be negatively impacted by *C. taxifolia* in ways not related directly to caulerpeyne. For example, *Caulerpa's* dense clumps of rhizomes and stolons can form obstructions to fish trying to feed on benthic invertebrates (Fig. 15.2). Levi and Francour (2004) documented obstructions with the striped red mullet *Mullus surmuletus*. Longpierre et al. (2005) additionally found that the mullet's foraging effort increased with increased *density of C. taxifolia* with significantly fewer large individuals in *Caulerpa* meadows (1.2%) vs. 27.8% in *Posidonia* seagrass beds. The number of individuals of the bivalve *Anadara trapezia* increased in areas of *C. taxifolia* relative to unvegetated controls in Australian waters (Gribben and Wright 2006), possibly the result of increased structural complexity. However, delayed reproductive development, changes in timing of spawning, and fewer oocytes and sperm were all associated with *Caulerpa* beds relative to controls (Gribben and Wright 2006).

15.3.7 Other Characteristics that Promote Invasiveness

Other aspects of the life history of the genus *Caulerpa* that promote "invasiveness" include (1) ability to survive burial in sediment, and (2) ability to extract nutrients from multiple sources. Typically, unicellular species such as *Caulerpa* can translocate chloroplasts away from portions of the thallus if buried or held in darkness. Glasby et al. (2005b) documented that partial burial of *Caulerpa* in sediment had very limited impacts on individuals, while total burial for 17 days resulted in only 35% survival. While many seagrasses obtain a large fraction of nutrients from the sediment via roots and leaf uptake is considered of secondary importance (Pedersen and Borum 1993; Ceccherelli and Cinelli 1997), *Caulerpa* utilizes both sediment and water column nutrients (Williams 1984; Chisholm and Jaubert 1997). *Caulerpa* also can modify organic and inorganic components of the sediment (Chisholm and Moulin 2003). Thus, *Caulerpa* may receive a selective advantage in nutrient-limited environments when competing with seagrasses (Williams 1984; Ceccherelli and Cinelli 1997, 1999b; Ceccherelli and Sechi 2002).

15.4 Popularity of *Caulerpa* in the Aquarium Industry

While many of the economic and ecological impacts of the aquarium hobbyist industry can be enumerated (e.g., Padilla and Williams 2004; Walters et al. 2006; Zaleski and Murray 2006), one critical aspect that cannot be quantified is the number of accidental and purposeful releases of organisms from aquaria into coastal waterways. In spite of missing information, some of the most harmful invasive species that have become established in global waters are presumed to be the result of aquarium releases (e.g., Whitfield et al. 2002; Semmens et al. 2004; Ruiz-Carus et al. 2006). The source of the US and Australian invasions of *C. taxifolia* will never be known, but the similarity to the Mediterranean invasion lends support to aquarium releases (Stam et al. 2006). Currently in the USA there are over 11 million aquarium hobbyists spending billions of dollars annually to have colorful marine communities in their homes or businesses (Kay and Hoyle 2001).

In spite of the invasive reputation, many members of the genus *Caulerpa* remain extremely popular with aquarium hobbyists (Walters et al. 2006; Zaleski and Murray 2006). *Caulerpa* sp. are quintessential-looking marine aquarium plants, difficult to kill, propagate easily, remove nutrients, and some are also fish food. In three 2006 publications, the popularity and ease with which *Caulerpa* is dispersed within US boundaries via the aquarium industry was documented. Zaleski and Murray (2006) focused on availability of the genus *Caulerpa* in retail shops in southern California immediately after the first Californian invasion was reported. Zaleski and Murray (2006) found no seaweeds for sale in large corporate/franchise pet stores, so focused on independent, nonfranchise stores that specialized in ornamental organisms for hobbyists. In total, ten species of *Caulerpa* were for sale by at least one shop for 52% of 50 stores visited between November 2000 and August 2001. Fourteen percent of the shops visited had *C. taxifolia* (Zaleski and Murray 2006). None was the invasive strain (Stam et al. 2006). In 2006–2007, S. Diaz and S. Murray (unpublished data) resurveyed the same southern California shops. Forty-four were still in business. In spite of the California code banning nine species of *Caulerpa*, including *C. taxifolia*, and all the publicity associated with the two Californian invasions, 52% of the 44 remaining shops still sold at least one species of *Caulerpa* and four had *C. taxifolia* (not identified to strain, S. Diaz and S. Murray unpublished data). Two other banned species, *C. racemosa* and feathery *C. sertularioides*, also were for sale (S. Diaz and S. Murray unpublished data).

