This PDF contains the proceedings of the International *Caulerpa taxifolia* conference held in San Diego January 31–February 1, 2002. The papers presented at the conference are included as well as the detailed results of the group discussions and breakout sessions.

It is hoped that this will provide an understanding of the biology of the invasive strain of *C. taxifolia*, the various options for its eradication and control, and the most successful strategies for education and outreach as an aid in the definition and refinement of future priorities in these areas.

The editors wish to thank all the many U.S. and international participants and the agencies who provided funding (credited in the acknowledgments), as well as the other contributors who helped to make the conference a success.

The distribution of these proceedings as a PDF allows for the inclusion of the entire proceedings as well as full color graphics and digital images.

—Ted Grosholz and Erin Williams, editors

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Introduction

Among the many invasions that have stressed coastal marine systems in recent years, none have had such broad-reaching biological and political impacts as the *Caulerpa taxifolia* invasions of the Mediterranean Sea, Australia, and the United States (U.S.). From its initial invasion of the northwest Mediterranean in 1984, to its discovery in Agua Hedionda Lagoon and Huntington Harbour in the summer of 2000 in California, this invasive alga has produced dramatic changes both in the biological landscape of coastal bays and estuaries and the political landscape of invasive species management.

Few could have predicted the coordinated response and the wealth of resources that have been directed to the *C. taxifolia* invasion in Southern California over the last two years. And though the efforts in Southern California in many ways represent a model of successful eradication for future invasions, many questions remain unanswered about the details of the eradication process and how the management, research, and education efforts here compare with similar efforts in Europe and Australia.

In order to evaluate the status of the eradication efforts, we felt it was important that the *C. taxifolia* eradication efforts in the U.S. learn from the successes and failures experienced in the other *Caulerpa taxifolia* invasions and that this information would help guide future efforts in the U.S. Much of the information from the European and Australian invasions had not been published or was not easily accessible in the U.S. Consequently, we brought key researchers, managers, and educators from Europe, Australia, and the U.S. who have been involved with *C. taxifolia,* or generally with introduced species issues in their region, to participate in a two-day conference. The main objective was to allow the opportunity for researchers, managers, and educators to share their experiences and expertise with one another with the overall goal of informing those involved in the current struggle to eradicate and prevent the further spread of *C. taxifolia* in California.

With these goals in mind, we sponsored this two-day conference in San Diego, California with financial assistance from the California Department of Fish and Game, the United States Fish and Wildlife Service, and the California Sea Grant College Program. We invited scientists, managers, and educators from France, Italy, the Netherlands, Croatia, Mexico, Australia, and the U.S. to present their work and to provide their own personal experiences. The first day of the conference involved scientific presentations by researchers and managers from all three invasions, with additional presentations about the U.S. invasion and the current status of management, research, and education in California. The second day focused on bringing together information available in group discussions to develop a listing of options and priorities for management, research and education for the U.S. invasion.

The results of these presentations and discussions are presented within the following proceedings with a few omissions. The proceedings include summary papers containing both previously published and unpublished work on a wide range of issues concerning the invasion of *Caulerpa* and issues concerning similar invasive species and their habitats. We have attempted to put together all the information presented in a way that accurately reflects how this information was presented at the conference. We hope that this information will help guide future eradication efforts in both the U.S. and elsewhere.

Edwin Grosholz
Erin Williams
University of California, Davis

Caulerpa taxifolia . . .

International
Caulerpa taxifolia
Conference
Proceedings
Abstracts

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Overview of the Genus *Caulerpa*

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Caulerpa is one of the most distinctive genera of seaweeds, being identifiable solely on the basis of its habit. The thallus, a nonseptate siphonous structure, consists of a creeping rhizome that produces tufts of colorless rhizoids downward and photosynthetic branches (assimilators) upward. A thin layer of cytoplasm, containing countless numbers of each type of organelle, is appressed to the wall. The assimilators assume many different forms. This distinctive habit was recognized as a generic character in 1809 by Lamouroux, who initially placed eight species in the genus, including five that had previously been described as species of *Fucus*.

In addition to its habit, *Caulerpa* has a distinctive suite of anatomical, cytological, and biochemical characters, including reinforcement of the siphonous structure by anastomosing strands of wall material (trabeculae), division of labor between photosynthetic chloroplasts and starch-storing leucoplasts (heteroplastidy), presence of siphonaxanthin and siphonein as photosynthetically active pigments, and replacement of cellulose by xylan as the skeletal constituent of the wall. While these characters are of great importance in relating *Caulerpa* to other siphonous genera, they are not demonstrably useful in infrageneric taxonomy.

Approximately 75 species are currently recognized, all of which inhabit warm waters. The polymorphism of certain species of *Caulerpa* is well known. From a taxonomic standpoint, the *C. racemosa-laetevirens-peltata* complex is notoriously difficult. Experimental analysis is essential to determine the effects of genetics vis-à-vis environment in this polymorphism. Many species show relatively little variation, and vegetative reproduction occurs readily by fragmentation. Sexual reproduction is uncommon, but when it does occur almost all of the protoplast of a thallus is converted into biflagellate gametes, which are discharged through papillae. The zygote develops into a protonema, which then forms a typical diploid thallus. *Caulerpa*, like *Bryopsis* and *Codium*, produces weedy strains, whose relationship to well-behaved strains is poorly known.

Introduction for the International *Caulerpa taxifolia* Conference

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The tropical green alga *Caulerpa taxifolia* is still spreading in the Mediterranean since its introduction in 1984. At the end of 2000, approximately 131 km^2 of seashore are affected by 103 independent colonies established along 191 km of coastline in six countries (Spain, France, Monaco, Italy, Croatia and Tunisia). The temperate Pacific waters of California, Japan, and Southern Australia are also invaded by *C. taxifolia*. Large regions neighboring the invaded areas appear favorable to further colonization; thus, there is no reason to believe that the spread will slow down in the following years.

We will discuss our progress after ten years of research on this important marine invader. The main topics are sexual reproduction, growth rates, biomass, vegetative development, morphology, resistance to cold water, repellant toxins, genetics, and karyology. All of our studies show the peculiarities of the invading strain suspected to be a vegetative clone selected after 20 years of aquarium culture, coming originally from the region of Moreton Bay, Australia. In the largest invaded regions, the dominance of *C. taxifolia* impacts the biodiversity of many algae, invertebrates and fishes. Two characteristics increase these problems: the alga is ubiquitous, growing in a large range of the littoral ecosystems, and it is not grazed by temperate fishes or invertebrates. This important invader requires management efforts and international awareness.

Tracing Invasions With Genetic Markers

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Comparative sequence data from the rDNA ITS have proven very useful in species identification and identifying major biogeographic groups of *Caulerpa taxifolia*. However, the low variability of the sequence, its mode of evolution, and the need to screen hundreds of samples have limited its utility for population level studies. Here we report on the performance of two new markers suitable for population level screening: the chloroplast rDNA 16S intron 2 and inter-simple-sequence-repeat fingerprints (ISSRs). Variability of the new chloroplast marker (also compared against ITS2) and ISSR fingerprints were tested in 110 individuals. A new analysis of ITS1 insertion-deletion patterns was also conducted using all available sequences (>200).

A number of new insights have emerged. First, the invasive aquarium strain (Mediterranean and Carlsbad, California) is clearly from Brisbane, but the Brisbane populations themselves may be the result of an introduction from Northern Australia. Second, an analyses of the new data in conjunction with an ITS1-insertion-deletion analysis further suggests that the Mediterranean populations may be the result of not one, but two separate introductions. Third, intrapopulation genetic diversity between invasive Mediterranean and "native" Australian populations revealed the occurrence of two divergent and widespread clades. The first clade grouped nontropical invasive populations with coastal inshore populations of Australia, while the second clustered all offshore/oceanic populations studied to date. *Caulerpa taxifolia*, therefore, exists as a complex of independent ecotypes that probably represent nascent species. Fourth, despite our finding of nine distinct nuclear and five distinct chloroplast profiles, strong linkage disequilibrium was found in most specimens, which indicates a predominance of asexual reproduction. However, nucleocytoplasmic recombination was detected in one case, supporting hybridization both within and between populations. Finally, we recommend that further population-genetic-level studies be undertaken in *Caulerpa* species—and also in the seagrass *Zostera marina*. Recent genetic surveys of meadow architecture in different geographic regions have revealed a wide range of diversity—from single clonal meadows to genetic mosaics. If the Carlsbad meadows of *Zostera marina* are old and clonal (which we suspect), then they may have substantially lower recovery chances following aggressive eradication efforts of *C. taxifolia.*

The Spread of *Caulerpa taxifolia* in the Mediterranean: Dispersal Strategy, Interactions With Native Species, and Competitive Ability

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The results of several experimental studies carried out in the field are presented as a contribution to understanding the performance of *Caulerpa taxifolia* in the Mediterranean. Identification of an efficient dispersal strategy, biotic factors that enhance performance, and considerations of its competitive ability are given. Evaluation of the importance of thallus fragmentation of *C. taxifolia* as a dispersal strategy revealed that a surprisingly high number of fragments reestablished at the margin of *Posidonia oceanica*, where they had dispersed. A descriptive study and an experimental manipulation of seagrass canopy type indicated that *P. oceanica* and *Cymodocea nodosa* stimulated the size and density of the alga by means of shelter rather than shade. The spread of *C. racemosa* and *C. taxifolia* in macroalgal assemblages of different complexity was also studied. Results showed that turf habitat was more favorable than encrusting species alone, while the least advantageous habitat was one where the macroalgal assemblage was left undisturbed and was the most structured (e.g., erect, turf, and encrusting). Overall, the performance (as stolon cover and blade density) of *C. taxifolia* was higher than that of *C. racemosa*. Evaluation of intra- and interspecific interactions between two introduced algae, *C. taxifolia* and *C. racemosa*, showed that positive interactions within species were very important. However, while there was a significant interspecific effect of *C. racemosa* on *C. taxifolia* stolon length, the reverse was not observed.

Appearance and Eradication of *Caulerpa taxifolia* in Croatia

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By the end of 2001, in the Croatian part of the Adriatic Sea, an invasive species *Caulerpa taxifolia* (Vahl) C. Agardh had been found in three distant areas: in Stari Grad Bay (Hvar Island) during the summer of 1994, in Malinska (Krk Island) at the end of 1994, and in Barbat Channel (between the Islands of Dolin and Rab) at the end of 1996. It was estimated that the alga was brought into the areas of Stari Grad Bay and Malinska in 1991, and into Barbat Channel in 1995.

At the time of first observation in Barbat Channel, this alga covered about 20 m^2 of the rocky and sandy bottom in depths ranging from 2.5 to 8 m. The colony was manually extracted after 130 hours of diving. During the summer of 2001, a large new colony of approximately 100 m^2 was found 200 m from an area which had been previously eradicated.

In the area of Malinska, four large stations on a muddy-sandy bottom between depths of 3 and 12 m were observed until the end of 2001. Eradication was performed during 1996 and 1997. The alga was pumped together with 10 cm of muddy bottom, using a suction water pump. The material was filtrated through a system of sieves.

The alga was completely eradicated from the area of the harbor, where it had covered about 1,300 m^2 of 16,000 m^2 of the affected sea bottom. In the other colonies (1,900 m^2 of the total covered surface), recolonization of the algae occurred due to the remains of algae thallus after eradication. Eradication efforts stopped in 1997 because of financial problems.

In Stari Grad Bay, until the end of 2001, one central and ten distant stations were infested. The affected area was 39 ha in the central station, and less than 100 m^2 in the distant stations. Although some of the distant colonies were established five years ago, systematic controls and eradication using suction pumps and covering with black PVC foil, restricted their spread and, in some cases, totally removed them.

The Introduction of *Caulerpa taxifolia* in New South Wales, Australia

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On the eastern seaboard of Australia, *Caulerpa taxifolia* is native as far south as the Nerang River, Southport, Queensland. It also occurs naturally at Lord Howe Island (geopolitically part of NSW), some 600 km northeast of Sydney. The first population of *C. taxifolia* was discovered in Port Hacking just south of Sydney Harbour, in April 2000. It is estimated to cover approximately 2 hectares. The second population (about 10 hectares) was discovered in the almost landlocked Lake Conjola, about 200 km south of Sydney. In December 2000, a small, 400 sq m population was found at Careel Bay, in Pittwater (next to the Royal Sydney Yacht Squadron), just north of Sydney. In February 2001, a population was found in Lake Macquarie, again just north of Sydney, and in April 2001, a population in Lake Burrill, near Batemans Bay, was also confirmed. In all situations, the plants are growing associated with *Posidonia australis* seagrass beds, in shallow water (1–10 m) and in very sheltered estuaries. The cold tolerant (10˚C), fast growing (4 cm/day) strain is smothering these beds.

Genetic information (see Jousson et al. 2000, Nature vol. 408, November 9, 2000), suggests that there have been two separate introductions. Those from Lake Conjola are related to Moreton Bay, Queensland, populations and those from Port Hacking from Gladstone, Queensland. The alga was listed as a Noxious Species by the parliament of New South Wales (NSW) on October 1, 2000; it cannot be bought, sold, traded, or kept in an aquarium in NSW. Eradication has been deemed impossible, but preliminary attempts showed that a 4 sq m patch could be cleared by two divers (without any mechanical suction device) in one hour. This patch grew back in six months. Smothering with rock (sea) salt has shown partial success in that it kills the *C. taxifolia* assimilators, but the health of the rhizoids imbedded in the soft sediment has yet to be determined.

Morphological Plasticity and Invasive Potential of Some *Caulerpa* Species

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No general rules have been developed to explain why some plant species are more invasive than others. Nevertheless, invasiveness has been predictable in some species on the basis of a small number of simple biological characters. The biological traits associated with the invasiveness of *Caulerpa taxifolia* are: a) high growth rate; b) nutrient uptake from sediments; c) tolerance to low water temperature; d) lack of consumers; and e) clonal growth form. Clonality allows *Caulerpa* to cover new areas through vegetative growth, disperse by fragmentation, avoid senescence by continual production of modules, and use resources opportunistically by modifying morphology and physiology. These attributes have been described for other *Caulerpa* species, which means that some of them are potentially invaders. In this presentation I will focus on morphological plasticity as a key invasive attribute, comparing this trait among seven *Caulerpa* species native to the Caribbean Sea. In field studies, particular growth forms characterized different reef habitats, and each species had different ranges of morphological and physiological plasticity. Species with compact forms were associated with general reef conditions. In contrast, species with open forms were present in lagoon conditions. *C. cupressoides* was the only species that appeared in both forms, and this phenotypic plasticity allowed it to live in both reef and lagoon conditions. Further, this particular species produces toxins against herbivores and incorporates nutrients from sediments, so it is a strong candidate to become an invasive species if introduced into different regions. The genus *Caulerpa* includes 73 species worldwide with several in the aquarium trade. Comparative studies among *Caulerpa* spp. using key attributes will aid the development of scientifically sound import policies to avoid future introductions.

Chemical Ecology of *Caulerpa* spp. With an Emphasis on Invasive *Caulerpa taxifolia*

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Green algae of the family Caulerpaceae, represented by the single genus *Caulerpa*, are found worldwide, generally in shallow water tropical and subtropical marine habitats. All species, which are traditionally separated by their distinct morphologies, possess a rhizome that produces erect blades and rhizoids that penetrate sediments. The natural products of at least 14 species of *Caulerpa* from around the world have been studied, and most species, including the Mediterranean *C. taxifolia*, produce the sesquiterpene caulerpenyne as a major metabolite. Caulerpenyne concentrations are often 2% or more of algal dry mass and are higher in the erect blades than in the rhizoids. Various biological effects including toxicity have been attributed to caulerpenyne; however, the activities of the compound against ecologically relevant organisms have been studied in only a few cases. In the tropics, most species of *Caulerpa* are readily consumed by herbivorous reef fishes such as rabbitfishes (Siganidae) and surgeonfishes (Acanthuridae). Crude extracts of several species of *Caulerpa* as well as caulerpenyne do not deter feeding by any species of herbivorous fishes against which they have been tested. A few tropical species of *Caulerpa* including *C. ashmeadii* and *C. bikinensis*, which produce sesquiterpene aldehydes instead of caulerpenyne, have chemical defenses against herbivorous reef fishes. Mediterranean collections of *C. taxifolia* are known to produce caulerpenyne, oxytoxins, taxifolials and other terpenes. Recently, a wound-activated transformation of caulerpenyne to oxytoxins has been described for Mediterranean *C. taxifolia. Caulerpa taxifolia* is unpalatable to generalist herbivores in the Mediterranean (where herbivorous fishes are not present) and can affect the physiology of sympatric fishes. The chemical defenses of *C. taxifolia* appear to have facilitated this biological invasion, which is greatly affecting the benthic community structure in areas where it occurs.

Invasion Ecology of *Codium fragile* ssp. *tomentosoides*: Implications for *Caulerpa taxifolia* Incursions

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Several taxonomically and ecologically diverse macroalgae have become aquatic nuisance species, or even pest species, after anthropogenic introduction to new geographic regions. Research on native and introduced subspecies of *Codium fragile* (Chlorophyta) has important implications for *Caulerpa taxifolia* management. (1) *Codium* and *Caulerpa* are two of the most species-rich genera of marine algae; within each genus, different species, subspecies, or strains exhibit a highly variable degree of invasiveness. Comparisons of suites of related taxa reveal which attributes render some taxa particularly good at establishment and spread. (2) *Codium* and *Caulerpa* belong to different algal orders but share numerous structural, functional, and ecological attributes. Both taxa are coenocytic and have small, robust chloroplasts; both are preyed on by specialized, suctorial herbivores (sacoglossan sea slugs). Many species of *Codium* and *Caulerpa* exhibit thallus fragmentation and extensive regeneration, possibly precluding any eradication efforts. (3) Past ecological research on invasive species of *Codium* and *Caulerpa* has been insufficiently rigorous to provide resource managers with a comprehensive understanding of the risks of establishment and invasive spread. Research on the nature and magnitude of interspecific interactions, particularly with native grazers, is critically needed. Experimental research on sacoglossan host-switching and herbivory demonstrates a high risk associated with biological control proposals.

The Availability of *Caulerpa* spp. and "Live Rock" in Retail Aquarium Outlets in Southern California

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During the last two years, invasive populations of *Caulerpa taxifolia* were found in the coastal waters of southern California. This has attracted much attention because this exotic seaweed is thought to have significantly altered the structure of marine ecosystems in the Mediterranean Sea following its 1984 invasion. The local inoculation of *C. taxifolia* is believed to have resulted from the release of aquarium specimens. In addition to *C. taxifolia*, other species of *Caulerpa* being sold for aquarium use also may have the potential to invade Californian waters. As a first step towards making this determination, an investigation was conducted on the availability (percentage of frequency) of *Caulerpa* species sold in southern California for aquarium use. Fifty retail saltwater aquarium stores were visited in Los Angeles, Orange, and San Diego counties between November 2000 and August 2001. At least one of 16 identified *Caulerpa* taxa were sold at 52% of these stores. The most commonly sold species were "*Caulerpa taxifolia,*" Mediterranean form, which was offered for sale in 10% of the stores visited, *Caulerpa serrulata var. hummii* (18%), *C. racemosa* (14%), and *C. racemosa var. lamourouxii* (also 14%). In addition, "live rock" (with attached marine plants and animals), was sold in more than 90% of the visited outlets. These data indicate that the aquarium industry is bringing into the region many other species of *Caulerpa* besides *C. taxifolia*, and an unknown number of additional exotic marine species are being offered for sale as "live rock." Some of these species may also have the potential to invade temperate southern California waters.

The Role of Science in Management of the *Caulerpa taxifolia* Invasion in Southern California

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A consensus has formed in the United States that management of marine life should be based on science and take an ecosystem approach. In California, this perspective was mandated in the Marine Life Management Act (Assembly Bill 1241) in 1998. A keystone of the act is that marine ecosystems will be maintained to provide sustainable fisheries and that management of marine life will be based on science. Scientific peer review is the tool mandated to help achieve science-based resource management. Science is needed to address management questions regarding the *Caulerpa taxifolia* invasion in California; for example: to what degree does *C. taxifolia* threaten our marine ecosystems, how far and fast can it spread, is eradication/control effective, how can new introductions be prevented? I will summarize the ongoing science of the California invasion and pose specific scientific questions of critical importance to management that remain to be addressed.

Caulerpa taxifolia in the United States:
Rapid Response and Eradication Program

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Less that four weeks following the June 12, 2000 discovery of *Caulerpa taxifolia* in Agua Hedionda lagoon near Carlsbad, California, containment and chemical treatments began. Colonies of plants were covered and sealed beneath PVC tarps and liquid chlorine was injected. In some cases solid chlorine tablets were used. Monitoring so far has not revealed any open-coast populations. A coalition of essentially "ad hoc" agencies and other interested stakeholders formed the Southern California *Caulerpa* Action Team (SCCAT) within two weeks after the discovery. The Southern California *Caulerpa* Action Team provided a highly effective advisory forum, the focus, direction, and energy needed to develop and sustain the eradication program, as well as critically important educational outreach. Additionally, SCCAT facilitated an effective campaign that resulted in the state legislation to ban C. *taxifolia* and eight other species in September, 2001. With the subsequent discovery of *C. taxifolia* at Huntington Harbour, SCCAT reacted quickly to tailor eradication methods to fit that site. The SCCAT Steering Committee includes representatives from California Department of Food and Agriculture, California Department of Fish and Game, San Diego Regional Water Quality Control Board, US Department of Agriculture–Agricultural Research Service, and the National Marine Fisheries Service.

Several key processes and related decisions made this "rapid response" possible: (1) confirmation of species sufficiently quick; (2) communication to appropriate state and federal resource and research agencies immediate; (3) institutional "learning curve" steep, but short due to documented impacts of *C. taxifolia* in the Mediterranean *and* to prior experience and successes with other invasive aquatic plants (e.g., *Hydrilla verticillata*); (4) early consensus to eradicate (rather than "manage"); (5) resolution of regulatory and "permitting" issues; (6) field crew in place with funds and other resources sufficient to act (Merkel and Associates); (7) cooperative, dedicated, and committed people.

First year program costs were approximately $1.1 million; a similar amount is needed for the second and continuing years to support monitoring, surveillance and eradication. To date, funding has come from a variety of public agencies, and some private sources. In December 2001, sediment cores were taken to assess eradication efforts. Placed in controlled, "grow-out" conditions, cores from treated areas have not produced any *C. taxifolia* up to 76 days post-sampling. Additional bioassay assessments will be conducted over the next 5 years to document and insure eradication.

Summary of Mediterranean Invasion and Management

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Since its introduction at Monaco in 1984, *Caulerpa taxifolia* is still spreading in the Mediterranean Sea. Centralized monitoring efforts, within the framework of two European programs (Life DGXI) led to the regular survey of the *C. taxifolia* invasion until 1997. Since then, the spread of the alga has been monitored independently country-by-country by several international groups. These observations, coming from the countries concerned with the *C. taxifolia* invasion, have been brought together in an effort to assess current invasion status. Consequently, standardized methods were established to measure the temporal and spatial scale of the spread of this alga. Thus, regional or global status can be described and compared from one year to the next.

At the end of 2000, approximately 131 km^2 of benthos were infested by 103 independent colonies of *C. taxifolia* along 191 km of coastline in six countries (Spain, France, Monaco, Italy, Croatia, and Tunisia). In France in the summer of 2001, more than 30 new independent areas of colonization were discovered. The main characteristics of the invasion in each country will be presented. These include changes in surface area, the number of independently colonized areas, the linear extent of coastline adjacent to the colonies, the organization of the monitoring efforts, and any local eradication measures that may have affected the spread.

Management Successes and Failures in the Mediterranean

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Monitoring (mapping) and public awareness was the only effort made by the concerned countries. Control of the invasion was never a priority for most of them.

In France, regular control of the alga only occurs in the waters of the national park of Port-Cros, where control efforts (manual removal or application of a cloth soaked in copper salts) have been performed annually since 1994. Fifteen tiny isolated colonies have been successfully eradicated.