Walters et al. (2006) surveyed 47 salt water aquarium retailers in central Florida. Fifty-three percent sold *Caulerpa*, but none had *C. taxifolia*. A total of 9 species of *Caulerpa* were available for sale in central Florida.

Electronic commerce (e-commerce) increasingly is the primary, if not only, shopping venue for aquarium hobbyists. From 30 internet commercial retailers and 60 internet auction sites (eBay), Walters et al. (2006) made online purchases of 12 species of *Caulerpa* from 25 US states and Great Britain (Walters et al. 2006; Stam et al. 2006). Fifty-two percent of the states were landlocked, suggesting prior transport by hobbyists or the US postal/private shipping services. Walters et al. (2006) purchased *Caulerpa taxifolia* only once from a commercial online retailer when listed as "green feather *Caulerpa*" on the seller's web site. The purchased *Caulerpa* was shipped from a southern California retailer to Florida in November 2004 raising concern that this purchase might be the first documented case of human transport of the invasive strain of *C. taxifolia*. It, however, turned out to be a specimen of Caribbean origin based on the DNA sequence analysis (Stam et al. 2006). Hence, this clone of *C. taxifolia* was somehow transported from the Caribbean basin to California and then to Florida. On eBay you can buy entire aquarium setups that need to be collected in person. Walters et al. (2006) noted 13 auctions representing 10 states, but did not acquire *C. taxifolia* via this dispersal mechanism. They did, however, purchase *C. racemosa* and *C. mexicana* with one aquarium purchase.

Live rock is another way *Caulerpa* can be globally distributed (Walters et al. 2006). Live rock is coral (or other substrate) that is either directly quarried from reefs or kept in waters under aquaculture conditions to allow a diversity of organisms to attach. Live rock is extremely popular with hobbyists because the rock can be inexpensive and with each purchase there is the possibility of receiving a diversity of novel species. Zaleski and Murray (2006) found that 94% of southern California shops sold live rock and 18% of these had visible growth of *Caulerpa* on them. Walters et al. (2006) purchased live rock from ten retailers in central Florida and had small quantities of rock (≤10 kg) shipped to a Florida address from 11 internet retailers and 9 auction sites. After a minimum of 1 month in quarantine culture, *C. racemosa* was visible on three purchases of live rock, and *C. sertularioides*, *C. mexicana*, and *C. verticillata* were each found on one purchase. No *C. taxifolia* was transported via live rock in this study (Walters et al. 2006).

15.5 Control Methods Used to Try Dealing with Recent Invasions

There is significant pressure on marine managers to immediately remove or control any invasive marine species when an incursion occurs using the best science available (Bax et al. 2001). Thresher and Kuris (2004) list issues with the marine environment that make managing marine invasions very difficult. These include the following: (1) the ocean is perceived as an open system, (2) the public perceive oceans and coastlines as pristine, (3) a defeatist attitude by coastal managers, (4) limited knowledge about

Table 15.1 Control methods tested to eradicate invasive *Caulerpa taxifolia*

Method	Location	Success?
Manual harvest	Mediterranean, Australia	Not successful due to fragmentation, costs
Suction pumps	Mediterranean, Australia	Not successful due to fragmentation, residual attached biomass
Opaque tarpaulins	USA	Successful when combined with liquid chlorine (tarpaulins not tested alone in USA)
	Mediterranean	Not successful due to damage to tarps
	Australia	Not successful due to damage to tarps, cost for labor, nontarget mortality
Altering salinity	Australia	Successful
Liquid chlorine	USA	Successful
Copper	Mediterranean, USA	Not successful with short exposures as 100% mortality not achieved
Hydrogen peroxide	Mediterranean	Not successful with short exposures as 100% mortality not achieved
Aquatic herbicides	USA	Not successful with short exposures as 100% mortality not achieved
Coarse sea salt	Australia	Successful
Dry ice	Mediterranean	Not successful as 100% mortality not achieved
Heated water	Mediterranean	Not successful as 100% mortality not achieved
Ultrasound	Mediterranean	Not successful as 100% mortality not achieved
Biological control	Mediterranean	Not successful due to limited numbers of native herbivores and government restrictions on nonnative herbivores

the biology of most invasive species, and (5) uncertainty about control outcomes. With any marine invasive, it obviously is best to attempt eradication with a small infestation using methods that have limited ecosystem impacts. The ability of *C. taxifolia* to grow successfully from very small fragments has hampered many control efforts, but there have been some success stories. Some were based on well-planned experimental manipulations, while others were shotgun approaches. A variety of tested control methods and the reported effectiveness of each are described later and in Table 15.1. Mangers must remember that all relevant biotic and abiotic variables at the infestation site need to be considered when deciding on an eradication plan.

15.5.1 Manual Harvesting and Suction Pumps

In Mediterranean waters, harvesting by hand or with suction pumps was one of the first eradication methods attempted. Unfortunately, all attempts were unsuccessful because of *C. taxifolia's* ability to propagate clonally from small fragments missed by divers and because any residual attached biomass regrew (Meinesz et al. 1993; Rierra et al. 1994). Zuljevic and Meinesz (2002) described later efforts to use suction pumps in Croatian waters. Eradication with suction pumps was tested in four locations in 1996 and 1997 after *C. taxifolia* invaded Croatia in 1994. There was extensive regrowth in three of the four locations. To be effective, Zuljevic and Meinesz (2002) noted that suction pumping needed to be repeated after short while and eradication was more effective if the patch was small. Initial eradication attempts in NSW, Australia also included physical removal by hand and suction pump (Glasby et al. 2005a). Again, hand removal was abandoned because of the intense labor involved (<1–3 m^2 per diver per hour) and fragmentation caused by the removal process (Glasby et al. 2005a). In only one place is hand removal continuing. At the French National Park of Port Cros, annual hand removal plus applying cloths soaked in copper salts has occurred since 1994 to remain local biodiversity for SCUBA divers (Rierra et al. 1994; Thibaut 2001; Madl and Yip 2005).

15.5.2 Smothering Colonies

Black tarpaulins (20–30-mil PVC), surrounded by PVC frames and weighted down by gravel-filled bags, were used in the successful eradication campaign in California (Anderson 2005). Chlorine was injected into the confined space under all tarps, so it was not possible to determine if both treatments were required for *C. taxifolia* eradication. In other locations, tarps to smother individuals or inhibit photosynthesis were not successful. Zuljevic and Meinesz (2002) tested 0.15-mm thick black plastic tarps that were 4-m wide and suggested that this technique would be useful for all types of substrata. However, success was limited because of damage to tarps from anchoring, fishing, and storm events (Zuljevic and Meinesz 2002). In NSW, heavy rubber conveyor belts and jute matting (hessian) were tested and soon abandoned because the method was excessively labor intensive, tears in the tarps allowed for survival of some *C. taxifolia*, and high mortality of many species in the impacted area (Glasby et al. 2005a).

15.5.3 Changes to Local Salinity

Caulerpa taxifolia was found in West Lakes and the upper reaches of the Port River in South Australia in 2002 (Cheshire et al. 2002; Westphalen and Rowling 2005), prompting a significant eradication program. The West Lakes system is an artificial marine water body constructed in the 1970s and filled from Gulf St. Vincent at the south end by the tide. With an average salinity of 35 ppt, the system extends 7 km from north to south, is less than 500-m wide, and ranges in depth from 3 to 7 m (Collings et al. 2004). After extensive literature review, understanding the local flow regime, and mesocosm salinity trials, managers closed West Lakes to the sea and replaced the saltwater with freshwater. Freshwater was pumped from the nearby Torrens River. Any negative impacts were deemed acceptable by managers because the river historically drained through the area that included West Lakes and infrastructure for transfer of water was mostly in place. Engineers designed a pumping station on the bank of the Torrens River, which transferred freshwater to the southern end of the lake by gravity. Pumping began on 23 July 2003. Two additional barge-mounted pumps were deployed on the lake to pump high salinity water out and into the Port River. The project was completed on 1 December 2003. Although limited mixing of fresh and saltwater slowed progress, there was a salinity reduction at the depth where *C. taxifolia* grew (Collings et al. 2004). Most locations in West Lakes went below 17 ppt for 0–30 days, although one area never dropped below 24.8 ppt. Fragments of *C. taxifolia* from West Lakes tested after 3 months failed to grow, and there was no evidence of any regrowth after salinity was increased. Within 2 weeks of refilling from the sea, normal salinity returned to West Lakes. No *C. taxifolia* has been found in West Lakes since 2003 (Collings et al. 2004).