In Spain, since the first discovery in 1992, regional authorities tried to slow down the spread of the alga by using an airlift sediment sucker, or exposing the alga to copper ions.

In Italy, except for a few eradication attempts made at the onset of the invasion, no control strategy has been established.

In Croatia, control measures have been implemented annually by covering isolated colonies with black plastic sheets and removing the alga with a suction pump.

In Tunisia, no control strategies have been made.

The present state of the Mediterranean invasion is critical and it is useless to try to eradicate the alga. The best option would be to preserve the biodiversity of selected sanctuaries against the invasion by regular control of new *C. taxifolia* recruitment.

Modeling the spread can help decision makers with their choice of strategy. A simulation model taking into account the biology of *C. taxifolia*, the season and the spatial characteristics is now used, as a predictive tool, in some places in the Mediterranean. Modeling results are accurate over 4–5 year time periods.

A global solution for the management of *C. taxifolia* could be biological control. The evaluation of Mediterranean and tropical specialist grazers (Mollusca, Opisthobranchia, Sacoglossa) show that the indigenous species are inefficient, but that the tropical *Elysia subornata* provides some hope, if a cold-resistant strain of this species could be found.

Reproduction of *Caulerpa taxifolia* in the Mediterranean Sea

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The introduced tropical alga *Caulerpa taxifolia* (Vahl) C. Agardh has been rapidly spreading since the mid-1980s throughout the Mediterranean Sea. This expansion is a result of wide ecological range of substrates, habitats, light, temperature and nutrients, and the lack of predatory species, and extremely successful vegetative reproduction. Regeneration of a whole alga is possible from each part of the algae thallus: fronds and pinnules, stolons or hairlike tiny rhizoids. In nature, vegetative reproduction most often occurred due to cuttings of fronds. At 25ºC, formation of a whole small plant including fronds, stolons and rhizoids, from a cutting, occurred within 10 days following a similar pattern of regeneration. The regeneration from small pieces of thalli becomes a great problem during eradication efforts, because such small fragments are almost impossible to find and collect in the field.

In tropical regions, this monoecious species also reproduces sexually by producing both types of gametes inside the same plant. In the Mediterranean Sea, thalli of *C. taxifolia* became fertile. They are easily detected in the field due to reticulate depigmentation and development of papillae mostly on the frond axes. The gametes are released around 27 minutes before sunrise. After release of gametes, the parental plant dies. In the Mediterranean Sea, only male gametes (without pigmentation) were observed. Despite prolific release of male gametes, sexual reproduction does not occur because female gametes are absent. The reason for the absence of female gametes remains unknown.

Caulerpa taxifolia . . .

International *Caulerpa taxifolia* Conference Manuscripts

January 31 – February 1, 2002
San Diego, California U.S.A.

Caulerpa taxifolia . . .

An Overview of the Genus *Caulerpa*

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Caulerpa is one of the most widespread, conspicuous, and abundant seaweeds in tropical, subtropical, and certain temperate waters. It has been used for food for many centuries by Japanese, Polynesians, Filipinos, and Indonesians. *Caulerpa* was first brought within the realm of western science by Samuel Gottlieb Gmelin who in 1768 described what came to be known as *C. sertularioides* from the West Indies (Fig. 1).

A few years later, four more species were described in a manuscript by the botanical collector Pehr Forsskål, a Danish naturalist who explored lower Egypt and the eastern side of the Red Sea. This work was edited and published in 1775 following his untimely death at the age of 31 (Fig. 2). However, because Forsskål's manuscript was not illustrated, many of his new species were of uncertain identity.

As far as the algae are concerned, this uncertainty was not settled until 1932, when another Danish naturalist, Frederick Børgesen, rediscovered specimens sent by Forsskål to Copenhagen. Among these were *C. prolifera* (Fig. 3), which Forsskål found at Alexandria and which has proved to be widespread throughout the Mediterranean, and three species from the Red Sea: *C. racemosa*, *C. serrulata*, and *C. plumaris*—the latter now believed to be conspecific with *C. sertularioides* from the West Indies. Two well-known species, *C. cupressoides* and *C. taxifolia* , were described exactly two centuries ago by still another Dane, Martin Vahl (Vahl 1802), on the basis of collections made at St. Croix in the Danish West Indies (renamed the Virgin Islands after being purchased by the United States in 1917). All of these were originally placed in the genus *Fucus* in accordance with the classification of Linnaeus ("Species Plantarum" 1753), who applied this name to a genus that comprised all fleshy forms of algae.

The genus *Caulerpa* was described near the beginning of the 19th century by Jean Vincent Félix Lamouroux, a French botanist of remarkable insight. Two important contributions were made by Lamouroux. He was the first to recognize the importance of pigmentation in the classification of seaweeds, thus providing the basis for currently accepted divisions or phyla of red algae (Rhodophyta), brown algae (Phaeophyta), and green algae (Chlorophyta). Equally important, he was one of the first to address the heterogeneity of the classical Linnaean genera of seaweeds by proposing segregate genera, one of which was *Caulerpa*. Hundreds of other species of fleshy seaweeds of widely divergent morphology had been described in the half-century following the publication of the "Species Plantarum," all of which had been assigned to *Fucus*.

Between 1809 and 1813, Lamouroux segregated numerous genera from this unwieldy mass, including such well-known genera as *Anadyomene* and *Bryopsis* in the greens, *Desmarestia*, *Dictyopteris*, *Dictyota*, and *Laminaria* in the browns, and *Amansia*, *Delesseria*, *Furcellaria*, and *Gelidium* in the reds. Among those organisms that Linnaeus considered to be neither typical plants nor typical animals, and which he therefore called zoophytes, Lamouroux described such well-known genera as *Acetabularia*, *Amphiroa*, *Cymopolia*, *Galaxaura*, *Halimeda*, *Jania*, *Liagora*, *Melobesia*, *Neomeris*, *Polyphysa*, and *Udotea*.

Caulerpa was conceived by Lamouroux (1809; Fig. 3) to comprise forms that had a horizontal, cylindrical, essentially hollow, creeping stem bearing fibrous rootlike structures downward, and leaflike structures upward. When Lamouroux observed the alga through his microscope, he could not discern a distinct structure. He recognized eight species in the genus, including four of the six species mentioned above. These four species, in addition to *C. peltata* (a newly described species), were illustrated by Lamouroux (Fig. 4).

Lamouroux made some interesting observations. Looking at the fibrous rootlike structures, he hypothesized that *Caulerpa* inhabited soft substrates, which were universally common, and therefore *Caulerpa* was probably much more abundant in nature than its representation in herbaria would indicate. This was further borne out by the fact that collectors routinely head for rocky outcrops or rummage through the drift, avoiding muddy shores. Perceiving *Caulerpa* to have animal-like characters as well as plant-like characters, Lamouroux sought guidance from a well-known chemist, Nicolas-Louis Vauquelin. Analysis of a sample of *Caulerpa* gave the following results:

1. A small quantity of water
2. A thick, reddish brown oil with an extremely fetid odor
3. Ammonium carbonate
4. Prussic acid (hydrocyanic acid, hydrogen cyanide)
5. An abundance of carbon

Lamouroux compared this analysis with previously published analyses of red and brown algae and concluded that more animal products were present than plant products. Still, the overall appearance of *Caulerpa* was plant-like. Obviously uncertain, he decided to assign the genus provisionally to the plant kingdom awaiting a definitive decision by some future worker. All subsequent authors, however, have accepted Lamouroux's decision as definitive rather than provisional.

Lamouroux formed the name of the genus from two Greek words, *caulos*, a masculine noun meaning "stem," and *erpo*, a verb meaning "I creep." Noting the brilliant color of certain species, he was tempted to name the genus *Lucidia*, but considered the habit of greater importance and thus decided on *Caulerpa.*

From the beginning, the resemblance of the leaflike uprights to the foliage of various genera of plants, both higher and lower, was noted and reflected in the selection of epithets. Thus we have *C. asplenioides* (like *Asplenium*, the spleenwort fern); *C. cactoides* (like cactus) (Fig. 5); *C. charoides* (like *Chara*, the stonewort); *C. cupressoides* (like *Cupressus*, the cypress tree); *C. sedoides* (like *Sedum*, the stonecrop); and *C. selaginoides* (like *Selaginella*, a clubmoss). Also, we have *C. ericifolia* (like the leaf of *Erica*, a heath); *C. taxifolia* (like the leaf of *Taxus*, the yew tree); *C. lycopodium* (recalling *Lycopodium*, a clubmoss); and *C. ophioglossum* (recalling *Ophioglossum*, the adder's tongue fern).

The habit of *Caulerpa* by itself proved to be a remarkably reliable guide for a succession of authors. In a compendium of seaweeds on a worldwide basis, C. Agardh, a Swedish botanist, recognized 19 species (1822) while his son, J. Agardh, published the first monographic study of the genus in 1873, in which he distributed 64 species among 13 sections. These sections, which had been treated as separate genera by a few authors in the middle of the 19th century, were based on the gross morphology of the uprights. Species without leaflike uprights (e.g., *C. fastigiata*) were placed in one group, contrasted with those with simple leaflike uprights (e.g., *C. prolifera*) (Fig. 6), those with pinnately divided leaflike uprights (e.g., *C. taxifolia*) (Fig. 7), and those with compoundly divided leaflike uprights (e.g., *C. cupressoides*).

The segregation of genera based on the habit was soon abandoned because it ignored the single most important unifying generic character, namely, the strengthening of the thallus by an internal network of strands of wall material that extend from one wall, across the lumen, to the opposite wall. These strands, which are called trabeculae, were first mentioned by Montagne (1837), a French cryptogamic botanist, in his description of *C. webbiana* from the Canary Islands.

In a more extensive study, Montagne (1838) found trabeculae in all eight species that he examined. He correctly concluded that they constituted a definitive generic character. He noted that Turner (1811: 93, pl. 173, figs. d and 3) had mentioned and illustrated these trabeculae for an Australian species, *Fucus hypnoides* R. Brown ex Turner [*C. hypnoides* (R. Brown ex Turner) C. Agardh], but considered their presence to be a specific character. Montagne was mildly critical of Turner for failing to determine the extent of this character among the many other species of *Caulerpa* that Turner treated (all as species of *Fucus*). The structure of these trabeculae was first studied by Nägeli (1844) and later, more precisely by Dippel (1876). In essence, an initial fibrillar core, which may anastomose with other cores, is strengthened by multiple layers of wall material deposited centripetally.

The maximum number of recognized species of *Caulerpa* was reached in the compilation by De Toni (1889), with a total of 80 species. Soon thereafter (1898), a monograph of the genus was published by Anna Weber-van Bosse, a Dutch phycologist, and none have been published subsequently. Retaining J. Agardh's sections, Weber-van Bosse recognized only 54 species, but in 23 of these she distinguished varieties and forms, a total of 36 and 58, respectively, excluding those infraspecific taxa that include the type of the specific name. Many of the varieties are based on previously published species, while the forms represent minute morphological differences.

When establishing *Caulerpa*, Lamouroux had commented on the presence of intermediate forms, and he wondered whether his new species *C. ocellata* (from the Mediterranean) might be merely a variant of *C. prolifera*. Observations by subsequent workers support this synonymy. *Caulerpa* is similar to other large genera of algae, indeed of all plants, in that approximately half of the species are clearly defined, showing relatively little morphological variation. The remainder of the genus, as in all large genera, poses taxonomic problems of varying difficulty, ranging from morphologically variable species with a clearly defined range of variability, to the unmanageable polymorphic complex centering on *C. racemosa*, *C. laetevirens*, and *C. peltata*. There are numerous anecdotal accounts of morphological variability in this complex, including reports of the occurrence of more than one nomenclaturally recognized growth form on the same thallus. In situ observations confirm this situation, with shaded parts of a plant developing peltate uprights, while parts exposed to high light intensity develop cylindrical uprights. This interrelationship has been demonstrated elegantly by Ohba and Enomoto (1987) and Ohba et al. (1992), using a cross-gradient apparatus that combined five different temperatures with five different light intensities, yielding 25 different environments.

Knowing the cause of morphological variability, however, does little to help the taxonomist who is faced with a bewildering array of forms. In a recent paper on the marine green algae of Papua, New Guinea, for example, the authors (Coppejans et al. 2001) recognize 16 species and 13 nontypical infraspecific taxa of *Caulerpa*. They also provide five entries for intermediates between pairs of forms or varieties.

At the present time, approximately 75 species are recognized, with the richest area in number of species being the coast extending from western Australia through southern Australia and Victoria to Queensland. About 27 species are found in this area, and 22 species are recognized in the western Atlantic. Eighteen species are recognized in Japan.

On the Pacific Coast of North America, the northernmost populations of indigenous *Caulerpa* are found at Islam Guadalupe at 29˚N, out of range of coastal upwelling. On the Baja California mainland, however, the northern limit is 24º 30′N. In contrast, *Caulerpa* occurs on the Atlantic coast as far north as Onslow Bay, North Carolina, at latitude 34˚ 30′N. At this northern limit, however, the habitat is restricted to the subtidal (15–48 m), where the water is warmed by the Gulf Stream. The Pacific Coast of South America is truly deficient in *Caulerpa*, which occurs only as far south as Islas de Lobos in Peru at latitude 6˚ 30′S.

The unique structure of *Caulerpa* was considered worthy of taxonomic recognition at a level higher than genus as early as 1830, when Greville (1830: lxiii) proposed the monotypic family Caulerpaceae ("Calipee"), but without giving a description to validate the name. Validation was provided by Kützing (1843: 302), to whom we are indebted for many currently recognized algal families.

The Caulerpaceae has always been associated with other families of siphonous green algae, to which the name Siphonales has been applied. This name, however, may not be used because an ordinal name must be based on the legitimate name of an included genus. When the order to which the Caulerpaceae is assigned excludes the Bryopsidaceae, the correct name is Caulerpales J. Feldmann (1946: 753), but when it includes the Bryopsidaceae the correct name is Bryopsidales Schaffner (1922: 133). In an early example of hierarchical inflation, Bessey (1907) recognized two classes of siphonous algae. The Vaucheriophyceae ("Vaucherioideae") included several families of fungi together with the Cladophoraceae and genera now placed in the Codiaceae, Halimedaceae, and Udoteaceae. The Bryopsidophyceae ("Bryopsidoideae") included the Chytridiaceae together with the Botrydiaceae, Valoniaceae, Derbesiaceae, Bryopsidaceae, Dasycladaceae, and Caulerpaceae. Bessey placed these two classes in their own phylum, the "Siphonophyceae."

Considering the size, abundance, and unique structure of *Caulerpa* plants, one might expect them to engage the imagination of those biologists who were trying to determine how marine algae met their daily challenges. Because many of the better-known marine laboratories, such as Plymouth, Woods Hole, and Helgoland, were in *Caulerpa*-free areas, research was initially restricted to the Mediterranean, where *C. prolifera* was readily available at such laboratories as Villefranche-sur-Mer (near Nice) and Naples.

Early investigators (e.g., Janse 1889) were fascinated by protoplasmic streaming, which heretofore had been observed almost exclusively in the giant internodal cells of *Chara* and *Nitella*. Morphogenesis proved to be a source of amusement for several workers (e.g., Janse 1904, 1905, 1906,

1910) whose experiments showed that the frond of *C. prolifera* was both polar and medusoid. A piece of the blade would produce rhizoids basally and proliferous blades somewhat below the apex. Polarity could be overruled by geotropism, so that a blade positioned upside down would produce rhizoids from the tip. In the words of Fritsch (1935, p. 383),

> [Vegetative reproduction] takes place abundantly by a gradual dying away of the older parts of the rhizomes, whereby the branches become independent plants; by this means rapid local multiplication is effected. Dispersal is attained by detached fragments which are able rapidly to heal any exposed surface and possess a remarkable power of regenerating new plants when lodged in a suitable position.

These observations foretold of impending invasive strains.

An important physiological character of *Caulerpa*—the division of labor among plastids between photosynthetic chloroplasts and starch-storing amyloplasts—was first studied by Nägeli (1844) and later, in greater detail, by such workers as Czurda (1928). *Caulerpa* shares this character (heteroplastidy) with three other families of siphonous green algae, namely, Dichotomosiphonaceae, Halimedaceae, and Udoteaceae.

The composition of the pigments in the chloroplasts of *Caulerpa*, which are characteristic of siphonous green algae but not unique to that group, was first determined by Strain (1949), who named the distinctive xanthophyll "siphonaxanthin" and the distinctive carotene "siphonein." The first comprehensive study of the biology of *Caulerpa* was published in 1844 by Nägeli, the great Swiss botanist who was a pioneer in the study of developmental morphology, anatomy, and cytology. The standard histochemical test for cellulose at that time (and even now) is hydrolysis with sulfuric acid followed or accompanied by staining of the hydrolysate with iodine potassium iodide (IKI) solution; the hydrolysate from cellulose stains blue. When Nägeli tried this test on the wall of *C. prolifera*, the hydrolysate stained yellowish or brown. Nägeli concluded that the wall of *Caulerpa* was not like that of higher plants or other green algae, but he did not pursue the matter further.

Doubts as to Nägeli's results were expressed by two subsequent investigators but were firmly put to rest by Correns (1895). Like Nägeli, however, Correns did not attempt to determine the chemical composition of the wall. Many years later, this question was assigned to a French graduate student, Robert Mirande. Mirande (1913) concluded that the chief components of the wall were callose and pectic compounds. Callose is a complex carbohydrate found in sieve elements of higher plants. It remained for Mackie and Percival in 1959 to show that the so-called callose in *Caulerpa* was a beta-1,3 linked D-xylose or xylan. Further work in Percival's laboratory and elsewhere showed that xylan replaces cellulose in members of the Bryopsidaceae, Dichotomosiphonaceae, Halimedaceae, and Udoteaceae as well as in *Caulerpa*, while a beta-1,4 linked D-mannose or mannan replaces cellulose in *Codium* and in the Dasycladales.

For nearly a century after Lamouroux described *Caulerpa*, it was assumed that sexual reproduction in the genus was lacking. Some observers reported seeing papillae on the thallus and a reticulate pattern of the protoplast, suggesting some sort of reproductive activity. The problem was not addressed specifically, however, until the summer of 1927, when Rudolf Dostál, a Czech botanist, was working at Villefranche-sur-Mer. Dostál saw papillae on the blade of *C. prolifera*, from some of which a glob of mucilaginous material was being exuded. Buried in the mucilage were several small green cells, which he thought most likely were macrogametes. He also thought that the papilla was probably a macrogametangium. These results were published in May 1928 (Dostál 1928a). However, in summer 1928 Dostál corrected his misimpressions of the previous year. He observed holocarpic reproduction, with most of the protoplast forming swarmers, which he called spores because he did not observe copulation. These results were published in October 1928, within a month of Dostál's return to Brno (Dostál 1928b).

In February of that same year (1928), Bruno Schussnig, a professor in Vienna, took up residence at the zoological station in Naples, having received a fellowship in support of his morphological studies of marine green algae. Upon seeing Dostál's first paper, Schussnig turned his attention to *C. prolifera* and soon observed the release of anisogametes through the papillae on the blade. These observations were published in January 1929 (Schussnig 1929a). The overlapping investigations led to the publication of two polemics in successive issues of the same journal, Dostál (1929) claiming priority of discovery and accusing Schussnig of taking unwarranted credit, Schussnig (1929b) claiming independence while conceding priority.

In 1972, Ian Price showed that the quadriflagellate zygote settles on the substrate, loses its flagella, and enlarges to form a spherical body before germinating in a bipolar fashion. The germling develops into a protonema of stout green axes and pale slender rhizoids. The green axes produce uprights, thus showing that the life history of *Caulerpa* is haplobiontic with the somatic phase being diploid.

Clifton (1997) has recorded the mass release of gametes by siphonous green algae (the order Bryopsidales) on a Panamanian coral reef in intermittent predawn episodes that show no lunar or tidal cycling. Several genera, including *Halimeda* and members of the Udoteaceae, discharge gametes along with *Caulerpa*. The surrounding waters become cloudy, and the remaining colorless thalli soon disappear from the reef.

The discovery in 1984 that an aquarium strain of *C. taxifolia* had begun to colonize the area around Monaco, followed by reports on its invasion of many other areas of the Mediterranean, including the Adriatic Sea, has served as an enormous stimulus to research on *Caulerpa*. Currently, BIOSIS lists 240 references, most of which deal with some aspect of *C. taxifolia*, such as its mode and rate of spreading, possible means of control, and its biochemistry, especially the neurotoxin caulerpenyne (an acetylenic sesquiterpene) and the hormone caulerpin (a dimer of indole-3-acrylic acid).

A fascinating account of the Mediterranean invasion has been published by Meinesz (1999), who chronicles the devastation of indigenous ecosystems resulting from failure by government agencies to recognize the seriousness of the situation. Everyone involved in the California invasion would do well to heed this warning.

Acknowledgments

I thank Richard L. Moe for his critical reading of the manuscript and Max E. Chacana for preparing the illustrations.

Figures . . .

HISTORIA
FVCORVM

AVCTORE
SAMVEL GOTTLIEB GMELIN,
MED. DOCT. ACADEM. IMPER. PETROPOL. BOTANICES PROFESSORE ET MEMBRO ORDINARIO

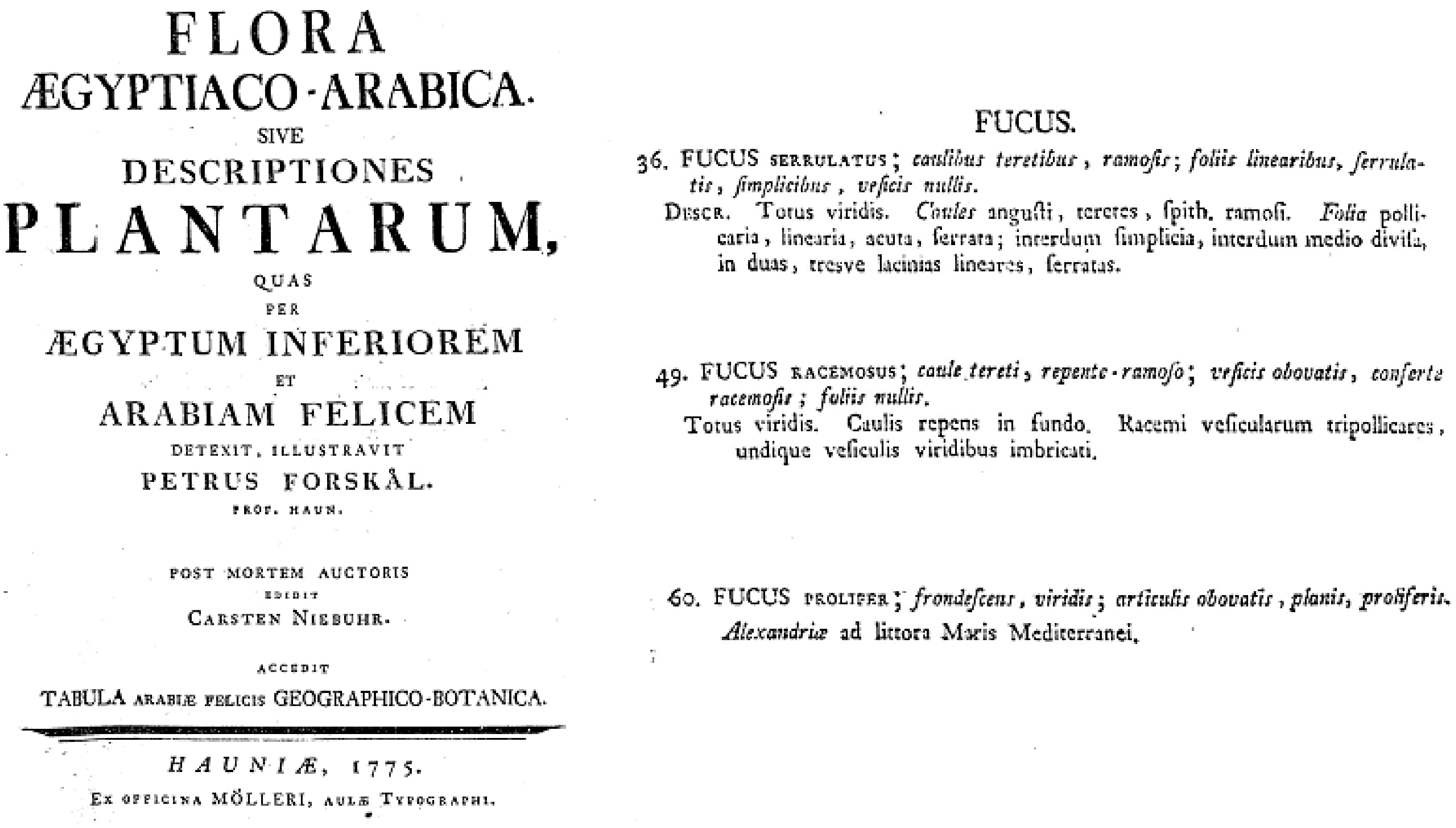
PETROPOLI
EX TYPOGRAPHIA ACADEMIAE SCIENTIARVM
cIↃ IↃCC LXVIII.

SPECIALIS. 151

FVCVS SERTVLARIOIDES.

Deſcriptio.

Figure 1. Description of *Caulerpa sertularioides* (as *Fucus sertularioides*), the first species of *Caulerpa* to be described (Gmelin 1768).



FLORA
ÆGYPTIACO-ARABICA.
SIVE
DESCRIPTIONES
PLANTARUM,
QUAS
PER
ÆGYPTUM INFERIOREM
ET
ARABIAM FELICEM
DETEXIT, ILLUSTRAVIT
PETRUS FORSKÅL.
PROF. HAUN.

POST MORTEM AUCTORIS
EDIDIT
CARSTEN NIEBUHR.

ACCEDIT
TABULA ARABIÆ FELICIS GEOGRAPHICO-BOTANICA.

HAUNIÆ, 1775.
EX OFFICINA MÖLLERI, AULÆ TYPOGRAPHI.

FUCUS.

36. FUCUS SERRULATUS; *caulibus teretibus, ramoſis; foliis linearibus, ſerrulatis, ſimplicibus, veſicis nullis.*

DESCR. Totus viridis. *Caules* anguſti, teretes, ſpith. ramoſi. *Folia* pollicaria, linearia, acuta, ſerrata; interdum ſimplicia, interdum medio diviſa, in duas, tresve lacinias lineares, ſerratas.

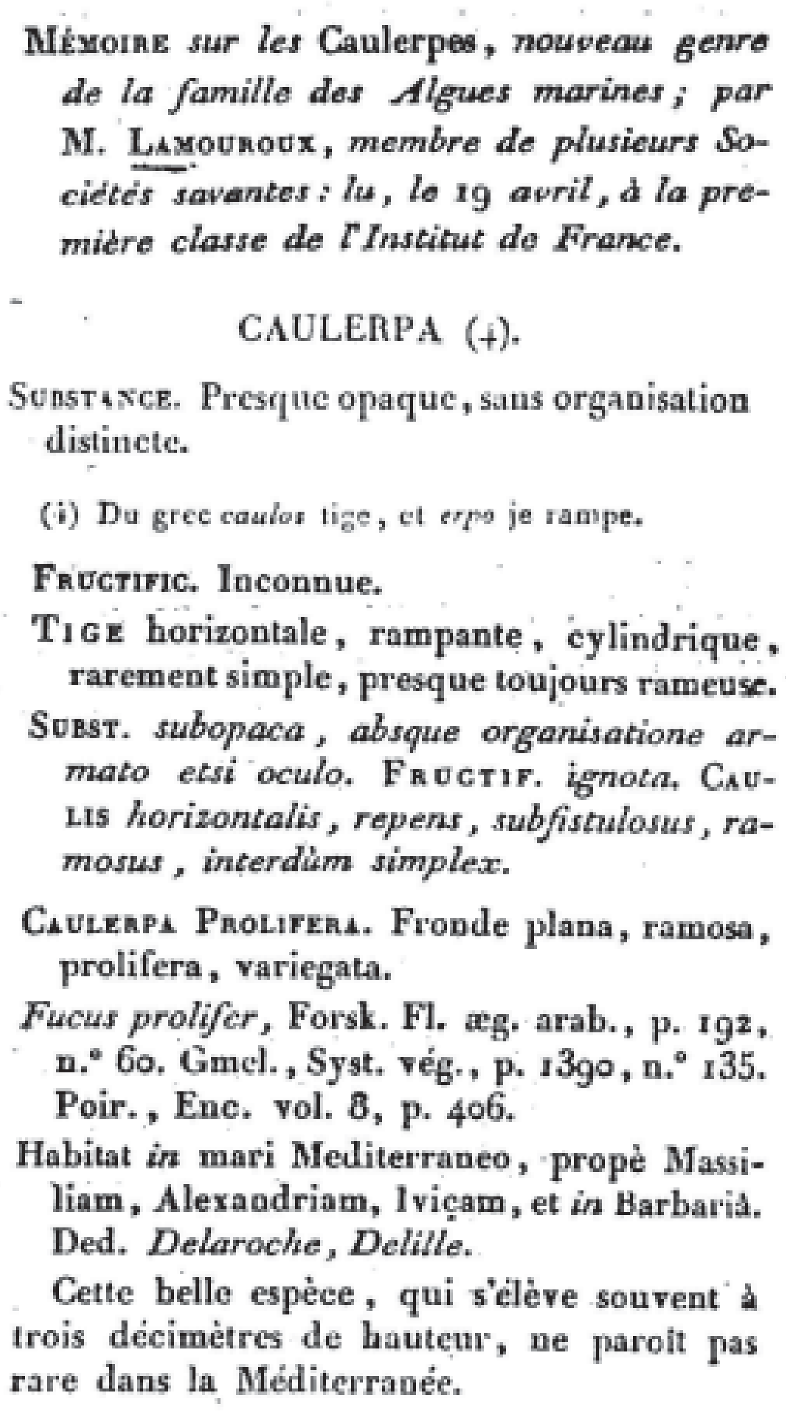
49. FUCUS RACEMOSUS; *caule tereti, repente-ramoſo; veſicis obovatis, conſerte racemoſis; foliis nullis.*

Totus viridis. Caulis repens in fundo. Racemi veſicularum tripollicares, undique veſiculis viridibus imbricati.

60. FUCUS PROLIFER; *frondeſcens, viridis; articulis obovatis, planis, proliferis.*

Alexandriæ ad littora Maris Mediterranei.

Figure 2. Original descriptions of *Caulerpa serrulata*, *C. racemosa*, and *C. prolifera*, all as species of *Fucus* (Forsskål 1775).



MÉMOIRE *sur les* Caulerpes, *nouveau genre de la famille des Algues marines; par* M. LAMOUROUX, *membre de plusieurs Sociétés savantes : lu, le* 19 *avril, à la première classe de l'Institut de France.*

CAULERPA (1).

SUBSTANCE. Presque opaque, sans organisation distincte.

(1) Du grec *caulos* tige, et *erpo* je rampe.

FRUCTIFIC. Inconnue.

TIGE horizontale, rampante, cylindrique, rarement simple, presque toujours rameuse.

SUBST. *subopaca, absque organisatione armato etsi oculo.* FRUCTIF. *ignota.* CAULIS *horizontalis, repens, subfistulosus, ramosus, interdùm simplex.*

CAULERPA PROLIFERA. Fronde plana, ramosa, prolifera, variegata.

Fucus prolifer, Forsk. Fl. æg. arab., p. 192, n.° 60. Gmel., Syst. vég., p. 1390, n.° 135. Poir., Enc. vol. 8, p. 406.

Habitat *in* mari Mediterraneo, propè Massiliam, Alexandriam, Iviçam, et *in* Barbariâ. Ded. *Delaroche, Delille.*

Cette belle espèce, qui s'élève souvent à trois décimètres de hauteur, ne paroît pas rare dans la Méditerranée.

Figure 3. Original description of the genus *Caulerpa* (Lamouroux 1809).

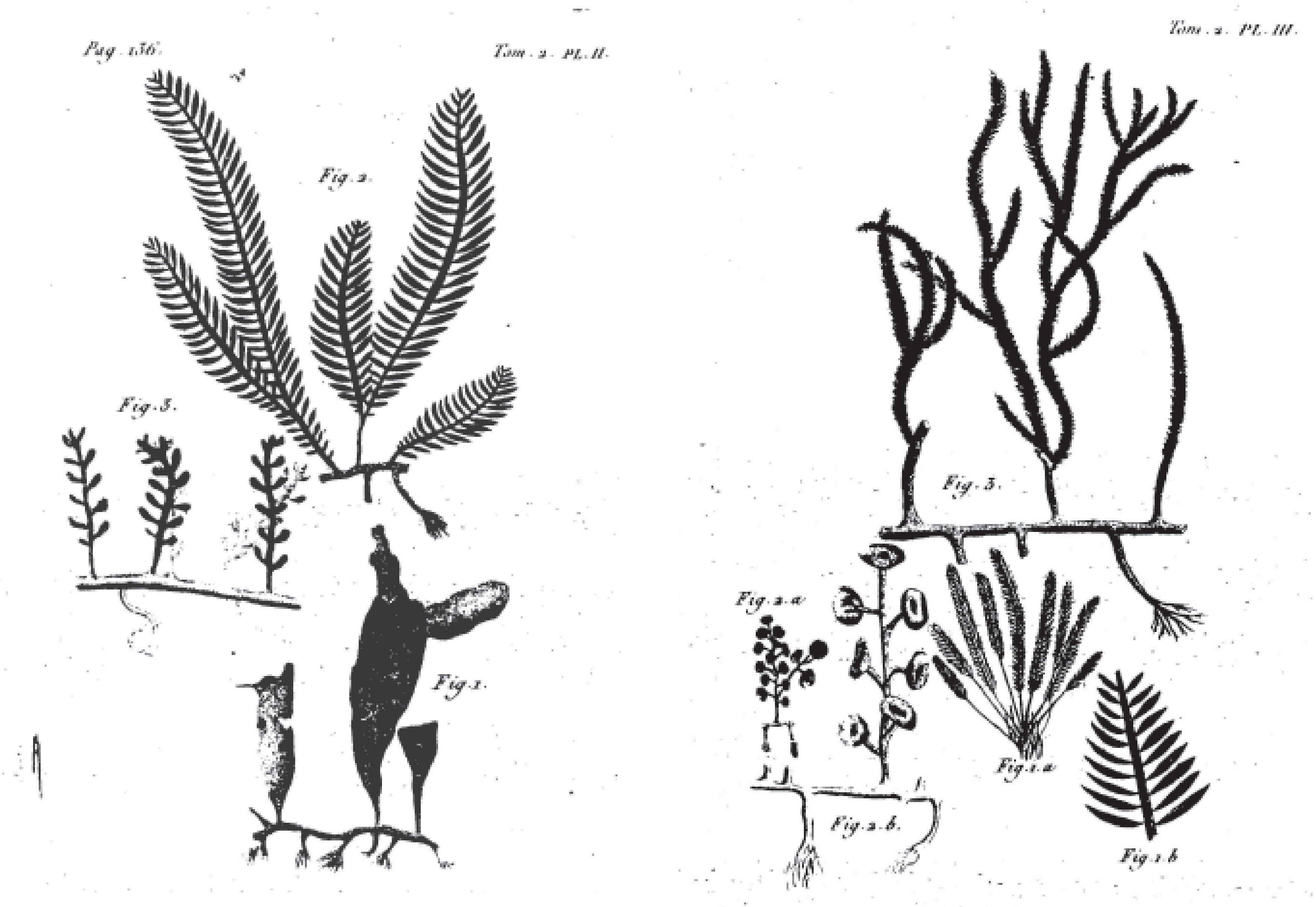


Figure 4. Lamouroux's illustrations of *Caulerpa* (Lamouroux 1809). Left-hand plate: Fig. 1. *C. prolifera*; Fig. 2. *C. taxifolia*; Fig. 3. *C. racemosa*. Right-hand plate: Fig. 2. *C. peltata*; Fig. 3. *C. cupressoides*.

Figure 5. *Caulerpa cactoides* from Australia.

Figure 6. *Caulerpa prolifera* from Mediterranean France.

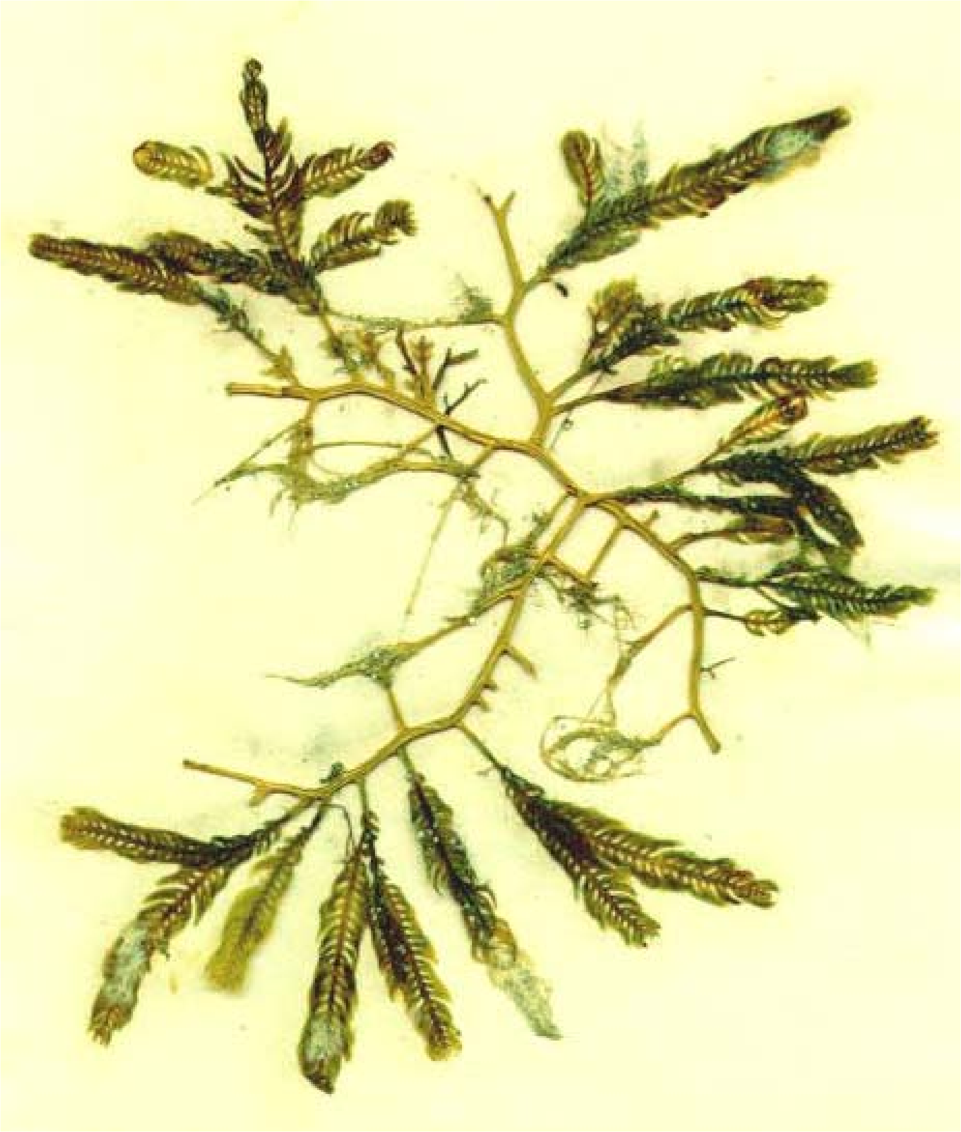


Figure 7. *Caulerpa taxifolia* from Guadeloupe, French Antilles.

Figure 8. C*aulerpa taxifolia* from Agua Hedionda, San Diego County, California.

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Caulerpa taxifolia . . .

Introduction for the International *Caulerpa taxifolia* Conference

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Introduction

The tropical green alga *Caulerpa taxifolia* has spread steadily throughout the northwestern Mediterranean Sea since its introduction in 1984. At the end of 2000, approximately 131 km^2 had been colonized along the coastline of six countries (Spain, France, Monaco, Italy, Croatia, and Tunisia). Since 2000, other regions have also been colonized by this invasive species. Invasions have also occurred in the temperate Pacific Ocean in California, Japan, and Southern Australia. Large regions in each of these invasions appear favorable for further colonization so it is unlikely that the rate of spread will decrease in years to come. Based on the information resulting from research on presently invaded areas over the last ten years, I will summarize the current state of knowledge of this important marine invader.

Taxonomy and Distribution

There are more than 70 species of *Caulerpa* and more than 50 subspecies and varieties. Most of these are tropical, while the natural distribution of *C. taxifolia* is circumtropical. *Caulerpa taxifolia* is limited by the winter Sea Surface Temperature (SST) and it does not survive temperatures below 19^o C, except populations in Moreton Bay (Queensland, Australia) where the winter SST drops to 16^o C. As far as we know, the invasive strain of *C. taxifolia* is only in temperate waters where the SST drops to 10^o C in winter.

Common Characteristics of the Genus *Caulerpa*

Coenocytic

The principal characteristic of the genus *Caulerpa* is the coenocytic thallus. They have no internal cell walls anywhere in their life cycle and, therefore, have no specialized cells. The plant is composed of three elements:

1. The upright photosynthetic axes of fronds bearing lateral ramuli or pinnules
2. The horizontal axes, or stolon, which is the main part of the plant
3. The rhizoids, sometimes at the end of pillars

Pseudoperennial

The stolon can grow by nearly 2 cm per day throughout the summer and fall. While the axis elongates at one end, it dies back at the other, so that no part of the thallus lives more than a year. Therefore, the same genetic individual can perpetuate itself by unlimited growth (i.e., pseudoperennial type of growth).

Vegetative reproduction by fragmentation

A fragment from any part of this alga can produce a new plant, as long as that fragment contains a nucleus and other organelles. This is an important point for the management of invasive *C. taxifolia*. Fragmentation occurs naturally due to disturbance by storms, invertebrates, etc., and produces clonal propagation. The fragments, which are denser than seawater, do not float so dispersal of fragments is presumed to be limited and will most likely enhance local colonization. However, these fragments can also be dispersed by pleasure boats and by fishing nets far from invaded areas.

Life history and sexual reproduction

Most of the *Caulerpa* species, such as native *C. taxifolia*, are monoecious. The thallus dies after release of gametes (holocarpy). After the fusion of the gametes, the zygote produces an intermediate stage called the *protosphaera* before becoming an adult plant.

Karyology

The state of understanding the alternate phases (n and 2n) of the genus *Caulerpa* is still imprecise and presents different interpretations. The use of DAPI staining and immuofluorescent labeling, together with confocal microscopy observations, indicate there is a large range of nucleus sizes (from 0.6 to 4.7 µm) with n = 3 chromosomes. What guides the change of the phases in different life history stages and the different ploidy levels (haploid, diploid, and polyploid) is still unknown.

Characteristics of the Introduced Strain of *Caulerpa taxifolia*

Giant fronds in low light conditions

When the plant is exposed to reduced light levels (late autumn or at greater depth), the frond length can be greater than 60 cm (maximum 80 cm). This length has never been found in other strains.

No sexual reproduction

Sexual reproduction has never been observed in the invasive aquarium strain of *C. taxifolia* because only male gametes are produced.

Resistance to low water temperature

Data from aquaria culture and inferred from the present distribution of *C. taxifolia* in the Mediterranean Sea indicate that the invasive strain can survive up to 3 months at 10^{o} C under low light conditions.

High concentration of Caulerpenyne

The toxic terpene Caulerpenyne, presumed to be a chemical defense of the alga, is produced in large amount in the invasive strain.

Ubiquitous, forming large, dense colonies

In the Mediterranean Sea, *C. taxifolia* forms large, dense colonies that are competitively dominant, in contrast to tropical seas, where such colonies never develop.

Origin of the Invasion

History as an aquarium strain

Prior investigations established that *C. taxifolia* was cultivated in aquariums in northern Europe since the end of 1960. In the beginning of 1980, *C. taxifolia* was in the aquaria of the Museum of Monaco. In the Mediterranean Sea, *C. taxifolia* had never been documented prior to the first record in 1984 in a 1 m^2 area just beneath the Museum of Monaco. Oral testimony shows that this alga was accidentally introduced from the aquarium of the Museum of Monaco. A similar introduction occurred in the Sea of Japan (Notojima) via a public aquarium, but after spreading across a 3 m^2 area in open water, it died during the winter due to SSTs under 8^{o} C.

Genetic studies

Studies of genetic relatedness of invasive *C. taxifolia* strains over the last decade have largely invalidated alternative hypotheses for the introduction of *C. taxifolia* into the Mediterranean Sea (dispersal from the Red Sea, "metamorphosis" from *C. mexicana,* cryptic-dormant species) put forth by the research team from Monaco. All the specimens from the Mediterranean Sea and California, and from European and Japanese aquaria, are identical and close to natural populations of Moreton Bay (Queensland, Australia) and recently introduced populations south of Sydney (Jousson et al 1998; 2000; Olsen 1998; Wiedenmann et al. 2001; Meusnier et al. 2001).

Impacts

In the largest invaded regions, the dominance of *C. taxifolia* has been shown to impact the biodiversity of many species of algae, benthic invertebrates, and fishes. These changes are amplified by several characteristics of *C. taxifolia*: the alga is ubiquitous, perennial, fast-growing on a very large scale in a variety of littoral ecosystems, and is not subject to herbivory by temperate fishes or invertebrates. Thus, this important invader needs to be the focus of active management and international awareness.

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Caulerpa taxifolia . . .

The Spread of *Caulerpa taxifolia* in the Mediterranean:

Dispersal Strategy, Interactions With Native Species, and Competitive Ability

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Introduction

Caulerpa taxifolia (Vahl) C. Agardh is a fast-spreading introduced species in the Mediterranean that has caused great concern in recent years (Meinesz and Hesse 1991, Boudouresque et al. 1992, Meinesz et al. 1993). As a contribution to the knowledge of the performance of the green, tropical alga, results of several experimental studies carried out in the field are presented. Identification of an efficient dispersal strategy of biotic factors that enhance the performance and considerations on the competitive ability are given. Overall, comparisons with the performance of another introduced *Caulerpa* species in the Mediterranean, *Caulerpa racemosa* (Forsskål) J. Agardh, are included.

Thallus Fragmentation as a Dispersal Strategy

The rapid expansion of *C. taxifolia* has led to a dramatic increase in the number of permanent populations, mostly along the French and the Italian coasts. In this regard, evaluation of the importance of thallus fragmentation of *C. taxifolia* as a dispersal strategy has been investigated by means of a multifactorial experiment (Ceccherelli and Cinelli 1999a). The experiment tested the hypotheses that there were seasonal differences in patterns of establishment of vegetative fragments, whether this process changes with depth and whether these patterns were consistent at different spatial and temporal scales. The experimental approach consisted of dispersing drifting fragments of *C. taxifolia* along the margin of a *Posidonia oceanica* bed and recording the number of fragments established after one month.

The study was carried out from October 1995 until September 1996. On three dates randomly chosen within each season, 20 fragments 15 cm long with stolon, blades, and rhizoids were manually uprooted from the same habitat and dispersed along replicate margins (each 3 m in length). On each date, 20 fragments were spread at each of the 3 replicate margins in each of 2 areas randomly chosen at each of 2 depths (3 m and 10 m).

Results have revealed that a surprisingly high number of fragments reestablished at the margin of *P. oceanica*, right where they were dispersed, especially during summer (Fig. 1). Differences among areas were also found: high variability in establishment of fragments depended on the site and time within season. Results indicate that dispersal by fragmentation can greatly contribute to the wide spread of the alga in the Mediterranean. The prediction is that spread will be greatest during summer, when a large proportion of fragments can reattach to the substratum, even at shallow sites.