15.5.4 Chemical Controls, Including Chlorine and Sea Salt

Many chemicals have been tested in the laboratory and in the field with *C. taxifolia*. These include chlorine, copper (electrodes and cloths soaked in copper salts), hydrogen peroxide, and domestic herbicides known to kill nuisance freshwater algae and angiosperms (e.g., Uchimura et al. 2000; Thibaut 2001; Madl and Yip 2005). While some chemicals produced the desired results at high doses, toxicity extended to all organisms in the locality. Possible exceptions included liquid chlorine (California) and sea salt (Australia). Liquid chlorine (sodium hypochlorite) at a 12% stock solution was injected under black tarpaulins in California shortly after the infestation was reported (Anderson 2005). Over time, liquid sodium hypochlorite was replaced with 2.5-cm diameter, solid, chlorine-releasing tablets used for swimming pools (Anderson 2005). Monitoring of sediments under the tarps occurred in December 2001 and August 2002 to determine if the treated sediments continued to preclude growth of fragments of *C. taxifolia* (Anderson 2005). Cores from untreated areas promoted fragment growth while none emerged in treated sediments. Anderson (2005) did find, however, that seagrass and living invertebrates were present in all cores. Williams and Schroeder (2004) examined the role of chlorine for eradication of *C. taxifolia* in finer detail in the laboratory. They tested apical fragments at 10, 15, 50, and 125 ppm doses at three temperature regimes (7–10°C shocks, 10–11°C, 20–23°C). At the highest temperatures, chlorine at 50 ppm killed all but one fragment of *C. taxifolia* and at 125 ppm killed all fragments. Williams and Schroeder (2004) concluded that field eradication would require a chlorine concentration of 125 ppm for at least 30 min in the water column directly surrounding the *C. taxifolia* blades. Chlorine must also penetrate a minimum of 15 cm into sediments to reach rhizoids and buried stolons (Williams and Schroeder 2004).

Although chlorine was successful in the USA, chlorine has not been investigated in Australia. The most popular chemical treatment in Australia has been coarse sea salt (99.5% NaCl, mean particle diameter: 2.7 mm) and the most effective dosage was determined experimentally to be 50 kg/m^2 (Glasby et al. 2005a). The salt dissolved within 10 h and killed the alga via osmotic shock and cell lysis while having only minor effects on native biota. Additionally, no fronds were present in salted areas 6 months later (Glasby et al. 2005a; O'Neill et al. 2007). Researchers determined that the salting process worked best in cooler months when *C. taxifolia* died back naturally and that a thick, continuous covering of salt worked significantly better than salting discrete patches. For deploying salt, researchers compared hand dispersal vs. using a hopper on a flat-bottomed boat. Although waters deeper than 5 m allowed for too much horizontal dispersal in the water column for salting to be successful, in shallower waters the hopper method cost $A7 per square meter (2005 values) (Glasby et al. 2005a). Salt deployment by hand cost an average of $30 per square meter at the same time. Glasby et al. (2005a) suggested that colonies should be mapped during the warm season, followed by repeated salting of the infestations during colder months. Glasby et al. (2005a) additionally calculated a cost of over $A60 million to cover all *C. taxifolia* in NSW with one application of salt, using the hopper method.

15.5.5 Other Treatments: Temperature Shock, Ultrasound, and Genetic Control

A variety of additional methods to kill *C. taxifolia* under field conditions have been tried unsuccessfully. While cold shock killed fragments in the laboratory (Williams and Schroeder 2004), dry ice applications were not successful in the field. With dry ice, only sublethal necrosis was obtained (Thibaut 2001). Likewise, when fragments of *C. taxifolia* in the laboratory were heat-shocked at 72°C for 1 or 2 h, the fragments died (Williams and Schroeder 2004). However, underwater applications of hot water at or above 40°C appeared to work initially, but recovery was observed after 3 weeks (Thibaut 2001). Underwater welding devices to boil the plants also were not successful (Madl and Yip 2005). In situ application of ultrasound did not destroy plant tissue (Boudouresque et al. 1996). However, in a feasibility study for genetic control of *C. taxifolia*, Thresher and Grewe (2004) stated that a species-specific biocide based on an enzyme critical for photosynthesis or osmoregulation could be developed and then delivered in pellet form.

15.5.6 Biological Control

Many scientists and managers hypothesize that the only hope for control of *C. taxifolia* will involve biological control. Thresher and Kuris (2004) suggested that most current efforts to eradicate or control high-impact marine invasive species that are deemed acceptable to stakeholders are low risk and publically acceptable, while biological control remains more contentious for both social and political reasons. Thresher and Kuris (2004) continue by stating that contentious possibilities will not occur on a large-scale until scientists and managers learn more about biological control agents.

Two biological control agents initially deemed most likely to reduce *C. taxifolia* biomass in Mediterranean waters were the native sea slugs *Oxynoe olivacea* and *Lobiger serradifalci*. Both species perforated cell walls with uniserial radula and sucked up the algal contents. Both species have been tested in aquariums and in open ocean waters as potential biological control agents of *C. taxifolia* (Thibaut and Meinesz 2000). In later laboratory studies, *L. serradifalci* created viable fragments of *C. taxifolia* when feeding; *Oxynoe olivacea* did not produce fragments (Zuljevic et al. 2001). The nonnative, tropical sea slug *Elysia subornata* was also tested (Meinesz 2002). At 21°C, *E. subornata* fed on *C. taxifolia* at rates 2–11 times higher than the native ascoglossan species (Thibaut et al. 2001). Meinesz et al. (1995) projected that 1,000 *E. subornata*/m^2 were required to have a significant impact on the Mediterranean sea floor with 5,000 fronds/m^2. Unfortunately, a cold-resistant strain of this species could not be readily cultivated (Meinesz 2002) and, in 1997, the International Council for the Exploration of the Sea (ICES) stated that nonnative ascoglossans could not be introduced to Mediterranean Sea for biocontrol. The French Ministry of the Environment shared the same attitude based on (1) possible dietary switching by the herbivore, (2) competition with other important groups of herbivores in the event of eradication of the target food source, (3) introduction of pathogens, and (4) spread of the introduced herbivore itself.

15.5.7 Outreach, Signage, and Closures

The most cost-effective management strategy is to prevent the introduction of *C. taxifolia* into coastal waters. To ultimately be effective, outreach concerns need to be addressed at local, regional, national, and international levels (Hewitt 2003). Many countries have provided public and private funds for creating a wealth of outreach materials (animated videos, fact sheets, identification keys, lesson plans for educators, etc.) designed to change behaviors for every age and interest group that may contact *C. taxifolia*. The next goal is to get the information into the right hands. As aquarium releases are an important, intangible source of marine invasions, aquarium hobbyists and custom agents who inspect international aquarium shipments are prime outreach targets. However, both audiences are fluid with new customers entering the hobby every day and new individuals assigned to rapidly assess live aquarium shipments for illegal importation. For example, Zaleski and Walters (unpublished data) surveyed participants at MACNA 2006, the annual meeting of the Marine Aquarium Societies of North America in Houston, TX and found that 29% of the visitors had never heard of *C. taxifolia*, while an additional 25% had very limited understanding of the biology or global invasions of *C. taxifolia*.

In areas such as the Mediterranean and Australia that may never be able to eradicate *C. taxifolia*, outreach can slow additional spread. In infested Australian waters, signs are posted at all areas where boaters launch their craft and mandatory “wash-down” stations are provided (Fig. 15.5). NSW visibly marks and bans anchoring at

Fig. 15.5 Signage used in NSW, Australia to limit further dispersal of *Caulerpa taxifolia*

sites newly invaded by *C. taxifolia* (Glasby et al. 2005a). Additionally, when new infestations are found in NSW, NSW Fisheries establishes fishing closures to prevent hauling or mesh-netting in infested areas under the Fisheries Management Act of 1994.

15.5.8 Posteradication Surveys

Eradication only is successful when no living *Caulerpa* is present at a previously infested location. Although easy to describe, documentation of eradication can be difficult to obtain based on prevailing currents, water clarity, and epiphytism. In California, significant effort was devoted to surveying and developing defendable survey techniques once *C. taxifolia* was no longer located by trained divers. During both pre- and posteradication monitoring, diver teams followed prescribed parallel transect lines from GPS coordinates. The grid provided sufficient overlap to minimize missing *C. taxifolia* that was present (Anderson 2005). In Huntington Harbor, a full survey took 5 days. In Agua Hedionda Lagoon, a full survey of the lagoon involved swimming more than 500 miles and took 2–3 months (Anderson 2005). To ensure divers were searching effectively and not just missing plants, *C. taxifolia* mimics (plastic aquarium plants) were deployed in locations unknown to the divers (Anderson 2005). Survey efficacy varied substantially with water clarity and bottom type. The efficacy study was necessary to estimate how many surveys were necessary to find every last plant. After 24 months of monitoring with no sightings of live *C. taxifolia*, but continued sightings of mimics, California deemed eradication successful in July 2006.