The Positive Influence of Native Seagrasses on *C. taxifolia*

Commonly, competitive and facilitative interactions between plants are known to directly influence their morphology and physiology (e.g., Callaway 1994, Callaway et al. 1996) as well as patterns of distribution and abundance (e.g., Tilman 1988). Patterns of spatial and temporal variation in size of *C. taxifolia* was investigated in 3 distinct habitat types: 1.) at the margin of *P. oceanica*, 2.) within *Cymodocea nodosa*, and 3.) on sand and cobbles (Ceccherelli and Cinelli 1998). To provide a basis for further experimental investigations of the factors affecting its performance, this study was carried out so that the size of blades was measured throughout two years. In each habitat, 4 areas out of 8 were randomly chosen and varied. The length of two blades was measured in situ in each replicate (10 x 10 cm quadrant). Four randomly chosen replicates were sampled in each area.

Besides the strong effects of seasonality, an obvious habitat effect was found for both response variables suggesting a positive effect of seagrasses on *C. taxifolia* (Fig. 2). For the whole study period, the longest blades of *C. taxifolia* were found at the edge of *P. oceanica*, while the shortest were found on sand and cobbles. Intermediate lengths occurred within *Cymodocea nodosa*.

The response of *C. taxifolia* size was also investigated in an experimental manipulation of seagrass canopy-type (Ceccherelli and Cinelli 1999b). We used *P. oceanica*-mimic plants made of transparent plastic strips that were able to protect, but not shade the alga. Controls for plastic material and for the frame were also included in the design. Treatments were replicated for natural leaf length versus reduced length.

Our results indicate that the positive effect of seagrass is due to the protection and not to the shade, but this comes with a cost. In fact, larger *C. taxifolia* were found next to “transparent plants” relative to “shading plants,” independent of length (Fig. 3). Also, intermediate depth or shoot density of the seagrass was a good compromise between protection and shading.

The Spread of *C. taxifolia* and *C. racemosa* in Native Macroalgal Assemblages of Different Complexity

One of the important goals for ecologists is to understand why and how successful invasions occur. Although all systems do not appear to be equally invasible (Lonsdale 2000), factors determining the susceptibility of a community to invasion remain unclear. Theory predicts that communities rich in species should be less susceptible to invasion (Rejmánek 1989; Stachowicz et al. 1999; Prieur-Richard and Lavorel 2000). Since Elton (1958), some descriptive studies support a positive relation between biodiversity and invasion resistance.

This study is a short-term field experiment with the aim to identify characteristics of Mediterranean macroalgal subtidal assemblages that are conducive to successful spread of the two introduced *Caulerpa* species. It was designed to identify layers of Mediterranean macroalgal assemblage that encourage successful spread of *C. racemosa* and *C. taxifolia* in macroalgal assemblages of different complexity.

By manipulation of macroalgal presence, we obtained plots of different assemblage structure with either one or the other *Caulerpa* transplanted. The performance of both species was investigated relative to the experimental assemblage complexity. Complexity of macroalgal assemblages is defined to be proportional to the presence of different vegetation layers such as erect, turf, and encrusting (Verlaque and Fritayre 1994; Airoldi et al. 1995a; Piazzi et al. 2001). With this study, we tested the hypothesis that the performance of both species increases with decreasing habitat complexity.

By manipulation of algae species, three differently structured assemblages were obtained for the experiment: 1.) encrusting algae, by removal of the turf and erect species; 2.) encrusting and turfing algae, by removal of erect species; 3.) encrusting, turfing, and erect algae leaving assemblages unmanipulated, which served as a control. Fragments of the two introduced species *C. taxifolia* and *C. racemosa* were transplanted into each of the three habitats. Plant colony width, blade density, and percent of the substrate covered by the two species were the response variables examined.

The susceptibility of the indigenous community to the spread was related to assemblage type. Blade density and the percent covered by the two *Caulerpa* species were different and generally higher for *C. taxifolia* than for *C. racemosa* (Fig. 4). Overall, the spread of these species was strongly dependent on habitat type, but not directly on the complexity level: turf habitat is more favourable than encrusting species alone, while the least advantageous one is where macroalgal assemblage is composed of encrusting, turf, and erect species. In other words, species richness of the assemblage affects invasion of the *Caulerpa* species conferring greater resistance and the species type is likely to be more important than species number. The presence of turf species seems to promote the spread of *Caulerpa* species.

Intra- and Interspecific Competition Between *C. taxifolia* and *C. racemosa*

When two or more introduced species co-occur, competitive interactions between them or synergistic deleterious effects on indigenous species could occur. One of the important goals for ecologists is to understand interactions among invasive species in order to predict possible effects on colonized communities.

Competitive interactions between the two introduced algae, *C. taxifolia* and *C. racemosa*, were studied in two experiments (Piazzi and Ceccherelli 2002). The first evaluated separately the interspecific and intraspecific effects on both species by manipulating their abundance. To achieve these objectives, two reciprocal experiments (competition experiments) were performed through manipulation of the abundance of the species. The controls consisted of a chosen density (2 fragments) of one species, which were then contrasted to experimental plots with different densities (2+2 and 2+4 fragments) of each species alone or in combination with the other species. Hence, each experiment consisted in the following five treatments seen in Table 1. The comparison among treatments 1, 2, and 3 detects intraspecific interactions in each species while interspecific competition is detected by the comparison among treatment 1, 4, and 5 (Underwood 1997). Treatments were interspersed and there were three replicates for each treatment, about 5 m apart. The whole experimental area was about 250 m^2 large.

The second experiment investigated the fate of fragments of *C. taxifolia* transplanted into patches of *C. racemosa* in contrast to those established on algal turfs. *Caulerpa racemosa* and *C. taxifolia* had similar temporal trends in growth, but reached very different sizes (Fig. 5). The overall increase in stolon length at higher densities for both species suggested that positive interactions are very important. However, there was a significant interspecific effect on *C. taxifolia* stolon length, but no effect on *C. racemosa*. Furthermore, *C. taxifolia* fragments transplanted on *C. racemosa* patches showed clear signals of stress with respect to those transplanted on algal turfs; blades became bleached and eroded.

Overall, the results of this study suggest that growth increases with the density augmentation, therefore suggesting that invasive characteristics of the species may increase with the time of colonization. Both species tend to spread faster at higher density. Overall, where both species co-occur we predict that *C. racemosa* would be the favoured species from the outcome of the competition.

Figures . . .

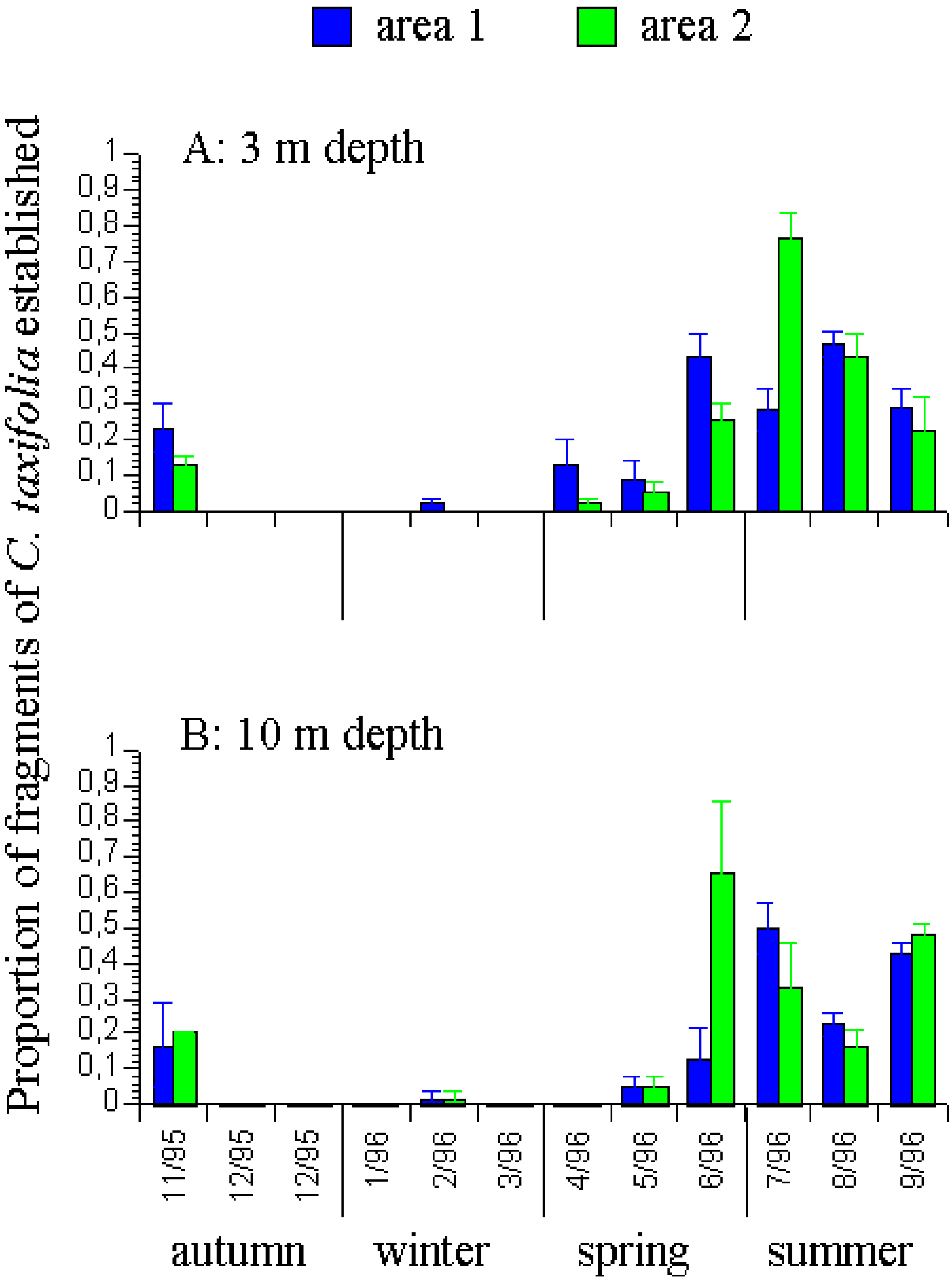


Figure 1. Mean proportion (+SE) of the number of *Caulerpa taxifolia* fragments established at the margin of *Posidonia oceanica*, dispersed 3 times in each season at 2 different depths (3 and 10 m). For each treatment, data for each area are shown. *(Figure reprinted with the permission of the Marine Ecology Progress Series.)*

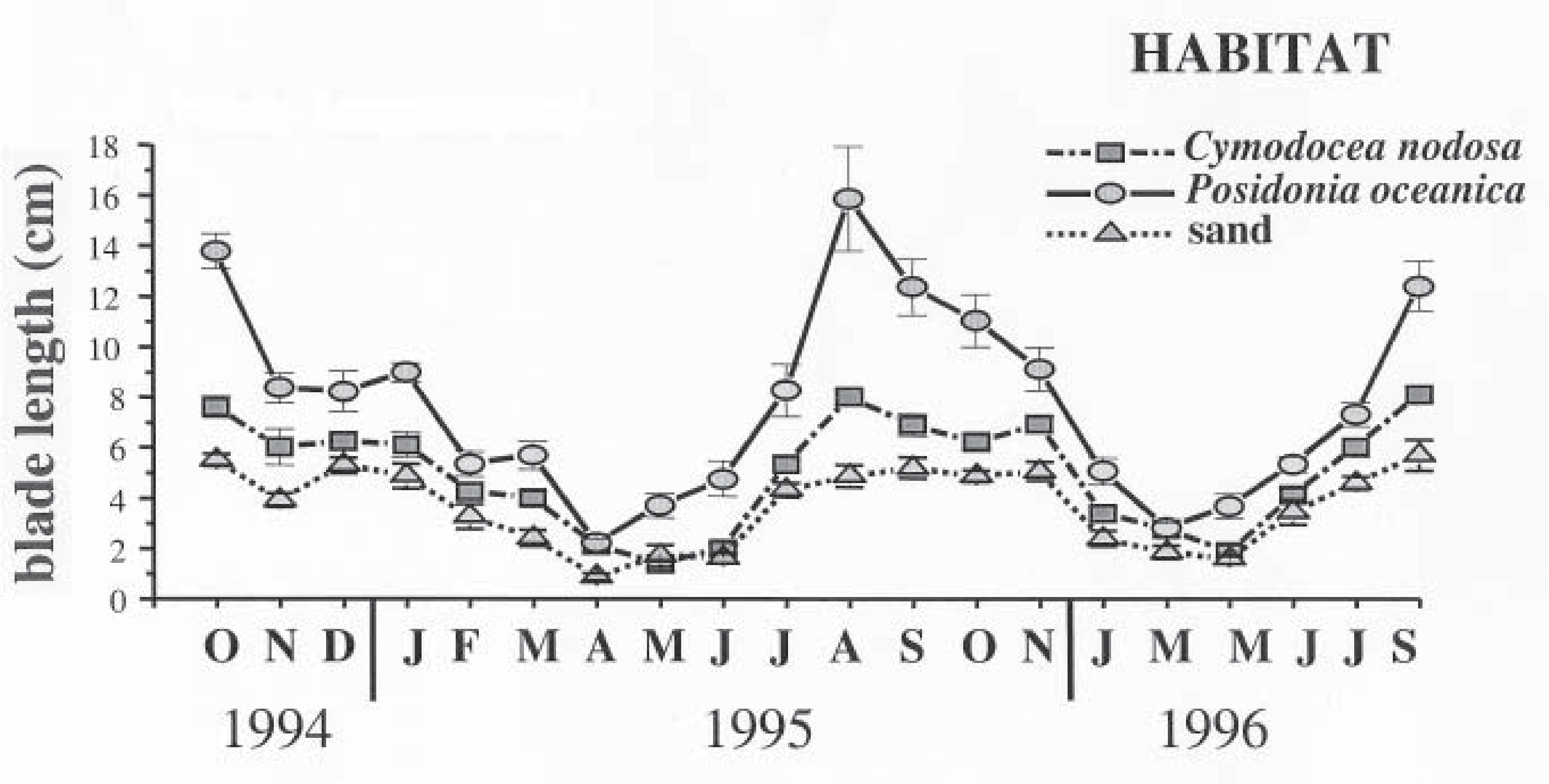


Figure 2. Temporal changes in mean blade length (±SE) during the study period in the 3 habitats (*Cymodocea nodosa, Posidonia oceanica*, and sand/cobbles). Each value represents the mean of 16 observations (4 replicates in each of the 4 areas).

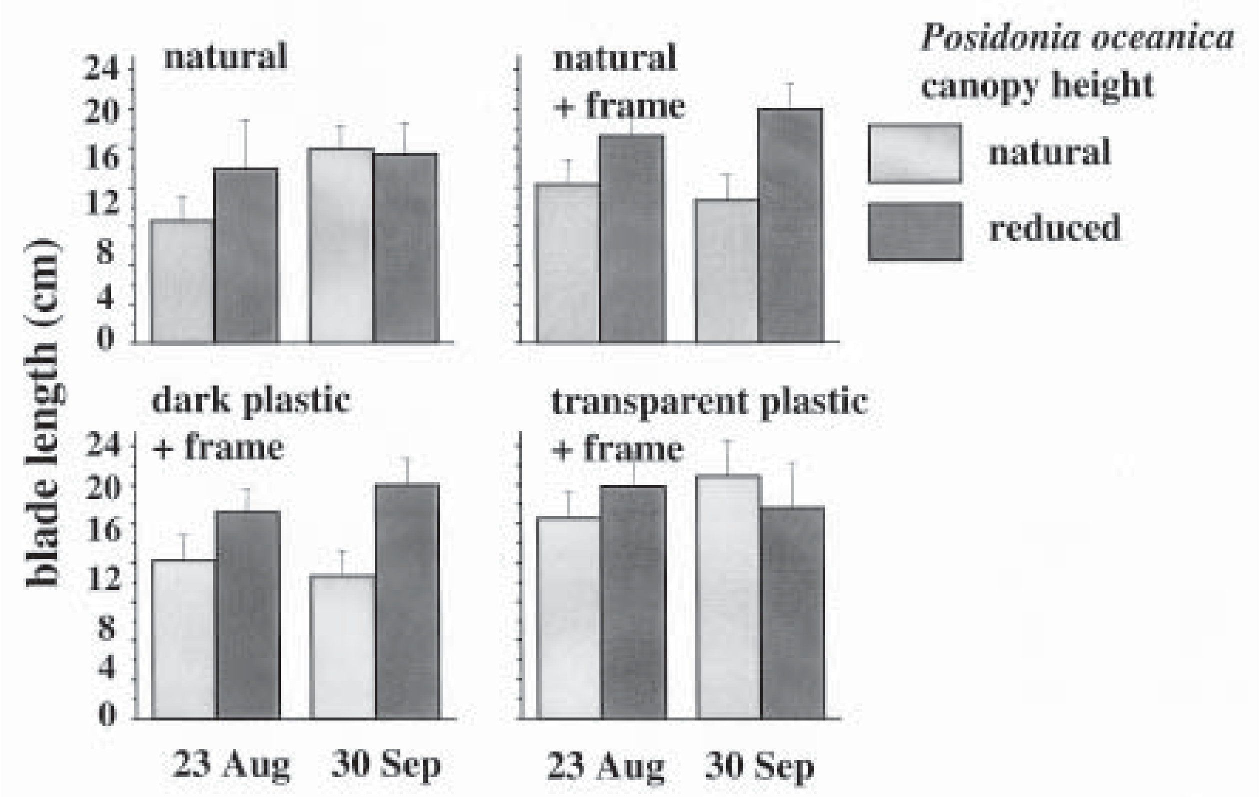


Figure 3. Mean (+ SE) *C. taxifolia* blade size at the two sampling times at the edge of *P. oceanica* canopy (natural, natural + frame, dark plastic + frame) of natural and reduced canopy height in each area (n=12). *(Figure reprinted with the permission of the Journal of Experimental Marine Biology and Ecology.)*

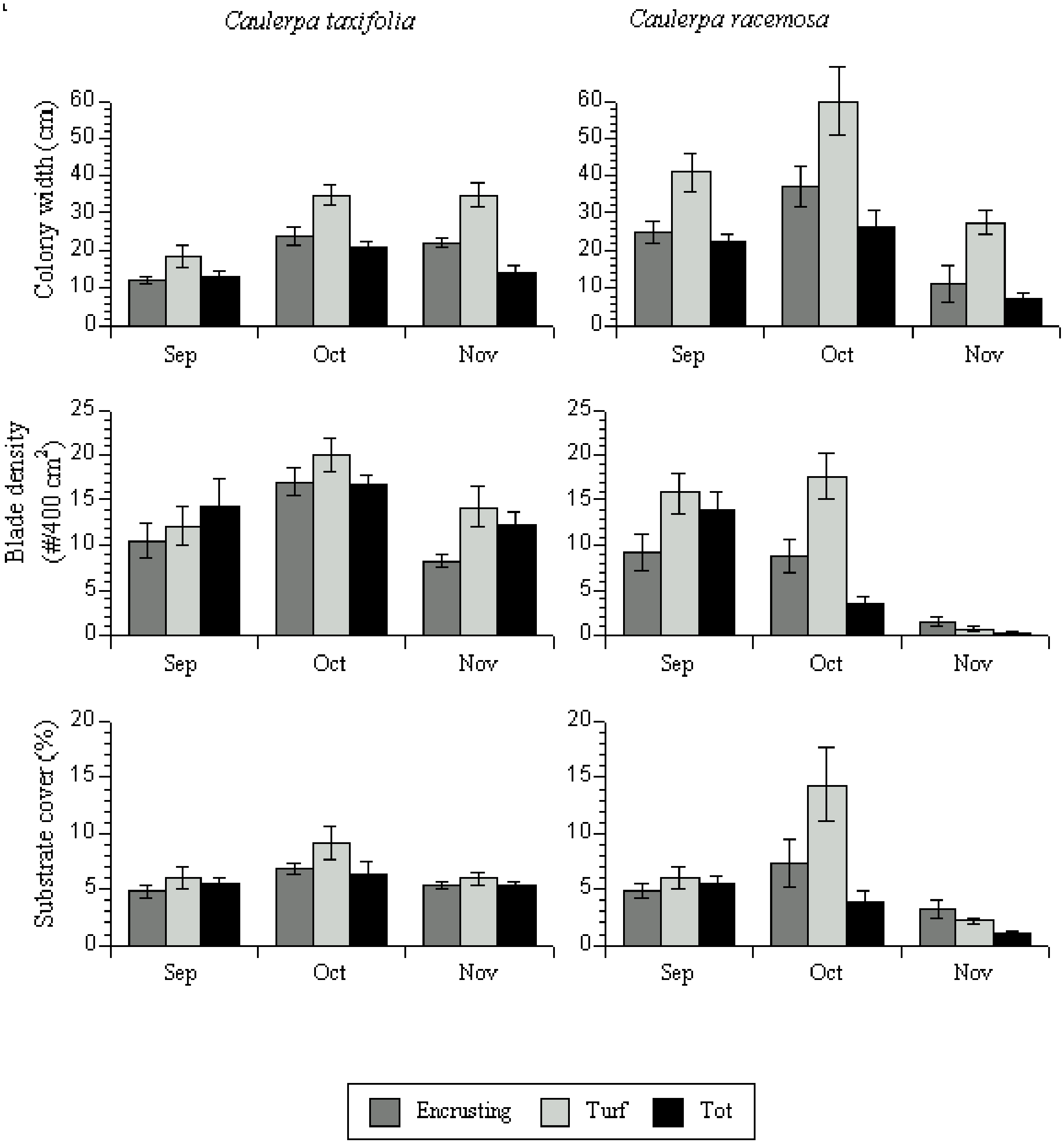


Figure 4. Temporal variation of mean (±SE) percent of substrate covered by stolons, blade density, and colony width of *Caulerpa taxifolia* and *Caulerpa racemosa* in assemblages of different macroalgal complexity (n=3).