In March 2007, California adopted a new survey protocol for persons applying for permits to disturb the benthos in areas where *C. taxifolia* was once found. Before commencing any permitted sediment-disturbing activity, a preconstruction *Caulerpa* survey of the area that covers at least 20% of the bottom that will be affected must be completed. The affected bottom includes the project footprint, areas where equipment were stored/moored, areas where vessel prop-wash could occur, and in-water disposal areas for sediment. The survey must be completed not earlier than 90 days prior and not later than 30 days prior. If any *C. taxifolia* is found, activity must be halted until the infestation was isolated, treated, and any risk eliminated. If work is to be undertaken in *Caulerpa*-infected waters, two surveys not less than 60 days apart must occur, one at the high intensity level (50% of bottom covered) and one at the eradication level (100% of bottom covered). If the project extends over 90 calendar days, additional surveys at the high-intensity level will be required. Additional surveys of dredged materials may also be required.

15.5.9 Modeling

Models allow managers to focus limited resources to survey only the most suitable sites for an invasive species, such as *C. taxifolia*. Glardon et al. (2008) have developed such a model for the genus *Caulerpa* in Florida waters. Glardon et al. (2008) conducted field surveys of 24 coastal areas around Florida in each of six zones chosen in a stratified manner and evaluated the association of potential indicators for the presence of *Caulerpa*. In total, 14 species of *Caulerpa*, but not *C. taxifolia*, were found at 31 of the 132 sites. Latitude, presence of seagrass beds, human population density, and proximity to marinas were simultaneously considered. A positive correlation between *Caulerpa* spp. presence and seagrass beds and proximity to marinas was documented while a negative correlation with latitude and human population density was also noted. The parameters in the logistic regression model assessing the association of *Caulerpa* occurrence with the measured variables then were used to predict current and future probabilities of *Caulerpa* spp. presence throughout the state. Percent correct for this model was 61.5% for presence and 98.1% for absence. While aquarium dumping provides an explanation for the positive correlation with marinas, the human population density results were surprising. This may be because, in Florida waters, high population densities enhance pollutant loads, freshwater inputs, and nutrient runoff, and these factors may decrease macroalgal growth.

A second type of useful model is one that accurately predicts the pace of an invasion once it has begun so that managers know how best to undertake eradication. Ruesink and Collado-Vides (2006) found that the model that best describes actual field distributions of *C. taxifolia* invokes local growth via rhizome expansion plus low levels of fragment dispersal and attachment (increases of 4–14-fold annually). The model goes on to suggest that the most effective plan for maximizing eradication is removal of established patches before summer and removal of fragments in the fall (Ruesink and Collado-Vides 2006). The times corresponded to just before maximum growth and just after maximum fragment production, respectively. Only a mixed strategy that combined 99% removal of all fragments and annual removal of 99% of established patches was predicted to entirely eliminate *C. taxifolia* (Ruesink and Collado-Vides 2006). This level of effort is only likely to be possible early in an invasion.

15.6 Reducing the Likelihood of Future Invasions Through Biosecurity Regulations

Marine algal invasions can transcend national boundaries, so the problem must be considered an international problem (Inderjit et al. 2006). To be successful, a global rapid response plan should be in place as well as immediate access to adequate funding. If biological invasions are treated the same way that governments respond to hurricanes, tornados, fires, floods, oil spills, or disease outbreaks, then rapid response should be possible. Anderson (2005) suggested that to be prepared to deal with an invasion, a drill must be performed to determine who will provide (1) biological experts, (2) ownership of the waterway, (3) knowledge of potentially successful eradication strategies, and (4) funding. Although many countries are concerned about future *C. taxifolia* invasions, currently only NZ appears ready to respond if an invasion were reported tomorrow.

In New Zealand, marine biological security is defined as protection of the marine environment from nonnative species. Biosecurity is a high profile topic, mainly because of the country's dependence on shipping (Hewitt et al. 2004). The NZ Marine Biosecurity Team was established in 1998 under the Biosecurity Act of 1993 with the dual goals of working on reducing knowledge gaps and establishing management frameworks. Active awareness campaigns by the government have led to a greater awareness of many nonnative species in the general population relative to other countries. Additionally, no discharge of unexchanged ballast water is permitted in NZ from any country unless exempted on the grounds of safety. Preborder and border management is likewise paramount to promote prevention, early detection, and rapid response (Wotton and Hewitt 2004). New Zealand is already on high alert, expecting *C. taxifolia* to arrive at any time. The decision making process in NZ for a *C. taxifolia* sighting follows a mostly universal rapid response protocol and would involve (1) confirming the genus species in NZ waters, (2) establishing the nature and magnitude of the incursion, and (3) risk analysis to determine the likelihood of an impact if the incursion was left untreated (insignificant, minor, moderate, major, catastrophic). Containment, management, or eradication would then be initiated if sustained, cost-effective action was possible and the organism posed an unacceptable risk. More than likely, any *C. taxifolia* in NZ waters would be considered an unacceptable risk. The actual level of response would then depend on the (1) potential impacts of the invasive organism on the environment, the economy, and people, (2) technical feasibility of response options, (3) ability to target the invasive species, (4) risks associated with treatment, (5) degree of public concern, and (6) likelihood of the organism being eradicated or managed. Monitoring and review of the response process itself completes this protocol.

In the USA, the US Department of the Interior was alerted to problems with *C. taxifolia* Mediterranean strain and the threat it posed to US coastal waters in 1998. The scientific community requested the Secretary of the Interior to be proactive and initiate action to prevent introduction of *C. taxifolia* into US waters. *Caulerpa taxifolia* was determined to pose a significant threat, so a comprehensive prevention plan was requested and the Mediterranean strain of *C. taxifolia* was banned from importation, entry, exportation, or movement in interstate commerce by the US Department of Agriculture (USDA) under the federal Noxious Weed Act (1999) and the federal Plant Protection Act (2000). Before the plan could be implemented and before importers/retailers knew about the ban, the invasive aquarium strain of *C. taxifolia* was discovered in California. The US was lucky that the invasion of *C. taxifolia* happened in southern California. Within 3 days of contract divers finding an unfamiliar macroalga in Agua Hediona Lagoon, specialists received and morphologically confirmed the unknown as *C. taxifolia*. DNA forensics shortly thereafter confirmed that the unknown alga was the invasive Mediterranean strain (Jousson et al. 2000). The Southern California *Caulerpa* Action Team (SCCAT) was created and included local, state, and federal agencies, university researchers, the San Diego and Santa Ana Regional Water Quality Control Boards, the local power company, and key local stakeholders (Anderson 2005). Treatment combining black tarpaulins and liquid chlorine began within days and rapidly was followed by new regulations at the state and county levels. California legislators banned nine species of *Caulerpa* after a public outcry by aquarists stated that a ban at the genus level would have dire effects on their industry. On 25 September 2001, California Fish and Game Code 2300 became law and prohibited the sale, possession, import, transport, transfer, release, or giving away of *C. taxifolia, C. cupressoides, C. mexicana, C. setularioides, C. floridana, C. ashmeadii, C. racemosa, C. verticillata*, and *C. scapelliformis*. All banned species were either known to be invasive in some location or were feathery look-alikes of *C. taxifolia*. Possession was permitted only for scientific research and any violators were subject to a civil penalty of not less than $500 and not more than $10,000 for each violation. Next, the city of San Diego, California adopted an ordinance that prohibited the sale and possession of all *Caulerpa* species within city limits. This comprehensive ban demonstrated the commitment of the city to protect its coastal resources. At the federal level in the USA, a National Management Plan was released in October 2005 for the genus *Caulerpa*. On a positive side, the plan identified research information gaps and how these gaps should be addressed. It also provided much-needed funding for research and outreach. The plan, however, did not have strong wording to create a federal ban at the genus or species level, so some states (Oregon, Massachusetts, South Carolina) were proactive and banned all strains of *C. taxifolia*. Dr. Susan Williams submitted a federal petition to increase the ban to the genus or species level. Williams correctly argued that current US regulations do not protect ecosystems from invasive Australian strains or other invasive strains not yet described. She also argued that the current regulation relies on expensive, time-consuming DNA technology. This petition has not yet been resolved.