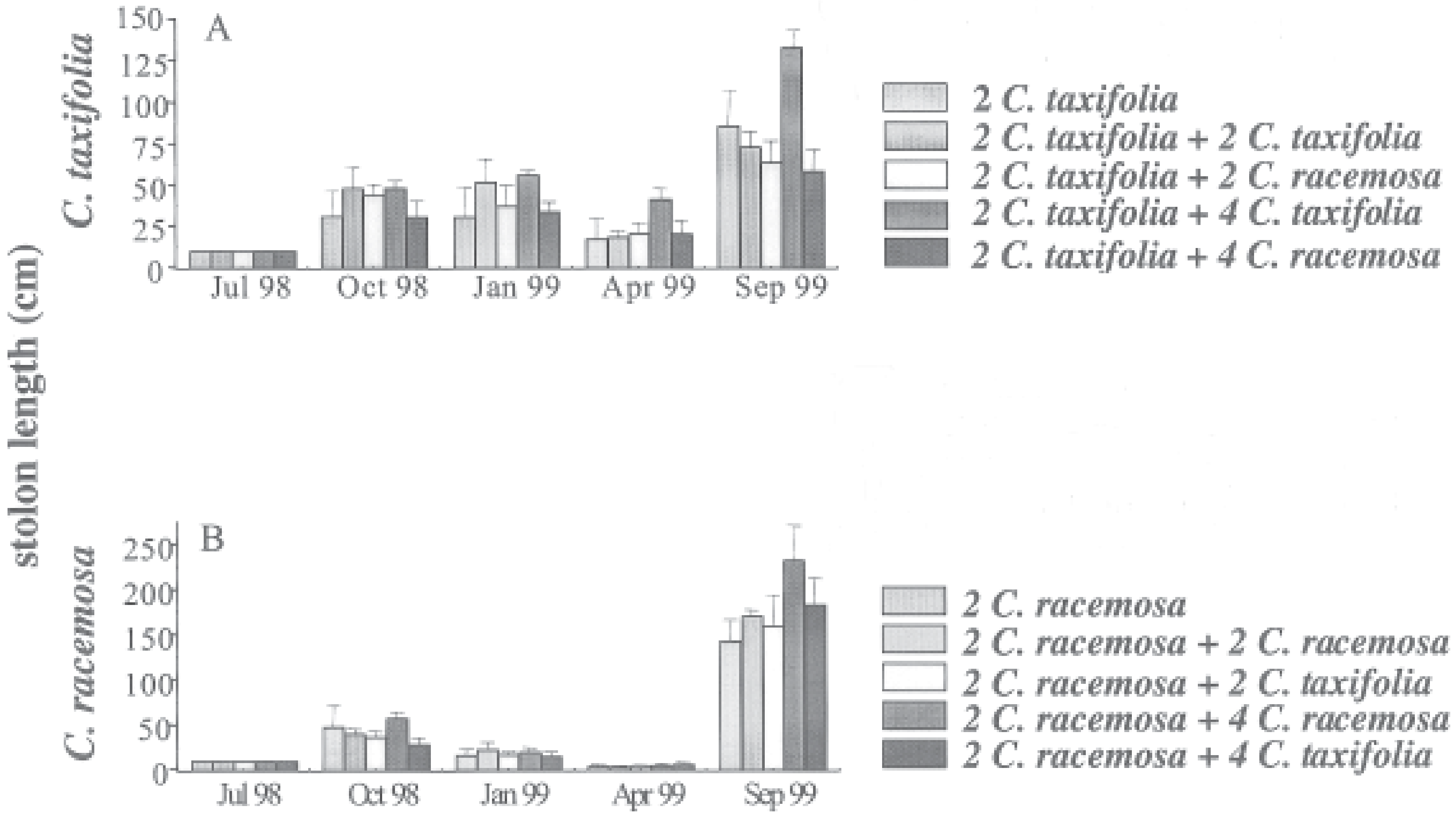
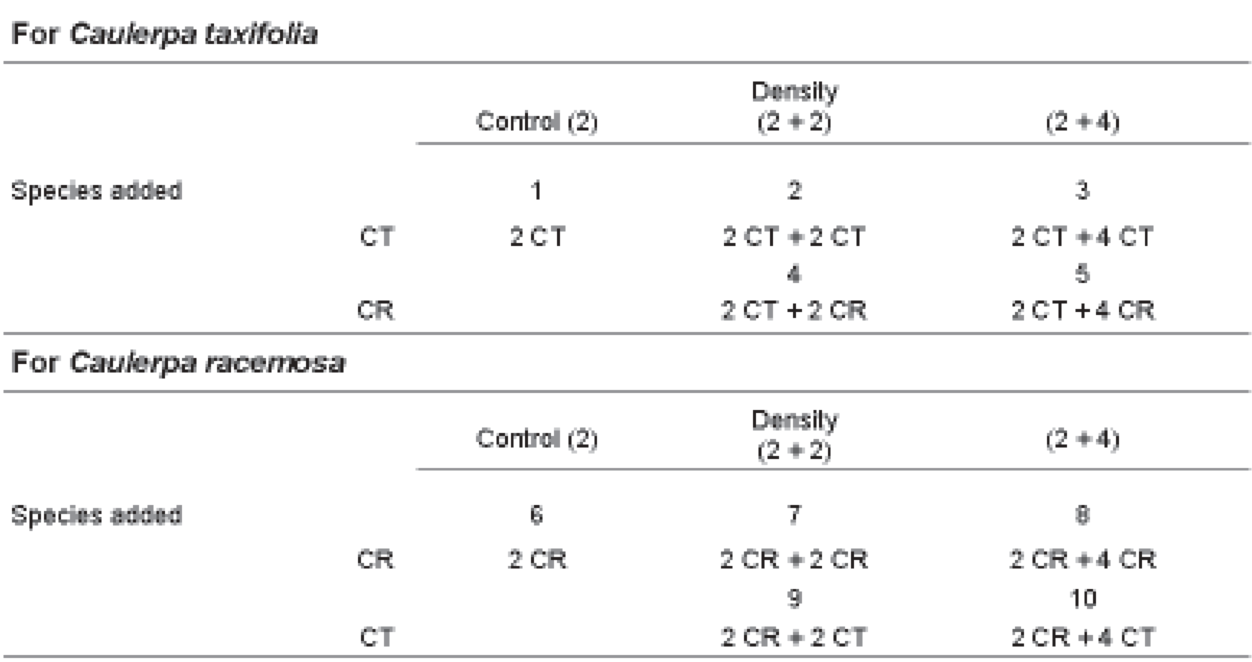


Figure 5. Competition experiments. Temporal variation during the study period of mean (± SE) stolon length of *C. taxifolia* (A) and *C. racemosa* (B) in treatments of different densities and different species added (n = 3). Numbers reported on legend refer to fragments used in treatments. *(Figure reprinted with the permission of the Marine Ecology Progress Series.)*

Tables . . .

Table 1. **Competition experiments. Experimental treatments to determine influences of inter- and intraspecific competition on blade density and stolon lengths of *Caulerpa taxifolia* (CT) and *Caulerpa racemosa* (CR) at several densities of fragments.**



For *Caulerpa taxifolia*

			Density	
		Control (2)	(2 + 2)	(2 + 4)
Species added		1	2	3
	CT	2 CT	2 CT + 2 CT	2 CT + 4 CT
			4	5
	CR		2 CT + 2 CR	2 CT + 4 CR

For *Caulerpa racemosa*

			Density	
		Control (2)	(2 + 2)	(2 + 4)
Species added		6	7	8
	CR	2 CR	2 CR + 2 CR	2 CR + 4 CR
			9	10
	CT		2 CR + 2 CT	2 CR + 4 CT

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Caulerpa taxifolia . . .

Appearance and Eradication of *Caulerpa taxifolia* in Croatia

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Until the end of 2001, in the Croatian part of the Adriatic Sea, an invasive species, *Caulerpa taxifolia* (Vahl) C. Agardh, had been found at a total of three distinct areas: Stari Grad Bay (Hvar Island), Malinska (Krk Island), and in Barbat Channel (between the Islands of Dolin and Rab). Because of the algae's fast-spreading and negative impact on the biological, ecological, and seascape diversity, eradication is being undertaken to prevent further expansion.

Barbat Channel

The tropical alga *C. taxifolia* was observed in the Barbat Channel (between the islands of Dolin and Rab) (44°44′16″N–16°53′32″E) for the first time in September 1996 by local divers. It was estimated that this alga was brought into the area in 1995. The algae was found in the photophilic biocenoses on hard substrate and in a *Cymodocea nodosa* seagrass bed on a sandy substrate between depths of 2.5 and 8 m. About 20 m^2 of surface was covered out of 350 m^2 of affected zone (Fig. 1).

Eradication was carried out from October 5–14, 1996. On the sandy substrate, each rhizoid pillar with bunches of rhizoids was unrooted manually with the aid of a fork. The algae attached to cobbles were picked from the sea together with the substrate. In total, approximately 130 hours of diving time was needed for this process.

Following eradication, during the next year there were a number of follow-up investigations of the eradicated area, as well as the surrounding area (± 1.5 km); no *C. taxifolia* was found. During the summer of 2001 a large new colony of approximately 100 m^2 was found 200 m from the previously eradicated one. This new colony is probably the result of a remaining fragment, which was dispersed by currents from the main colony in 1996, and was at that time too small to be noted.

Malinska

The alga was observed for the first time in 1994 in the area of Malinska (Krk Island) (45º7′30″N–14º31′56″E). It was estimated that the alga was introduced in 1991. Four algae stations on muddy-sandy substrate between depths of 3 and 12 m were observed until the end of 2001. Partial eradication was done during 1996 and 1997. The alga was pumped together with 10 cm of muddy bottom, using a suction water pump. The material was filtered through a system of sieves.

After two eradications, the alga was completely removed from the area of the harbor where it had densely covered about 1,300 m^2 of the 16,000 m^2 of affected sea bottom. In the other colonies (1900 m^2 of the covered surface in total), re-colonization of the algae occurred due to the remnants of algae fragments after eradication. Because of financial problems, the eradication efforts stopped in 1997. At the end of 2001, the alga was not found in the Port of Malinska, but it re-colonized the other stations.

Stari Grad Bay

In 8 km deep Stari Grad Bay (Hvar Island) (43º10’54”N–16º35’00”E) the alga was observed for the first time during the summer of 1994, and was probably introduced in 1991. Until the end of 2001, one central and 10 distant stations were found throughout the bay. The alga has been tracked since 1995 when the affected area was 7 ha. During 2001, the affected area at the central station was 39 ha, while at the distant stations the alga covered less than 100 m^2. Expansion of the stations is mostly caused by dissemination of fragments by waves and currents. The distant stations were colonized by transportation of the alga in fishing nets.

Although some of the distant colonies were colonized five years ago, due to systematic control and eradication using suction pumps and covering with black PVC foil, the colonies had not increased in size and some of them were even totally eradicated. At the beginning of a project of eradication during 1997, the affected area of the central station was 11 ha. The alga was found at depths between 0.5 and 20 m, on the hard substrate with photophilic and sciaphilic biocenoses and on the sandy and muddy substrate without vegetation or with seagrass beds (*Posidonia oceanica* (L.) Delile, *Cymodocea nodosa* (Ucr.) Ascher, and *Zostera noltii* Horn).

This area was too large for complete eradication. The aim of the program was to stop further spreading of the central station by eradicating the border colonies and completely eradicating distant stations. Eradication was done manually with the aid of air or water suction pumps and by covering the colonies with black plastic foil. With an annual budget of around $15,000, approximately 200 hours of diving time could be funded each year.

Eradication with suction pumps

Extraction with suction pumps is a fast method for eradication of alga thalli (up to 1 m in diameter) on a sandy and muddy substrate. The basic deficiency of the method is that the algae fragments including a rooted rhizoid usually remained after eradication. All of these small fragments are impossible to find and collect. So, it is important to repeat the eradication after a short period in which the fragments will start to regenerate into small, visible plants (Fig. 2c). On the other hand, the period between eradication should not be too long in order to avoid production of new fragments (Fig. 2d).

Covering by plastic foil

Covering the algae by plastic foil is a fast, cheap method useful for all types of substrata. *Caulerpa taxifolia* completely disappears under foil within 3 months. The 4 m wide, 0.15 mm thin, rolled black plastic foil is secured on the bottom by nails and stones. The problems are possible uncovered fragments and damage of the foil caused by fishing, anchoring, or storms during the three months in which the algae should be covered.

Taking into account an average dynamic of the algae colonies spread, until the beginning of 2001, without eradication the greatest part of the bay should be affected. Some of the stations like St. Ante Bay and Radocin dol Bay should have more than 10 ha of affected areas. Due to permanent eradication that did not happen the locations have remained small. Unfortunately, these methods could not be used for a complete eradication of large affected areas such as the central station in Stari Grad Bay.

Figures . . .

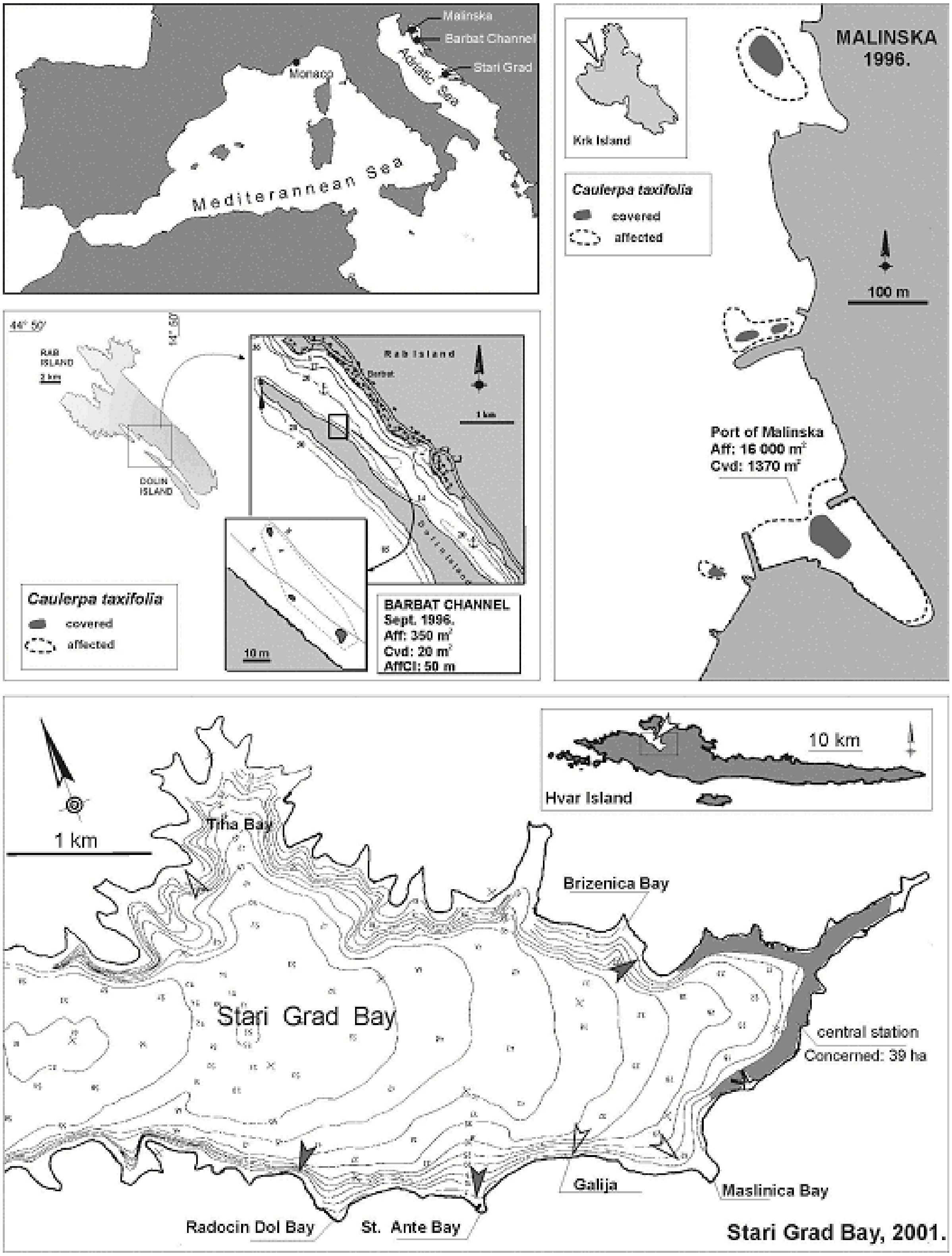
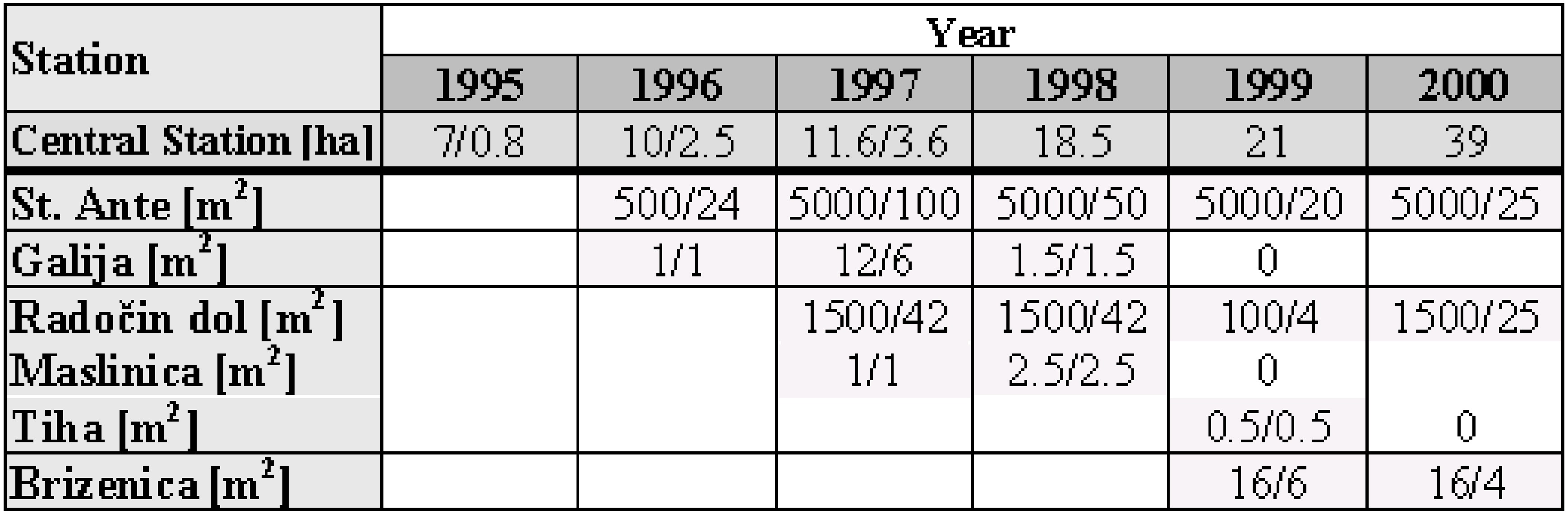


Figure 1. Distribution of *Caulerpa taxifolia* in the Adriatic Sea: Malinska in 1996, before eradication; Barbat Channel in 1996, before eradication; Stari Grad Bay at the end of 2001 with position of affected area of the central station and existing (full arrow) and eradicated (empty arrow) *Caulerpa* at distant stations.

Figure 2. Timing of eradication: a.) small colony with fragments before eradication; b.) remaining fragments after eradication; c.) beginning of fragments regeneration—ideal time for second eradication; d.) regenerated colony with new fragments—too late for successful eradication.

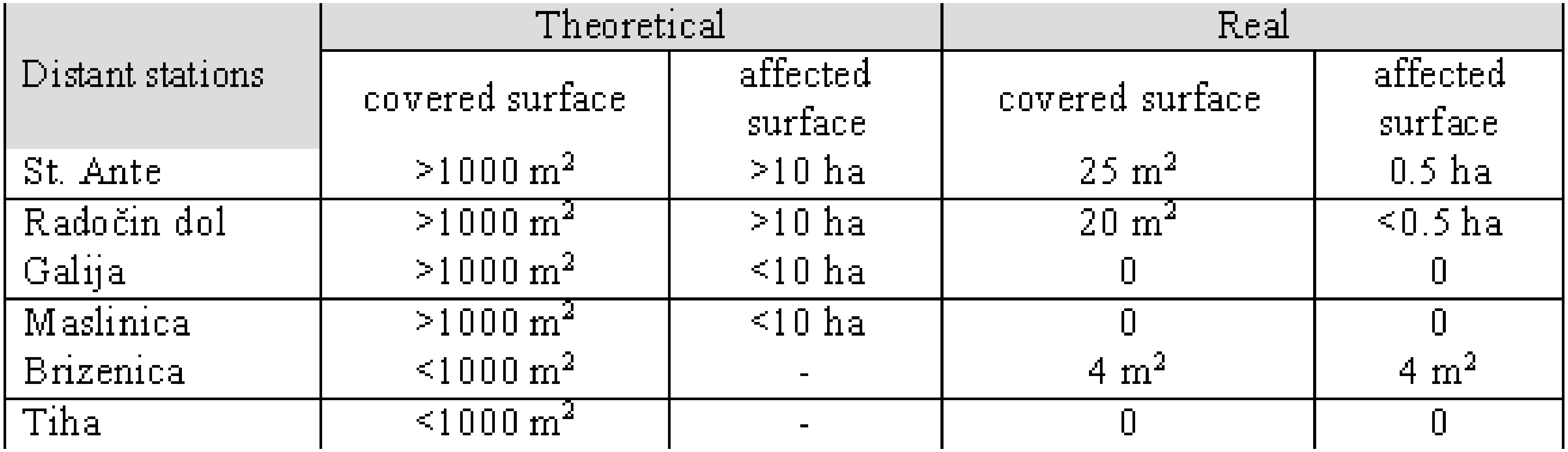
Tables . . .

Table 1. The area affected/covered by *Caulerpa taxifolia* in Stari Grad Bay from 1995–2000. The position and names of the stations are according to Fig. 1.



Station	Year					
	1995	1996	1997	1998	1999	2000
Central Station [ha]	7/0.8	10/2.5	11.6/3.6	18.5	21	39
St. Ante [m^2]		500/24	5000/100	5000/50	5000/20	5000/25
Galija [m^2]		1/1	12/6	1.5/1.5	0	
Radočin dol [m^2]			1500/42	1500/42	100/4	1500/25
Maslinica [m^2]			1/1	2.5/2.5	0	
Tiha [m^2]					0.5/0.5	0
Brizenica [m^2]					16/6	16/4

Table 2. **Distribution of the *Caulerpa taxifolia* at the distant station in the Stari Grad Bay at the end of 2000. Theoretical surface is the area on which the alga should be theoretically dispersed without eradication.**



Distant stations	Theoretical		Real	
	covered surface	affected surface	covered surface	affected surface
St. Ante	>1000 m²	>10 ha	25 m²	0.5 ha
Radočin dol	>1000 m²	>10 ha	20 m²	<0.5 ha
Galija	>1000 m²	<10 ha	0	0
Maslinica	>1000 m²	<10 ha	0	0
Brizenica	<1000 m²	-	4 m²	4 m²
Tiha	<1000 m²	-	0	0

Caulerpa taxifolia . . .

The Introduction of *Caulerpa taxifolia* in New South Wales, Australia

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Background and Biology

Within Australia, *Caulerpa taxifolia* grows naturally from the Montebello Islands in Western Australia's northwest region (Huisman, pers. comm.), presumably around the Northern Territory (no vouchers), and along the Great Barrier Reef (pers. obs.). On the eastern seaboard of Australia, it is native as far south as the Nerang River, Southport, Queensland. It is also native on Lord Howe Island, which although geopolitically in the waters of New South Wales (NSW), lies some 680 km northeast of Sydney in the Tasman Sea between Australia and New Zealand. In 200 years of European occupation and 150 years of collecting, *Caulerpa taxifolia* has never been recorded for the mainland of NSW (Millar and Kraft 1994) until now.

The first population was discovered on March 18, 2000 during a routine biodiversity survey. Two NSW Fisheries officers (Jack Hannan and Marcus Miller) found it in a small sheltered estuarine cove known as Fisherman's Bay near Maianbar, in Port Hacking some 25 km south of Sydney Harbour. Unsure of its identity, but knowing they had not seen it before during their surveys, they sent specimens to the author at the Royal Botanic Gardens Sydney. On confirmation of its identity and potentially invasive nature, further surveys were initiated. The Fisherman's Bay population was estimated to cover approximately 2 hectares. Another population (1 hectare) was then discovered a few weeks later at the main ferry wharf at Gunnamatta Bay at Cronulla on the opposite side of Port Hacking. The largest (about 10 hectares) and most severe infestation was subsequently found in the almost landlocked Lake Conjola, about 200 km south of Sydney, some two months (June 2000) after the Port Hacking discovery. In December 2000, a small population (400 sq m) was found at Careel Bay, in Pittwater (next to the Royal Sydney Yacht Squadron), just north of Sydney. In February 2001, a population was found in Lake Macquarie, again just north of Sydney, and in March of that year, a population in Burrill Lake, near Batemans Bay (south of Sydney), was confirmed.

The most recent outbreak (April 2001) was recorded at Towra Point Aquatic Reserve in Botany Bay just south of Sydney. A man fishing illegally in the reserve noticed the weed clogging his nets. He sent specimens to the author, while notifying NSW Fisheries of the possible outbreak. His honesty for reporting the discovery was rewarded with no fine being charged for his illegal activities.

In all situations, the plants are mostly associated with seagrass beds such as *Posidonia australis*, *Zostera capricorni,* and *Halophila ovalis* in shallow water (1–10 m) and in sheltered, mostly landlocked estuaries or ICOLs (Intermittently Closed and Open Lakes). We know from extensive seagrass mapping studies of regions such as Lake Conjola, that *C. taxifolia* was not present there in the mid-1980s. Judging by the size of the population, coupled with rough estimates of growth rate (4 cm per day), we believe the first introduction occurred sometime between 1985 and 1989. Few of the NSW populations consist of plants with their rhizoids imbedded in the soft sediment, but seem to be growing as entangled masses that have lodged around the fronds of the seagrasses. These *C. taxifolia* beds can be 20–30 cm deep and consist of plants no larger than 5–10 cm long fronds. In healthy, presumably rapidly growing stands, the seagrasses are completely smothered.

Based on the genetic information (see Jousson et al. 2000), it appears there have been at least two separate introductions to NSW waters. Populations from Lake Conjola are most closely related to those from Moreton Bay, Queensland, yet those from Port Hacking align closely with populations from Gladstone, Queensland. This is consistent with the anthropogenic origin theory whereby plants have been released into the various lakes from either aquarium tank discards or through boating activity. Although as yet untested, we believe that the NSW strain may well constitute a third strain of the species. While it is not identical to the official Mediterranean Aquarium strain, it is also not identical to the native Queensland or Lord Howe Island populations. The latter cannot tolerate water temperatures much below 19˚C. Genetically, the Mediterranean, San Diego, and NSW strains lack an intron normally found in native populations of *C. taxifolia*. (Fama et al. 2002).

The southernmost population in NSW occurs at Burrill Lake (35˚S) where winter minimum temperatures have been recorded as low as 10˚C, while the northernmost population at Lake Macquarie (33˚S) has summer maximums of 26–29˚C.

The theory that the NSW populations are merely natural range extensions of the otherwise native Queensland stocks is not supported, as there are no instances of *C. taxifolia* occurring along any open ocean section of the NSW coastline. The distance between Southport, Queensland, where the native population ceases, and Lake Macquarie is approximately 1000 km—a distance that no seaweed species would be expected to traverse within a 15-year period.

One of the largest unknown factors regarding the *C. taxifolia* populations in NSW is whether they are reproducing sexually or asexually by fragmentation. No reproductive plants have yet been observed and since *Caulerpa* species are holoblastic in which the entire fronds cytoplasm is converted into gametes or involved in their production, such 'bleached' plants would be immediately visible to random surveys by divers. During winter, instances of bleached plants have been observed, but these are assumed to be isolated frond deaths through depigmentation or smothering by surrounding plants. If the NSW populations were reproducing sexually, then eradication would be deemed impossible, whereas the latter method of reproduction (by fragmentation) would at least make it remotely possible in some of the enclosed lake environments to contain or eradicate them. Certainly containment of existing populations would be feasible. Additionally, we have no results or evidence yet that the *C. taxifolia* populations are reducing biodiversity in their immediate region. Such studies will be critical with respect to funding for eradication attempts. Marine life observed above the beds of *C. taxifolia* is limited in abundance and species numbers. Sites contain small numbers of yellowfin bream (*Acanthopagrus australis*) and sea mullet (*Mugil cephalus*). Fisherman's Bay has juvenile snapper (*Pagrus auratus*) and Tarwhine (*Rhabdosargus sarba*) as well as striped trumpeter (*Pelates sexlineatues*), with Gunnamatta Bay recording southern calamari (*Sepioteuthis australis*) around the pilings of the jetties.

Both the native and invasive strains of *C. taxifolia* are known to produce a toxic secondary metabolite known as caulerpenyne (a sesquiterpene), which acts as a major deterrent to all herbivores and epiphytes (Amade and Lemee 1998; Pesando et al. 1996), the former including sea slugs, abalone, and most sea urchins. The concentration of caulerpenyne varies with water depth and temperature, but is always higher in the invasive strain (Amade and Lemee 1998). Water temperatures above 19°C (spring to autumn) and depths of around 5 m are the optimum conditions for caulerpenyne production. Thus, only in deeper waters (10 m plus), and during the winter months, will the invasive *C. taxifolia* plants produce low concentrations of this toxin. Testing of toxicity levels of caulerpenyne in the NSW plants has not been conclusive, and based on field observations, it appears that invertebrates may coexist within the *C. taxifolia* beds, suggesting that levels are presumably low.

Presently known ecotoxological effects of *Caulerpa taxifolia* include:

1. Fatal behavioural changes to marine ciliate protists in very low sublethal concentrations (Ricci et al. 1999).
2. Detoxification of enzymes used by scorpionfish in predation deterrence (Uchimura et al. 1999).
3. Interference with DNA replication at metaphase stage in sea urchin embryos and eggs (Pesando et al. 1996).
4. Deleterious effects on mussel gills (Schroder et al. 1998).
5. Inhibition of first cleavage stages of many microorganisms and eggs of pluricellular animals living within close proximity to these plants (Pesando et al. 1996; Lemee et al. 1993).

None of these effects has been shown for NSW conditions.

Management Issues

The alga was listed as a Noxious Species by legislation rushed through the NSW parliament by the NSW Fisheries Minister on October 1, 2000. Penalties for spreading *C. taxifolia* are AUD$22,000 for individuals and AUD$110,000 for corporations. However, its noxious rating was listed as low, which means that although *C. taxifolia* cannot be bought, sold, or traded within NSW, specimens kept in aquaria do not have to be destroyed; i.e., you can still have it in your possession. A recent visit to the Sydney Aquarium in Darling Harbour (part of Sydney Harbour) found they were growing massive quantities of *C. taxifolia* that they had purchased from a Queensland supplier in order to feed their fish. The tank in which they were growing the plants had a flow-through system that emptied straight into the Harbour. No *C. taxifolia* has been found near the aquarium outlets at this stage and they have agreed to close off the tank and destroy the plants. The Manly Aquarium also has a supply of *C. taxifolia* purchased from the same Queensland supplier. We do not know how many other aquaria have plants, but we know of one in Victoria (where they have not yet brought in legislation) where they routinely give away bags of *C. taxifolia* with every new tank purchased. In their defense, a recent visit to that same aquarium showed that they had since destroyed their plants on the grounds that dealing with such an infamous and invasive species was not deemed profitable.

The Australian federal government has legislation in place regarding the introduction of marine pests. The Consultative Committee for Introduced Marine Pest Emergencies (CCIMPE) has the Mediterranean Aquarium strain of *C. taxifolia* as a trigger species. Unfortunately, because the genetics shows that the NSW populations were closely related to native Queensland populations and were not absolutely identical to the Mediterranean strain, CCIMPE consider *C. taxifolia* in NSW to be a range extension. Thus, it will not release money for studies or eradication from their emergency fund. Additionally, the monitoring, potential eradication, and research into growth rate and reproduction of the NSW populations fall within the jurisdiction of NSW Fisheries, and their existing budget. Until it is proved that *C. taxifolia* in NSW causes a loss in biodiversity, a decline in fish stocks, or a destruction of seagrass beds, funds will be hard to procure.

The recreational diving industry has been notified and they are offering to keep a close look out for *C. taxifolia* along the coast. This may be fruitless as it appears that *C. taxifolia* cannot cope with oceanic habitats in NSW or it would be growing there by now.

A substantial advertising and public education campaign in infected areas has been implemented. Signs have been placed at most boat ramps in affected areas. Boating closures and fishing restrictions have also been introduced in certain areas.

Risk Assessment for NSW Waters

If unchecked, the expansion of this introduced, invasive, cold-tolerant strain of *C. taxifolia* in NSW waters could:

1. Lead to a massive reduction in marine biodiversity (Meinesz 1999), thus seriously and irrevocably compromising the NSW Biodiversity Strategy.
2. Smother and kill all seagrass beds invaded (including the already reduced species *Posidonia australis*).
3. Exclude, to the possibility of extinction, many native and endemic marine algae and invertebrates (Meinesz 1999).
4. Lead to the development of monocultural stands of this most persistent, estuary-clogging alga (Keppner and Caplen 2000).
5. Reduce or potentially destroy recreational diving aesthetics in infested areas.
6. Hinder boating movements and commercial and recreational fishing within invaded areas by fouling fishing nets, lines and hooks, etc.
7. Reduce fish abundance and biomass in areas invaded by *C. taxifolia*.

Eradication Attempts

Preliminary eradication attempts resulted in a 4 sq m patch being cleared by two divers (without any mechanical suction device) in 1 hour. This patch grew back in 6 months.

Because we know the plants in Port Hacking are growing on a soft sediment seabed and not on a hard rocky substrate (as in the Mediterranean), the eradication of *C. taxifolia* is considered feasible. The entire plant consisting of erect fronds, creeping stolon, and descending rhizoids can be extracted from the soft sediment. The sediment is extremely fine and what is sucked up with the plants would be minor in comparison to the wet weight of the plant tissue itself. In our test eradication of 4 sq m, we collected 20 kg of wet plant material. The sediment stirred up or associated with the plants would have been less than 1 kg.

Using Pumps

Two divers are in the water, one with a rigid PVC pipe, to which is attached a water pump used to cause a strong lifting current/suction. A water pump is placed on the boat/barge, the seawater intake being over the side of the vessel. The pump hose attaches to the PVC pipe so that the water flow is directed up the pipe towards the surface.

Attached to the end of the rigid pipe is a length of collapsible or flexible firehose that ends up in the boat. The second diver picks up the individual plants and feeds them into the suction pipe being held by the first diver. The sediment itself is not “dug up” as such—only that which is associated with the plants is removed. The discharge of the fire hose empties into large Nelly bins that are covered with fly wire mesh. The plants are thus kept within the bin and the excess water and fine sediment spills over the sides of the bin(s) and back into the sea. Since the sediment came from that area of seafloor anyway, then returning it is not seen as a problem. Although the Nelly bins fill and overflow with water in seconds, the plants themselves are trapped underneath the mesh. The bins are full of plant material and need changing only after many thousands of litres of water are pumped through the mesh.

The size of any minute fragments of plants that might get through this mesh method is considered to make them essentially unviable.

Starting from the margins of the *C. taxifolia* population and working around in a circle reduces the amount of physical disturbance to areas thick with plants. Eradication by simply mowing through the middle of the population is not an option as it disperses fragments.

Smothering

Sand filled mattresses are biodegradable and do not appear to harm invertebrates in that they are quickly colonized by them. They do kill the seagrasses, however, and they are difficult to deploy.

Plastic sheeting and hard thick rubber matting (conveyer belt) are also hard to deploy over large areas and kill everything underneath including invertebrates and seagrasses.

Rock Salt

Smothering with rock (sea) salt has shown partial success in that it kills the *C. taxifolia* assimilators, but the health of the rhizoids imbedded in the soft sediment has yet to be determined. It appears, though, that the salt is not affecting associated or ambient invertebrates or finfish as it disperses rapidly (within hours). It also has not harmed the surrounding seagrass.

Problems arise in that the amount of salt required is approximately 1 tonne per 10 square metres, making it physically demanding on divers. A mechanical dispersal system is required. Its ecological impacts regarding salinity changes in shallow environments are also unknown at this stage.

All smothering methods are effective in killing *C. taxifolia* within three months and with the salt method, no regrowth has occurred after four months.

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Morphological Plasticity and Invasive Potential of Some *Caulerpa* Species

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Introduction

The arrival of animals and plants to new environments has happened naturally throughout earth's history (Elton 1958). Nevertheless, in modern times, the introduction (intentional or accidental) of exotic species has increased dramatically as a consequence of human activities (Elton 1958; Mooney et al. 1986; Cohen et al. 1995; Ruesink et al. 1995; Ruiz et al. 2000; Williamson 1996). In fact, biological invasions continue to cause biodiversity loss and negative economic impacts throughout the world, as species are transported across natural biogeographic boundaries.

The biological consequences of nonindigenous species result both from species-specific traits and the receptor environment. Some new species pose major threats to new environments; others cannot invade or remain rare and unimportant. In general, most new arrivals are due to human activities, most of those arrivals fail to establish, and few that establish become pests (Williamson 1996). Successful establishment increases with opportunity (number of individuals or times introduced) and may also be inhibited by biological characteristics of the receptor ecosystem, such as species richness, degree of disturbance, and healthy status of native communities (Williamson 1996; Levine and D'Antonio 2000).

We know very little about the biological characteristics associated with macroalgal invasions. Invasive macroalgae are relatively unstudied, although many cause damage to native communities (Curiel et al. 1998; Garbary et al. 2000; Jousson et al. 2000; Muller 2000; Schaffelke et al. 2000). Effects have been detected on biodiversity and on economies of human coastal communities (Riggio 1995; Verlaque 1994; Verlaque and Fritayre 1994). About 200 invasive marine algae have been detected in the Mediterranean Sea (Verlaque 1994; Muller 2000), the most remarkable of which is *C. taxifolia*. Worldwide, several additional species are recognized as high-impact invaders, including several red algae on the North Sea coasts (Maggs and Stegenga 1999), *Undaria pinnatifida* in the Atlantic Ocean (Floc'-h et al. 1996) and New Zealand (Walker and Kendrick 1998), and *Codium fragile* ssp. *tomentosoides* in New Zealand (Trowbridge 1998) and in the East Coast of North America (Garbary et al. 2000). Reefs in the Hawaiian Islands are invaded by *Acantophora spicifera* and *Hypnea musciformis* (Russell 1992; Russell and Balasz 1994) and many other introduced species have been detected (Coles et al. 1999). Around 18 marine algal species have been reported as possible nonindigenous species by Lindstrom (1999) for the Strait of Georgia, and Ruiz et al. (2000) mention a total 34 algal species for the United States.

The management options for invasive species have been:

1) Monitoring without intervention;
2) Management to reduce populations; and
3) Protection against invasions (Ribera and Boudouresque 1995).

Eradication and control of established macroalgal species is very difficult. Handpicking is a time-consuming technique with no clear effects in the long term (Trowbridge 1998). Herbivores may provide biological control of macroalgal invaders, but they actually can increase fragment production and dispersion in *C. taxifolia* (Zuljevic et al. 2001). Chemical control involves the use of herbicides, copper sulphate, sodium hydrochlorite or phytohormones, and their low specificity and persistence in the medium make them unsuitable for extended uses (Ribera and Boudouresque 1995). Prevention of new introductions is therefore a mandatory strategy for preventing harmful blooms of exotic macroalgae.

To predict which species are likely to invade and even become pests, several authors have suggested that it is important to understand what biological characteristics make a species a better invader, so that species can be screened to prevent future introductions (Goodwin et al. 1999). One of the few accepted generalizations is that if a nonindigenous species performs a novel function in the community, such as when a nitrogen-fixing plant invades a region with nitrogen poor soils (Vitousek and Walker 1989), the impact expected in the community is greater (Ruesink et al. 1995). Further, general characteristics identified as important determinants of plant invasiveness are: small, short-lived seeds that can germinate without pretreatment, short juvenile periods and short intervals between large seed crops, large size, long flowering period, vegetative reproduction and perfect flowers (Rejmánek and Richardson 1996; Reichard and Hamilton 1997). But Goodwin et al. (1999) found that only the original range of distribution was an effective predictor of invasiveness, which indicates that species that already have a wide distribution are likely to become be introduced accidentally or intentionally.

The genus *Caulerpa* includes about 73 species worldwide (Calvert et al. 1976; Satoh et al. 1992), many of which are highly valued as beautiful and hardy saltwater aquarium plants. Species are generally found in tropical waters, but also extend to some subtropical warm areas. Prud'homme van Reine et al. (1996) have described three major centers of biodiversity for *Caulerpa*: Malaysia (contact between Indian and Pacific Oceans) with 28 or 29 recorded species; the Caribbean with 22 species, including seven endemics (Calvert et al. 1976; Wynne 1986; Littler and Littler 2000); and Southern Australia with 18–20 species, with nine probably endemic (Womersley 1984). *Caulerpa taxifolia* occurs in all three major regions

(Littler and Littler 2000; Silva et al. 1987, 1996; Prud'homme van Reine et al. 1996). Because these species are transported widely, it is important to have scientifically sound import policies to avoid future introductions of the already invasive strain of *C. taxifolia*, as well as other potentially invasive *Caulerpa* spp.

In this report we address the following questions:

- What biological traits are associated with the successful invasion of *C. taxifolia*?
- Are these traits shared more generally within the genus?
- Specifically, to what extent do different *Caulerpa* species demonstrate phenotypic plasticity allowing them to live in multiple habitat types?

The goal of this work is to assess invasion potential of *Caulerpa* species from field observations and use this information to prevent future harmful introductions.

Biological Characteristics Promoting Invasion in *Caulerpa*

Several biological traits probably contribute to the successful invasion of *C. taxifolia*. The traits I summarize in this section allow *C. taxifolia* to live under a wide range of conditions (nutrient, temperature) and increase rapidly in abundance through growth and reproduction. *C. taxifolia* has traits of: a) high growth rate; b) nutrient uptake from sediments; c) tolerance to low water temperature; d) lack of consumers; and e) clonal growth form. Clonality allows *C. taxifolia* to cover new area through vegetative growth, disperse by fragmentation, avoid senescence by continual production of modules, and use resources opportunistically by modifying morphology and physiology.

Growth rate

Caulerpa species grow in three ways: stolon growth increases the area covered by a clone, new fronds emerge vertically from the stolon, and fronds grow longer. For stolons, growth rates of *C. taxifolia* in the Mediterranean Sea are higher in summer (5–14 mm/day) than in winter (0–3 mm/day), with yearly estimates of 1–2 m (Komatsu et al. 1997). These growth rates are in the range of those reported in the natural tropical environment for other native *Caulerpa* species. Williams et al. (1985) measured an average growth of 1 cm/day for *C. sertularioides*, *C. cupressoides* v. *lycompodium* f. *elegans*, *C. mexicana*, and *C. cupressoides* v. *flabellate* in the Virgin Islands. O'Neal and Price (1988) report a maximum growth rate of 16.8 mm/day for *C. paspaloides* in the Virgin Islands. It is evident that many species of the genus *Caulerpa* grow rapidly, both in their native and invaded environments. This rapid growth contributes to the potential for several *Caulerpa* spp. to form harmful blooms.

Lack of nutrient limitation

Macroalgae are thought to depend on absorption of nutrients from the water column because they lack roots to exploit nutrients from the sediments. Nevertheless all species of the genus *Caulerpa* have rhizoids embedded in the sediments. Williams (1984) experimentally demonstrated that *C. cupressoides* incorporated NH_4 from sediments, and that the sediments are the primary nitrogen source (Williams and Fisher 1985). Nutrient uptake from sediments is possible for other *Caulerpa* spp. as well. For instance, in *C. taxifolia*, tissue nutrient concentrations and photosynthetic rates do not correlate with water nutrient concentrations (Delgado et al. 1996). Chisholm et al. (1996) provided direct evidence of sediment ^{14}C-valine and ^{33}P uptake in *C. taxifolia* and translocation to photoassimilatory parts. Furthermore, they found bacteria covering the outer surfaces of the rhizoids and large numbers of bacterial rods (10^4–10^5 mm^{-3}) in the cytoplasm. One of the bacteria is a *Rhodopseudomonas*-like bacterium with the potential to fix N_2, but how the alga and bacteria interact, or even whether N_2 fixation occurs, remains unknown.

In the Mediterranean Sea, *C. taxifolia* does not experience nutrient limitation, as there is no growth response to N and P enrichment (Delgado et al. 1996). Similarly, *C. paspaloides* did not respond to nutrient enrichment in its native environment (O'Neal and Prince 1988). Nutrients appear not to control *Caulerpa* growth. However, because *Caulerpa* species can grow under low nutrient conditions, this capacity may contribute to their competitive dominance over other macroalgae and seagrasses (Delgado et al. 1996; Chisholm et al. 1996; Ceccherelli and Cinelli 1999b).

Tolerance to low water temperature

Caulerpa taxifolia growth was measurable between 15 and 35 ºC, with best growth from 20–30 ºC (Komatsu et al. 1997). Lethal upper limits were 31–32.5 ºC and lower limits were 9–10 ºC. These temperatures extend lower than the range experienced by wild strains in the native tropical environment. Other species of *Caulerpa* also have temperature-dependent growth, as indicated by comparisons of summer and winter growth in *C. paspaloides* in the Florida Keys (O'Neal and Price 1988). *Caulerpa* species can be expected to survive and grow to 15 ºC. Water temperatures in

Southern California range from 14–15 ºC in winter to 16–21ºC in summer. Northern California water temperatures are slightly lower (10–13 ºC in winter and 14 –20 ºC in summer). In Oregon and Washington, water temperatures are cooler still, from 5 –11 ºC in winter to 10–20 ºC in summer (NOAA-NODC 2001). Evidently, in the American Pacific, *Caulerpa* species will be able to grow mainly in Californian waters. However, more northerly latitudes could be invaded during relatively warm periods, for instance during summer, El Niño events, or in shallow bays.

Lack of consumers

Caulerpa taxifolia produces secondary metabolites such as caulerpenyne that repel predators, which may account for the lack of consumers in the Mediterranean Sea (Pesando et al. 1996; Paul and Van Alstyne 1988). Indeed, some of the invasive success of *C. taxifolia* may be due to escaping specialist consumers that keep it at low densities in its native range. Many other species of the genus also produce secondary metabolites; caulerpenyne has been isolated from at least nine (Paul and Fenical 1986). In addition, *C. cupressoides* from the Mexican Caribbean shows high ichthyotoxic activity (De-Lara-Issasi et al. 2001).

Specialized sea slugs (Sacoglossa) are known to graze on *Caulerpa* species, i.e. *Oxynoe olivacea*, *Lobiger serradifalci,* and *Elysia subornata* (Coquillard et al. 2000; Jensen 1980, 1993; Trowbridge 2002). No native sacoglossans are present in the Mediterranean Sea, but other sites of potential invasion may have some natural resistance to invasion through top-down control. However, careful studies are needed to evaluate the effect of herbivory on the growth and dispersal of species of the genus *Caulerpa*. One effect of herbivory is to break algae into small fragments. Sea slugs can actually facilitate the dispersal of native and introduced *Codium* spp. (Trowbridge 1993, 1997, 1998). In *Halimeda* spp., segments can survive and repopulate areas if they are not excessively damaged during biting or after physical damage by storms (Walters and Smith 1994). Thus, events considered to have negative impacts on algal populations appear to be able to increase plant numbers in reef habitats. Zuljevic et al. (2001) showed that the sacoglossan *Lobiger serradifalci* may facilitate *C. taxifolia* dispersal instead of controlling it in the Mediterranean Sea.

Clonal growth

Vegetative growth and asexual reproduction

Where it has invaded, *C. taxifolia* is reported to spread only by vegetative growth and dispersal of fragments (Zuljevic and Antolic 2000).

Successful sexual reproduction has not been observed, as all individuals are male. *C. racemosa*, which is also invasive in the Mediterranean, produces both female and male gametes but has a very low fertilization rate (5%) (Panayotidis and Zuljevic 2001). In their native environment, species of the genus *Caulerpa* have a monocarpic (plants die after reproduction) diplontic sexual life cycle with one vegetative phase (2N) and haploid (1N) biflagellated gametes with massive spawning (Clifton and Clifton 1999). In the absence of sexual reproduction, fragment production and fragment reattachment are crucial biological traits that affect the invasive potential of these species. Although vegetative growth certainly increases colony size, colonization of new areas by fragments is the major way that *C. taxifolia* has spread through the Mediterranean Sea (Ceccherelli and Cinelli 1999a; Belsher and Meinesz 1995; Meinesz et al. 1995; Sant el al. 1996; Smith and Walters 1999).