In spite of the US regulations, Walters et al. (2006) found that of 60 eBay auctions, only four vendors provided information on interstate transport regulations for *C. taxifolia*. eBay stated that the sellers, not eBay, were responsible for knowing all federal and state regulations for all live plant products sold and that vendors stand to have their accounts suspended and forfeit all eBay fees on cancelled listings for breaking regulations. With internet commercial retailers, the ratio was similar with only 2 of 30 providing consumers with information on *Caulerpa* restrictions. Some large internet distributors now provide fact sheets promoting alternatives to release for all aquarium and water garden flora/fauna. The US Postal Service now prohibits mailing the aquarium strain of *C. taxifolia* by designating the alga as a "nonmailable plant pest." As with eBay, the burden of identification resides with the sender. Common names are used so often in the marine aquarium trade that the seller/buyer may not even know that they are distributing a banned species. From e-commerce purchases, Walters et al. (2006) learned that eBay, internet, and local retailers frequently do not identify products scientifically; only 14.1% used genus species names and sellers correctly identified algae only 10.6% of the time at the species level. None identified macroalgae by strain. Walters et al. (unpublished data) found that common names that may be the aquarium strain of *C. taxifolia* included feather *Caulerpa*, feather algae, aquacultured *Caulerpa* algae, *Caulerpa* algae, marine macroalgae, assorted *Caulerpa* species, coral reef algae, fern *Caulerpa*, and green *Caulerpa* tang heaven. Common names greatly reduce the ability of agencies to remove a species from the market.

Although the origin of *C. taxifolia* in NSW, Australia remains unclear, scientists hypothesize that it was associated with the aquarium industry (Creese et al. 2004). Australia's initial response was much less aggressive than in the USA, in part because *C. taxifolia* is native to Queensland. Eventually, *C. taxifolia* was declared a noxious weed in NSW and South Australia. Sandwiched between the two invaded states, uninvaded Victoria declared *C. taxifolia* a noxious weed in 2004. After a 90-day amnesty period, it was illegal to bring into Victoria, or take, hatch, keep, possess, sell, transport, put in any container, or release *C. taxifolia*. While total eradication of *C. taxifolia* from NSW waterways is unlikely, hopefully resource managers will be able to prevent further spread of *C. taxifolia*. Both Australia and NZ have established national systems of port baseline surveys using standardized methods (Hewitt and Martin 2001; Ruiz and Hewitt 2002).

The response of countries surrounding the Mediterranean documents how difficult it can be to create multinational regulations. In 1994, 10 years after the Monaco invasion, the Barcelona Appeal was a call by scientists to list the spread of *C. taxifolia* as a major threat to Mediterranean ecosystems. In 1996, Article 13 of the Barcelona Convention Protocol on Specially Protected Areas provided legislation regarding the introduction of nonnative species. In 1998, a delegation recommended that all affected countries establish regulations to limit the invasion. Several governments and regional entities have since banned selling, buying, using, and dumping this seaweed. Currently, however, there is no coordinated, multinational effort underway to eradicate *C. taxifolia* in the Mediterranean.

15.7 Problems with Other Species in the Genus *Caulerpa* and Final Concerns with *C. taxifolia*

As little as we know about controlling and managing *C. taxifolia*, we know even less about other species of *Caulerpa* that may cause ecological and economic problems. Included is *Caulerpa racemosa* var. *cylindracea* (Sonder) Verlaque, Huisman et Boudouresque, a southwestern Australian variety, that is expanding dramatically in the Mediterranean and surrounding Atlantic waters (Belsher et al. 2003; Verlaque et al. 2000, 2003, 2004; Ruitton et al. 2005; Piazzi and Ceccherelli 2006). In Mediterranean waters, *C. racemosa* has been spreading faster and to more locations than *C. taxifolia* (Ruitton et al. 2005). In some cases in the Mediterranean, *C. taxifolia* outcompeted *C. racemosa* (Ruitton et al. 2005), while in other locations the reverse was true (Piazzi and Ceccherelli 2002; Piazzi et al. 2003). After over 2 years of rapid growth, natural disasters in the form of repeated hurricanes removed nonnative *Caulerpa brachypus forma parvifolia* from coral reef areas in south Florida (Lapointe et al. 2006). Although native, blooms of *Caulerpa* also can alter ecosystems. Blooms of *C. verticillata* (south Florida, Lapointe et al. 2006), *C. prolifera* (west coast of central Florida, Stafford and Bell 2005), and *C. sertularioides* (Costa Rica, Fernandez and Cortes 2004) have been described in recent years. Preventing new invasions, locating and eradicating invaded populations while small, and managing large populations once eradication is deemed impossible continue to be issues of global concern with *C. taxifolia* and many additional species in this genus. At the present time, we are a long way from being successful. Much more research is needed to make us globally proactive.

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