Fragmentation

Fragment establishment was examined experimentally for native clones of some *Caulerpa* species in Hawaii (Smith and Walters 1999). *Caulerpa taxifolia* fragments from the rhizoid failed to reattach, but fragments from the frond as small as 10 mm were able to produce new reattachment structures. Establishment increased with fragment size to 100% success in fragments of 15 and 20 mm. *Caulerpa prolifera* fragments that included stalk or rhizome tissue survived, and establishment success was 100% for fragments 40 mm in length; lamina fragments never survived. In contrast for *C. verticillata* only the fragments (fronds and rhizoids) of 40 mm survived, but any fragment was able to reattach over the course of 14 days. In a similar study, I found that stolon fragments of 4–5 cm of *C. cupressoides* from Puerto Morelos reef (Mexican Caribbean) were able to re-attach and resume growth after 15 days in aquarium conditions (L. Collado-Vides unpublished).

Escaping senescence

Based on long-term monitoring of patches, *C. taxifolia* has an annual cycle of growth and decay in which no single part of the thallus persists for more than a year, yet the patch as a whole persists indefinitely. Meinesz et al. (1995) tracked patches for one year within a 100 m^2 area at a depth of 9 m on the eastern side of Cape Martin, France. Fronds and stolons generally initiated growth in late winter and early spring, reaching maximum length in July and quickly decaying in September. Watkinson and White (1986) showed that clonal plants have mortality rates that are independent of age, because they constantly produce new modules and avoid senescence at the level of the whole individual. This seasonal pattern of maximal growth during late winter and early spring, while perennation allows whole-individual persistence, has been observed in both Mediterranean and tropical environments. Some examples are found in *C. racemosa* (Piazzi and Cinnelli 1999) and *C. prolifera* in the Mediterranean (Meinesz 1979), and *C. sertularioides* in Baja California coasts (Scrosati 2001).

Opportunistic use of resources—morphological and physiological plasticity

The capacity to change in size, form, and physiological behavior is an essential feature of living organisms, and such variation is well known in plants. Plasticity is one way organisms acclimate and/or adapt to different environmental conditions and, hence, amplify their distribution or avoid competition by diversification. This capacity of change in clonal plants has been widely described (Slade and Hutchings 1987a, b; de Kroon and Schieving 1990; Hutching and Mogie 1990). Decreased rhizome or stolon internode length and/or increased clonal branching in response to favorable environments is thought to be beneficial, since it should allow resource-acquiring parts of plants to become concentrated in the most rewarding areas of habitat, maximizing their acquisition of resources (Hutchings and Mogie 1990). The genus *Caulerpa* is characterized by extreme morphological variation. Svedelius (1906) and Boergesen (1907) mentioned that factors such as light intensity and degree of water movement possibly influenced morphology in *Caulerpa*. Barilotti (1970) demonstrated that the morphology of *C. prolifera* is influenced by light intensity. Particularly Meinesz (1979 a, c) reports seasonal morphological variation of *C. prolifera* and the ability to regenerate by vegetative propagation. Peterson (1972) showed that *C. racemosa* has the ability to change its growth form in altered light environments providing evidence for an environmental rather than genetic control of the wide morphological variation present in this species. In a study of morphological responses to reduced illumination, Calvert (1976) reports interesting morphological modification as responses to high or low light intensity in several species of *Caulerpa*. He demonstrated that the radial forms of shallow waters change to bilateral forms in deeper waters. Therefore, morphological plasticity is environmentally regulated for several species of *Caulerpa*, although this does not exclude a genetic component as a source of variation among strains, as in the case of *C. taxifolia* (Jousson et al. 1998, 2000; Wiedmann et al. 2001; Meusnier et al., 2001).

Morphological Plasticity in *Caulerpa* Species of the Mexican Caribbean

The general statement that all *Caulerpa* species are morphologically plastic has in fact not been tested. No comparative studies of morphological plasticity are available in the literature. Over several years one of us (LCV), has been examining the distributions of *Caulerpa* species, along with morphological and physiological traits, on Puerto Morelos barrier reef near the Yucatan peninsula in the Mexican Caribbean (20º48'N, 86º52'W) (Collado-Vides and Robledo 1999). A second study was done in the same locality to evaluate small, but important morphological variations using as a model *C. prolifera*, which has a heterogeneous distribution within lagoon habitats (Collado-Vides, in press). These studies allow a comparison of the range of morphological plasticity among species.

Caulerpa prolifera is restricted to the reef lagoon, mainly in shallow waters with sandy substrata, either intermixed with the seagrass *Thalassia testudinum* or in open habitats. Because morphology often varies across gradients of light intensity, two sites were selected for the study, both in the reef lagoon. One population was in a sunny area with a mixture of sandy and cobble substrate at a depth of 0.50 m and exposed to moderate wave action. A second population was in a shaded area within a *T. testudinum* bed with sandy substratum at 1.50 m depth and low water movement.

The light regime of both sites was characterized over a 12 hr cycle. Light readings were taken simultaneously with two light sensors (PAR, 4π attached to a LiCor 1000 Data Logger). Each sensor was fixed within the algal bed to read PAR at the lamina level (Fig. 1). At each site five quadrat samples (5 x 5 cm) were taken. All *C. prolifera* inside each quadrat was collected. Special care was taken to collect the whole clonal fragment including all ramets. The following morphometric measures were made: internode length, number of lamina per ramet, lamina length, stipe length and lamina thickness. A photocopy of the fresh material was made and scanned. Automatic calculations for surface area were made using the software for image analysis (SigmaScanPro 4.0, Jandel Scientific). After all morphometric measures were made, the material was separated into parts (lamina, stipe, stolon, and rhizoid), rhizoids were immersed in a 5% solution of phosphoric acid to remove the sand, then all parts were dried (10 hrs at 60º C). Dry weights of all parts were determined. Based on growth analysis (Pearcy et al. 1989), the following morphological parameters were calculated:

1. Total dry weight per quadrat
2. Lamina dry weight

3. Total lamina dry weight
4. Total stipe dry weight
5. Total rhizoid dry weight.

From those calculations the following parameters were obtained:

1. Lamina weight ratio (LWR): lamina dry weight/total of all parts dry weight.
2. Stipe weight ratio (SWR): stipe dry weight/total of all parts dry weight.
3. Rhizoid weight ratio (RWR): rhizoid dry weight/total of all parts dry weight.
4. Photosynthetic weight (PW): lamina + stipe dry weight.

Caulerpa prolifera growing in open well-lit environments differed significantly in morphology from plants growing within seagrass. In shade, laminas were regular and long, emerging from long stipes. In contrast, thick, irregularly shaped and short laminas from short stipes characterized populations in sunny environments (Tables 1 and 2). Shaded populations also invested more in photosynthetic area. Photosynthetic weight (sum of lamina and stipe dry weight) and stipe weight ratio were higher in shaded than sunny areas (Table 3).

Caulerpa prolifera shows morphological plasticity that can be correlated with light regimes, but its distribution is restricted to the lagoon, so the next question is, what is happening with the other species of the genus present in the Puerto Morelos reef system? An initial answer comes from a comparative study of seven *Caulerpa* species (Collado-Vides and Robledo 1999). Two species (*C. racemosa* and *C. verticillata)* are present in reef conditions, four (*C. prolifera*, *C. paspaloides*, *C. lanuginosa*, and *C. mexicana*) are found in the reef lagoon, and *C. cupressoides* is present in both habitats. Ten plants of each species at each of three reef and lagoon sites were sampled. Each sample included the total stolon, which was carefully unburied. The following morphometric measures were made: length of the total stolon, number of stolon ramifications, number of fronds, internode length, number of rhizoidal clusters. In this study, we made extraction of pigments to all seven species and P-I curves to five of the seven species: *Caulerpa cupressoides* (lagoon and reef), *C. prolifera*, *C. mexicana*, *C. paspaloides* and *C. racemosa*.

Morphologies differed substantially between reef and lagoon habitats. Small plants with short fronds and high frond density were found in reef conditions, whereas large plants with long fronds and low frond density were found in lagoon conditions (Figs. 2, 3 and 4). On the basis of a discriminant function analysis (DFA), the morphological features that separated the reef and lagoon species were: frond length ($p<0.001$), stolon ramification ($p<0.001$), stolon length ($p<0.001$) and frond density ($p<0.01$). *Caulerpa cupressoides* was found in both environments and had two significantly different morphs, with high frond density ($p<0.001$), short stolon length ($p<0.001$), and higher stolon branching ($p<0.001$) in reef individuals compared with lagoon individuals. Fronds from reef individuals were shorter but not significantly different from lagoon individuals. From these results we can conclude that all studied species have morphological variation, but in the Puerto Morelos system, *C. cupressoides* showed broadest plasticity and distribution.

The comparative physiological performance showed that reef species behave as sun tolerant species while in the lagoon *C. paspaloides* behave as sun tolerant and *C.lanuginose* and *C. mexicana* behave as shade tolerant species. In parallel with the morphological plasticity, *C. cupressoides* performed as a light tolerant alga in reef conditions and shade tolerant alga in lagoon conditions. Acclimation in this species gives it broad environmental tolerance relative to the other six species and probably contributes to its ability to survive in different environmental conditions.

We were able to demonstrate the presence of morphological plasticity and correlate it with some environmental parameters. Further, we were able to identify a morphological pattern associated with light and water motion in each habitat, and the only species that was able to colonize both environments changed its morphology to match all *Caulerpa* species found in each habitat.

Discussion

All the species of the genus *Caulerpa* are clonal plants. Clonality gives them the potential to disperse by fragmentation, achieve rapid vegetative growth, and compete strongly. *Caulerpa* species also have the unusual ability among macroalgae to input nutrients from the sediment. From those observations, many species of the genus may become invasive in new environments. Two particularly risky species are *C. racemosa* and *C. cupressoides*. In fact, *C. racemosa* has been reported to be invasive, spreads rapidly, and is becoming abundant in the Mediterranean Sea (Modena et al. 2000; Piazzi et al. 2001). *Caulerpa cupressoides* is a high risk species because it has high morphological and physiological plasticity (Collado-Vides and Robledo 1999), grows rapidly in native sites where it is able to incorporate nutrients from sediments (Williams and Dennison 1990; Collado-Vides, unpublished observations), and produces secondary metabolites with a high ichthyotoxic activity that deters consumers (De Lara-Isassi et al. 2000).

Other *Caulerpa* species may pose a lower risk of harmful introduction. *Caulerpa mexicana* (probably introduced) and *C. prolifera* (native) are present in the Mediterranean Sea but are considered noninvasive (Ribera and Boudouresque 1995). *Caulerpa prolifera* has a lower growth rate (Collado-Vides personal observations) and lower success of fragments than *C. taxifolia* (Smith and Walters 1999). High herbivory pressure by *Elysia* sp. is a possible explanation for a loss of *C. prolifera* populations in the Indian River lagoon, Florida (White and Snodgrass 1990).

A combination of a few biological characteristics can be useful in the evaluation of potential invasive species in the genus *Caulerpa*. Traits are relevant at three levels. At the individual level, risky species have few physiological limits to growth and plastic ability to use available resources. At the population level, risky species have effective reproduction, dispersal, perennation and colonization. At the community level, risky species avoid top-down control and have high competitive abilities. Based on those characteristics, all *Caulerpa* species are potentially invaders. What distinguishes species in large part appears to be their plasticity, although more comparative work is necessary. An additional consideration is evolution of strains during cultivation in aquaria, which could alter their expected range and impact if introduced. Propagule pressure or magnitude and frequency of introductions and particular characteristics of the receptor region are other determinants of invasion success.

Perspectives

Caulerpa taxifolia is an invasive alga that has already caused substantial damage. Yet no control mechanisms have been found. But the problem does not stop here, because many other *Caulerpa* species are potential invaders. For the dozens of other species in the genus, time remains to take steps to prevent harmful invasions. In our opinion we need to address the following questions in order to have a more realistic risk assessment of potential invaders.

a) Does the invasion of *Caulerpa* species have a direct relation with propagule pressure?
b) What is the minimum inoculum for a successful invasion? The clonal nature of all species of the genus may allow one fragment to start a successful invasion. On the other hand, control efforts may be successful if applied before the growing clone reaches a threshold size. Demographic models incorporating particularities of *Caulerpa* life cycle should be useful tools.

c) What are environmental characteristics of the potential receptor regions that facilitate or impede the success of species of the genus *Caulerpa?*
d) How do demographic models vary with environmental characteristics? This approach deals with the difficult prediction of where each species will have higher expectations of successful colonization.

The role of the aquaria: we need to experimentally demonstrate whether the invasive strain of *C. taxifolia* is a biological product from the aquarium.

a) Can we find in nature the invasive form? Is the robust morph of this species a human product or on the contrary, does the robust morph exist naturally and that strain was cultivated in the aquarium?
b) Does aquarium cultivation enhance the invasive characteristics of other species of the genus?

We need to identify all the possible vectors, not only for *C. taxifolia*, but also for other species of the genus.

All *Caulerpa* species should be banned from aquarium trade until we know which species are so restricted in their biological characteristics that invasion probability is low. This approach requires ecophysiological studies in a wider spectrum of species to give a scientific background to aquarium trade regulations.

Acknowledgments

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Figures . . .

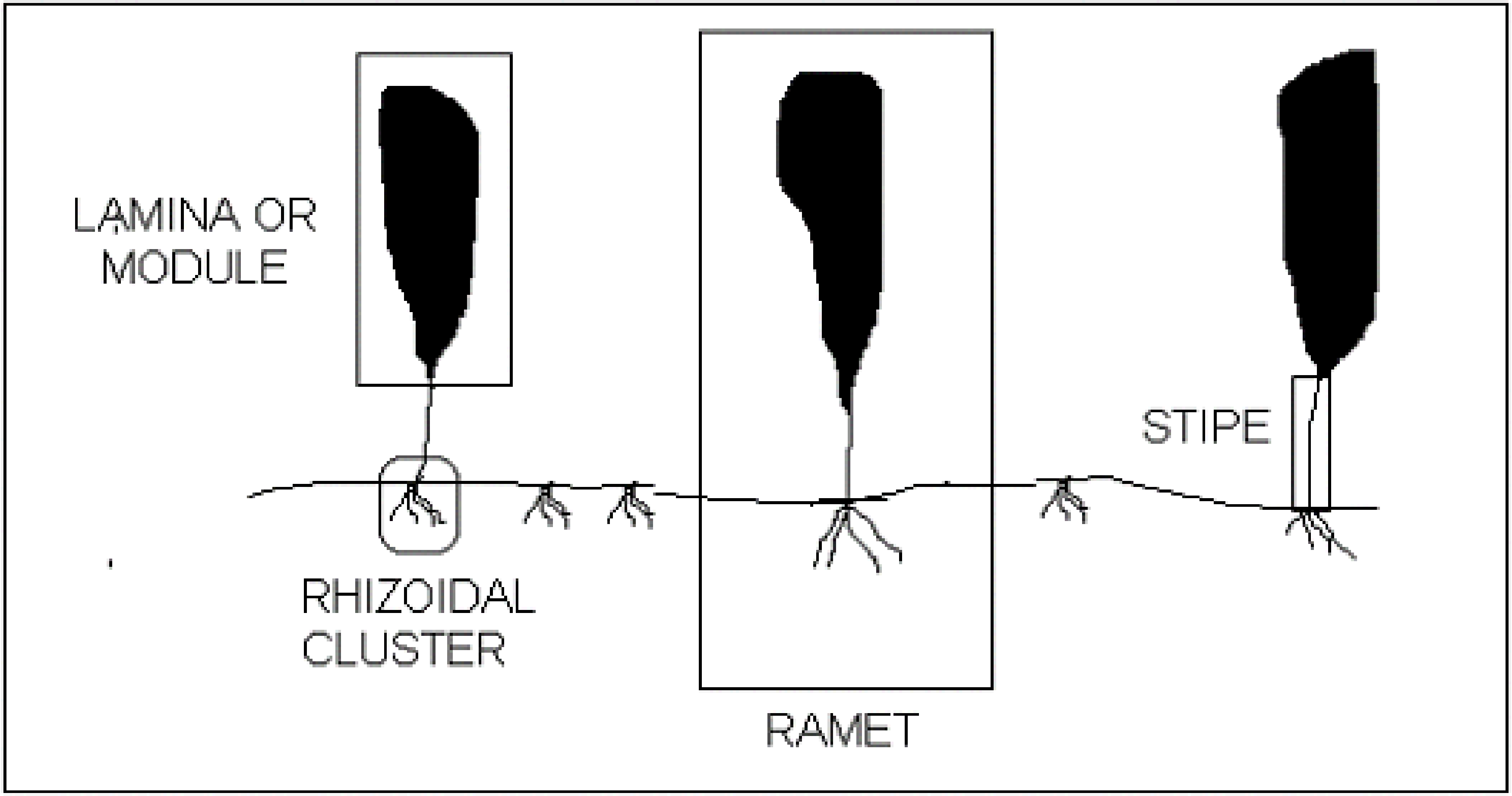

Figure 1. Schematic representation of the clonal parts of a clonal fragment showing the module or lamina, ramet, stipe, and rhizoidal cluster.

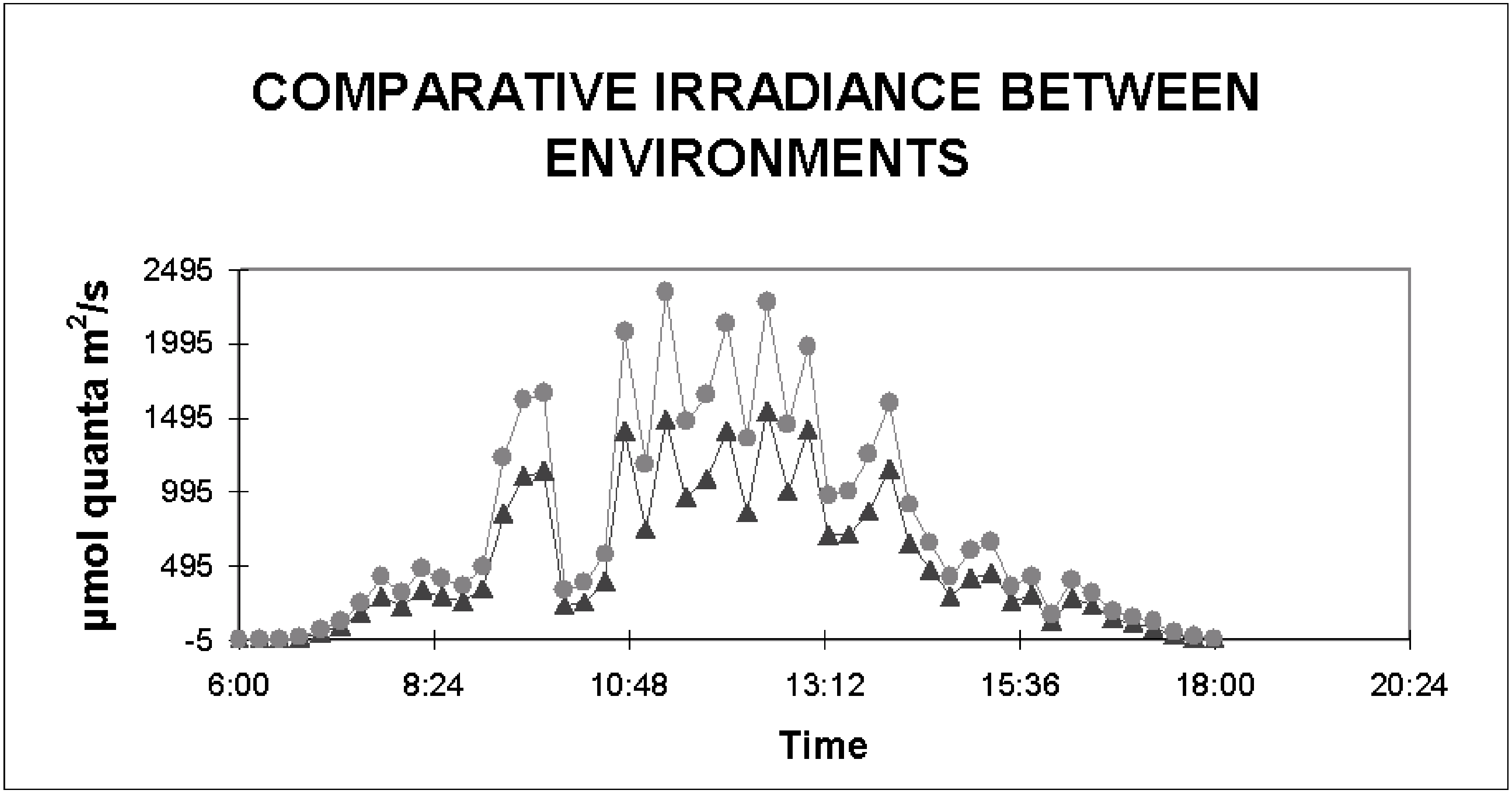

Figure 2. Comparative irradiance between sites o = Light, Δ = Shade. A 12 hr cycle of data collection of Photosynthetic Active Radiation (PAR) measured with a 4π sensor attached to a Li-Cor Datalogger.

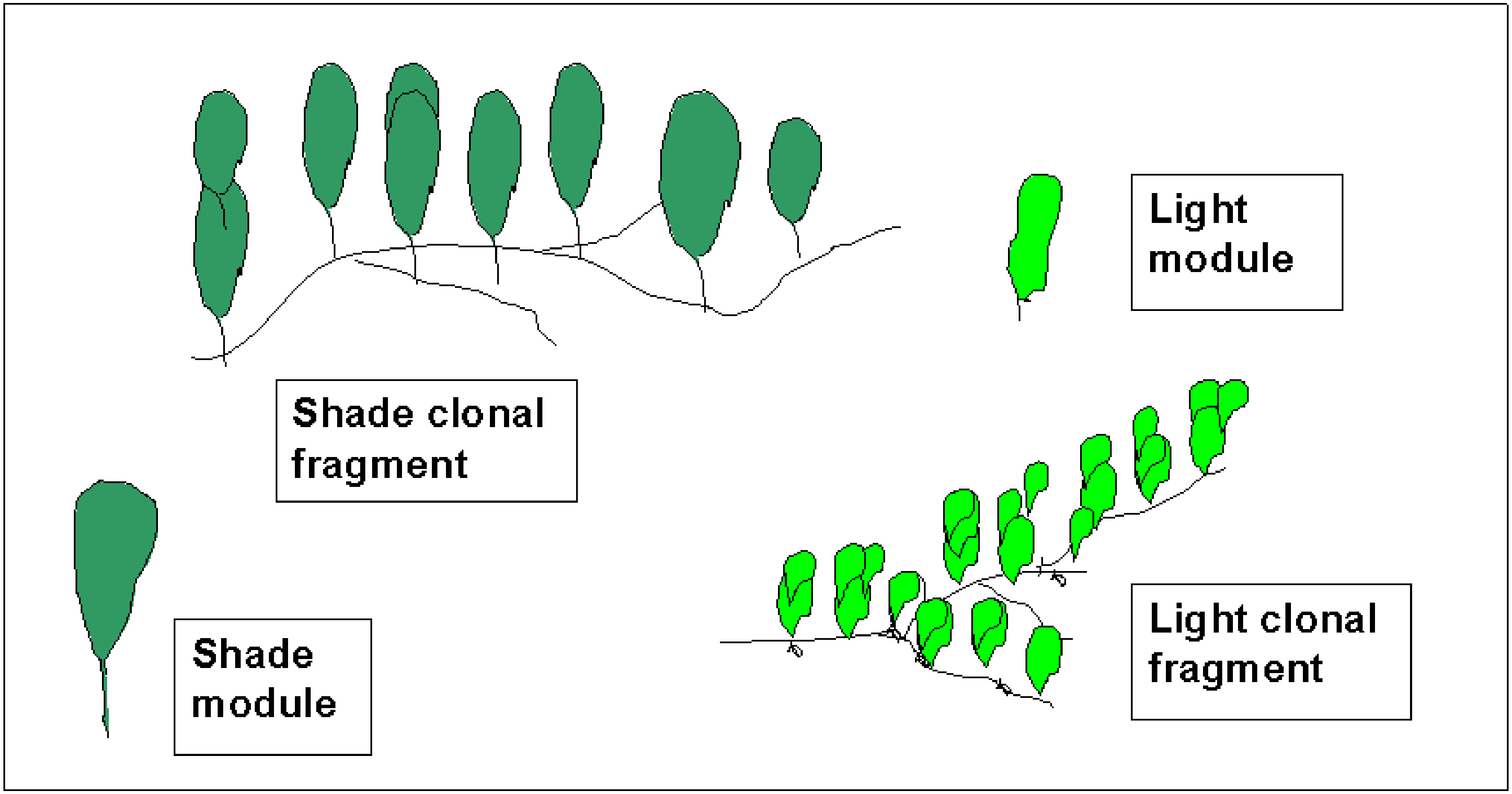

Figure 3. Schematic representation of clonal fragments of *Caulerpa prolifera* showing differences between shade and sunny clonal fragments.

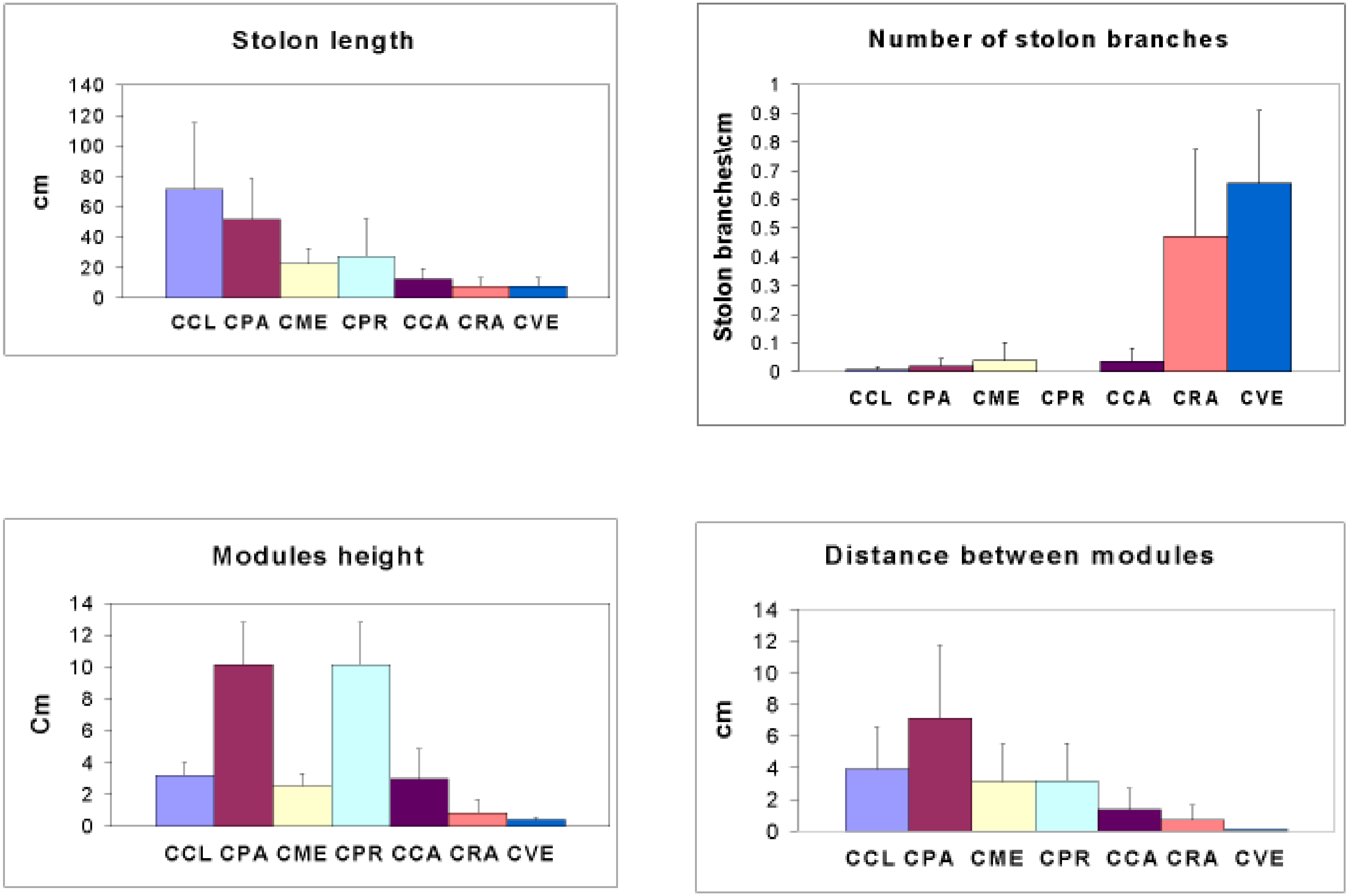

Figure 4. Graphs showing morphometric characteristics of the seven species of *Caulerpa*. CCL = *C. cupressoides* from the lagoon, CPA = *C. paspaloides*, CME = *C. mexicana*, CPR = *C. prolifera*, CCA = *Caulerpa cupressoides* from the reef, CRA = *C. racemosa*, and CVE = *C. verticillata*.

Tables . . .

Table 1. Morphometric parameters of the habit of *C. prolifera* and statistical analysis. ANOVA $P<0.05$. D/RAM = Distance between Ramets. Blade # = Number of blades per ramet. ST. L = Stipe length. ST.W = Stipe dry weight. RH.W. = Rhizoid dry weight. BL.W. = Blade dry weight.

	D/RAM.	BLADE #	ST.L	ST.W	RH.W.	BL.W.
LIGHT						
Mean	2.4591	2.6214	6.2315	0.2408	0.0146	0.2966
S.E.	0.1622	0.1474	1.0181	0.04122	0.00351	0.06132
S.D.	1.5215	1.4959	9.9233	0.09217	0.00786	0.13713
SHADE						
Mean	3.8703	1.9091	11.407	0.4984	0.027	0.9068
S.E.	0.3196	0.1652	0.6906	0.10517	0.01197	0.11629
S.D.	1.9441	1.0958	8.4868	0.23516	0.02676	0.26003
P<0.05	0.0001	0.005	0.000	0.05203	0.34938	0.002
F	18.906	8.100	19.864	5.20000	0.98800	21.542

Table 2. Morphometric parameters of blades and statistical analysis, ANOVA P<0.05. Thick = Blade thickness in mm. Length = Blade length in cm. Weight = Blade dry weight in g. Area = Projected area in cm^2.

	THICK	LENGTH	WEIGHT	AREA
LIGHT				
Mean	0.4029	2.5284	0.018	2.3654
S.E.	0.0084	0.1310	0.0011	0.1723
S.D.	0.0819	1.2770	0.0115	1.6798
SHADE				
Mean	0.24423	4.26688	0.03169	3.96811
S.E.	0.01220	0.16063	0.00219	0.18108
S.D.	0.15001	1.97395	0.02693	2.22518
$p<0.05$	0.0001	0.0001	0.0001	0.0001
F	91.848	55.564	20.702	42.315

Table 3. **Dry weight partitioning and statistical analysis. ANOVA $P<0.05$. BWR = Blade weight ratio (blade weight/total weight). SWR = Stipe weight ratio (stipe weight/total weight). RWR = Rhizoid weight ration (rhizoid weight/total weight). PW = photosynthetic weight (blade + stipe weight).**

	BWR	SWR	RWR	PW
LIGHT				
Mean	0.53442	0.43898	0.02658	0.5374
S.E.	0.02393	0.02134	0.00556	0.10041
S.D.	0.05351	0.04772	0.01244	0.22452
SHADE				
Mean	0.64407	0.33831	0.01761	1.4052
S.E.	0.04181	0.03673	0.00697	0.19528
S.D.	0.09348	0.08213	0.01559	0.43667
$p< 0.05$	0.052	0.045	0.344	0.004
F	5.18	5.616	1.011	15.617

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Caulerpa taxifolia . . .

Natural Products Chemistry and Chemical Ecology of *Caulerpa* spp. With an Emphasis on Invasive *Caulerpa taxifolia*

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Introduction

Green algae of the genus *Caulerpa* are found world-wide, generally in shallow-water tropical and subtropical marine habitats. These noncalcified algae can be found in abundance and sometimes in areas of significant herbivore populations. The taxonomy of the genus *Caulerpa* is generally based on the shape of the blades, which vary from flattened to bushy to cylindrical branchlets (Littler and Littler 2000). Even within a species the variation in forms is great. These algae grow vegetatively and can cover extensive areas.

In this paper I will review the natural products chemistry of *Caulerpa* species with an emphasis on comparing tropical species of *Caulerpa* with the invasive Mediterranean *C. taxifolia*. In the tropics, most species of *Caulerpa* are readily consumed by herbivorous reef fishes including rabbitfishes (Siganidae) and surgeonfishes (Acanthuridae) (Paul and Hay 1986, Paul et al. 1990), sea urchins such as *Diadema antillarum* (Morrison 1988), and specialist herbivores such as sacoglossan mollusks (Cimino and Ghiselin 1998, Williams and Walker 1999). Crude extracts of several species of *Caulerpa* as well as the purified terpene caulerpenyne do not deter feeding by any species of herbivorous fishes they have been tested against (Paul 1987, 1992, Paul et al. 1990, 1993, Meyer and Paul 1992, Meyer et al. 1994). Thus, tropical generalist herbivores, such as grazing fishes, do not appear to be affected by terpenes present in most species of *Caulerpa*. However, this is not the case for the temperate grazers (mostly invertebrates) in the Mediterranean and Southern California where *C. taxifolia* has invaded. These herbivores do not readily consume *C. taxifolia* (Boudouresque et al. 1996), and it is likely that the terpenes function as chemical defenses against these non-adapted herbivores (Paul et al. 2001). However, caulerpenyne, oxytoxins, and the other terpenes found in *C. taxifolia* have not been directly tested against Mediterranean or Californian herbivores; therefore, it difficult to draw any conclusions about the roles of these compounds in chemical defense in temperate habitats.

Natural Products Chemistry of *Caulerpa* species

Species of *Caulerpa* were the first algae of the related families Caulerpaceae and Udoteaceae that were investigated by natural products chemists. Australian workers studying *Caulerpa* species from southern Australia found various terpenes such as caulerpol, flexilin, and trifarin (Blackman and Wells, 1976, 1978). Caulerpenyne, a unique acetylenic sesquiterpenoid which is closely related to flexilin, was first isolated from a Mediterranean collection of *C. prolifera* (Amico et al. 1978) (Fig. 1).

These Caulerpa compounds were the first natural products isolated that possessed the bis-enol acetate functional group, which is a common feature among green algae of the genera *Caulerpa*, *Udotea*, *Halimeda*, *Penicillus* and related members of the families Caulerpaceae and Udoteaceae (Paul 1985). This functional group represents an acetylated dialdehyde group to which high biological activity is generally attributed. Continued investigation of the Mediterranean *C. prolifera* led to the isolation of several related metabolites such as furocaulerpin and fatty acid esters in minor amounts (De Napoli et al. 1981, 1983).

During subsequent investigations of the genus *Caulerpa*, caulerpenyne was isolated from nine other species of *Caulerpa* common in the tropical Pacific and Caribbean (Paul 1985, Paul and Hay 1986). These species include *C. prolifera* (Florida Keys, Bahamas), *C. racemosa* (Caribbean, Pacific Mexico, western Pacific), *C. mexicana* (Florida Keys), *C. sertularioides* (Florida Keys, Bahamas), *C. taxifolia* (Saipan), *C. paspaloides* (Bahamas), *C. lanuginosa* (Florida Keys), *C. cupressoides* (Florida Keys, Bahamas, Guam), and *C. verticillata* (Puerto Rico). Caulerpenyne has been reported to show antimicrobial activity (Hodgson 1984), larval toxicity and cytotoxicity toward sea urchin eggs (Paul and Fenical 1986), and feeding deterrence toward the sea urchin *Lytechinus variegatus* (McConnell et al. 1982). However, it does not effectively deter feeding by many tropical herbivorous reef fishes (Meyer and Paul 1992, Paul 1992).

Caulerpin is often a minor metabolite in these same algae (Fig. 1). This bright-orange, pigmented compound, probably derived from indole biosynthesis, has been found in over 50% of the *Caulerpa* species investigated (Maiti et al. 1978, Vest et al. 1983, Schwede et al. 1987). Although caulerpin was originally described as a bioactive compound, this compound seems to lack toxicity to fish or feeding deterrent effects (McConnell et al. 1982, Paul et al. 1987, Meyer and Paul 1992), and it is unclear whether caulerpin has a role in chemical defense in *Caulerpa* species. It has been suggested that caulerpin may function as a growth regulator for *Caulerpa* (Raub et al. 1987, Schwede et al. 1987).

Several monocyclic sesquiterpenes have been reported from species of *Caulerpa* including *C. bikinensis* from Palau (Paul and Fenical 1982), *C. flexilis* var. *muelleri* from western Australia (Capon et al. 1981), and *C. ashmeadii* from the Florida Keys (Paul et al. 1987). Major compounds usually contain the same bis-enol acetate group found in caulerpenyne and other linear terpenes from *Caulerpa* and related green algae. In addition, minor acetoxy-aldehydes and dialdehydes have been reported from these algae. The aldehydes from *C. ashmeadii* and *C. bikinensis* showed enhanced toxicity to fish relative to the bis-enol acetates (Paul and Fenical 1982, Paul et al. 1987). The aldehydes from *Caulerpa* are similar in structure to compounds that deter insect feeding such as warburgenal, polygodial, and the iridoid aldehydes (Kubo et al. 1976), and they could function as defensive agents by identical chemical mechanisms. The aldehyde functional group can react with proteins in a number of ways to inactivate protein or enzyme function.

The natural products chemistry of invasive *Caulerpa taxifolia* in the Mediterranean has been studied over the past decade. Much of the interest in the chemistry of this alga is because it has had such negative effects on the benthic environment of the Mediterranean since its introduction. Caulerpenyne is the major terpene produced by the Mediterranean populations of *C. taxifolia* (Guerriero et al. 1992, Amade and Lemee 1998, Dumay et al. 2002) (Fig. 2). Although it has been reported that this alga contains higher levels of caulerpenyne than tropical species of *Caulerpa* (Guerriero et al. 1992, Dumay et al. 2002), this is not always the case. Tropical species of *Caulerpa* are highly variable in their production of caulerpenyne, and, for example, concentrations of this compound in *C. sertularioides* from Guam are higher than those reported for the Mediterranean alga (Meyer and Paul 1992). In addition to caulerpenyne, other minor terpenes have been reported including oxytoxin 1, 10,11-epoxycaulerpenyne, taxifolials A-D, and taxifolione (Guerriero et al. 1992, 1993) (Fig. 2).

Recently, Mediterranean *C. taxifolia* has been shown to respond to tissue damage by transforming caulerpenyne to oxytoxins 1 and 2 and related acetoxy aldehydes that results from deacetylation of caulerpenyne (Jung and Pohnert 2001) (Fig. 3). This enzymatically mediated activation of caulerpenyne to the oxytoxins, which are presumably more potent defensive compounds, has been looked for, but not observed, in *Caulerpa prolifera* in the Mediterranean (Gavagnin et al. 1994). A similar wound-activated transformation has been reported for green algae of the genus *Halimeda* (Paul and Van Alstyne 1992). In many species of *Halimeda*, the halimedatetraacetate, which is a diterpene bis-enol acetate, converts to the aldehyde halimedatrial when algae are crushed or injured. Halimedatrial is a more potent toxin and feeding deterrent than its precursor halimedatetraacetate. Similarly, *Udotea flabellum* shows a wound-activated conversion from udoteal to petiodial (Paul 1992). Activated chemical defenses may be common among green seaweeds of the families Caulerpaceae and Udoteaceae.

Conclusion

Terpenoid natural products occur in most species of *Caulerpa* and related green seaweeds. Caulerpenyne, which is found as a major compound in many species of *Caulerpa* worldwide, occurs in high concentrations in the invasive *Caulerpa taxifolia* in the Mediterranean and can be enzymatically transformed to oxytoxins when the alga is wounded. Based on the aldehyde functional groups present in the oxytoxins, it is likely that they are more potent chemical defenses, although this has not been directly tested. The natural products chemistry of introduced *Caulerpa taxifolia* in California has not been studied; it may be similar to that of the Mediterranean strain. Many tropical generalist and specialist herbivores are not deterred from eating species of *Caulerpa* by their terpenoid natural products; however, non-adapted temperate herbivores in the Mediterranean and California may be more affected by these compounds. Much work concerning the chemical ecology of introduced *Caulerpa* species including *C. taxifolia* still needs to be done. The effects of extracts and isolated terpenes on temperate herbivores must be tested before we can understand the significance of caulerpenyne and related natural products as factors contributing to the invasion of *Caulerpa taxifolia* into nonnative habitats.

Acknowledgments

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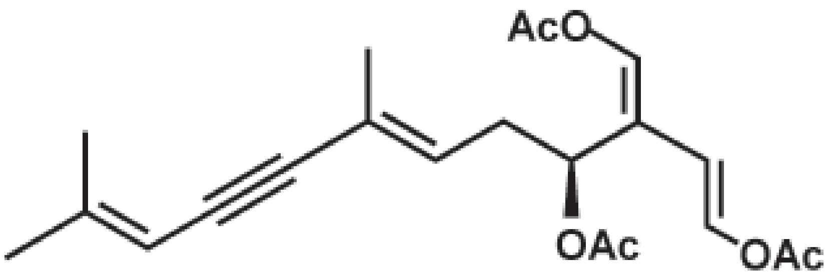
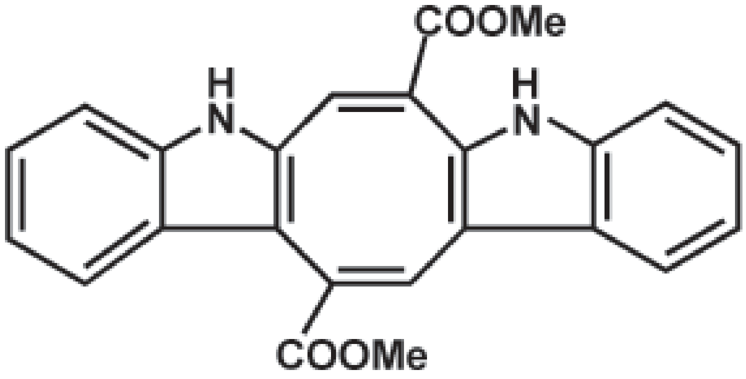
Figures . . .

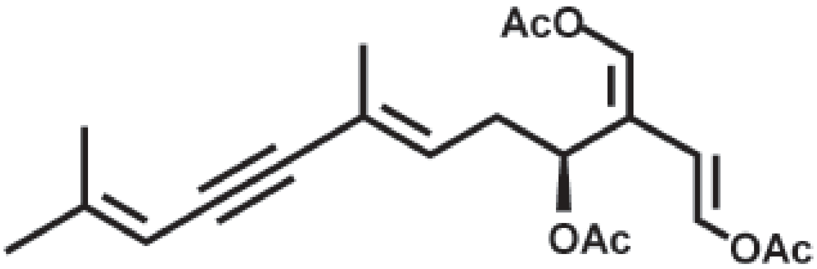


caulerpenyne

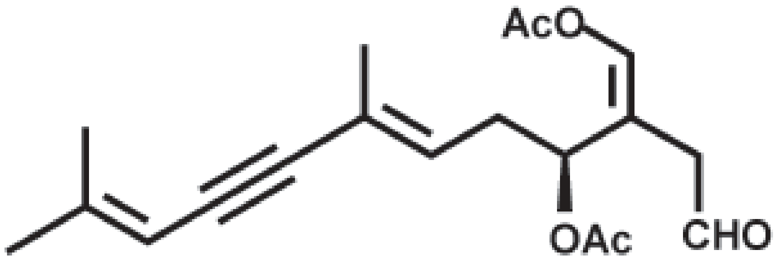


caulerpin

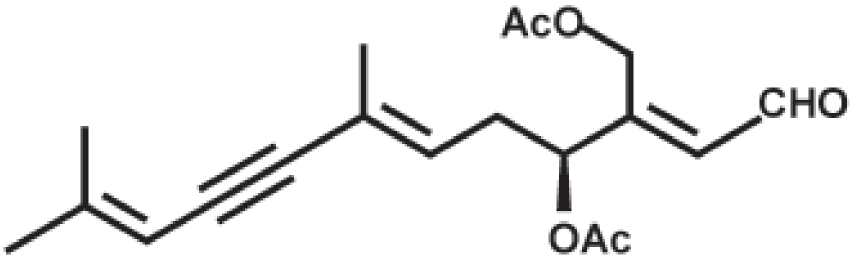
Figure 1. Caulerpenyne and Caulerpin



caulerpenyne



oxytoxin 1



taxifolial A

Figure 2. Caulerpenyne

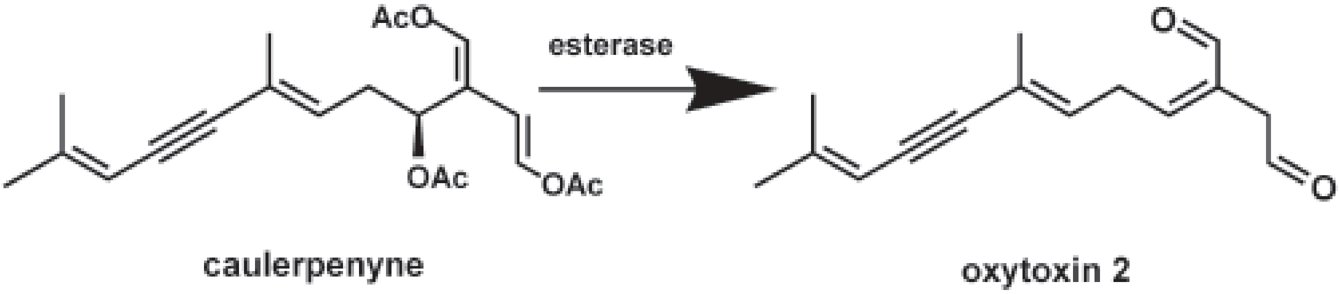


Figure 3. Caulerpenyne transforming to oxytoxin 2.

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Caulerpa taxifolia . . .

Invasion Ecology of *Codium fragile* ssp. *tomentosoides*:

Implications for *Caulerpa taxifolia* Incursions

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Introduction

Codium fragile ssp. *tomentosoides* (van Goor) Silva is a green macroalga with morphological similarities to specimens on northwestern Pacific shores, particularly Japan (Silva 1955, 1957). The alga appeared on European shores around the 1900s, then spread to the British Isles and the Mediterranean several decades later. Currently, the invasive alga is widely distributed around the British Isles and on Atlantic and Mediterranean shores of Europe (Norton 1985; Rueness 1989; Morton 1994; Verlaque 1994; Trowbridge and Todd 1999). In the 1950s, the alga appeared on northwestern Atlantic shores; details of the establishment and spread of *C. fragile* ssp. *tomentosoides* have been well reviewed by Carlton and Scanlon (1985) with more recent details documented by Harris and Mathieson (1999). In the 1970s, the alga was reported in San Francisco Bay, California (Silva 1979) and New Zealand (Dromgoole 1975, 1979). In the 1990s, *C. fragile* ssp. *tomentosoides* was observed in southeastern Australia and is now widely distributed in Victoria, Tasmania, and New South Wales (Campbell 1999; Trowbridge 1999, unpubl. data). The recent incursions were relatively cryptic as two native subspecies of *C. fragile* inhabit Australian shores as well as numerous species of superficially similar congeners (Trowbridge 1999). Potential vectors of introduction include shellfish transplants (particularly of the Pacific oyster, *Crassostrea gigas*) and hull-fouling of vessels and barges.

Comparisons

Among Subspecies

Comparison of invasive pests to closely related noninvasive taxa (species, subspecies, varieties, etc.) is a powerful approach for investigating nonindigenous species (NIS), including *Codium fragile* ssp. *tomentosoides* (Trowbridge 1996, 1998), *Sargassum muticum* (Paula and Eston 1987), and *Caulerpa taxifolia*. To evaluate the attributes that may enhance invasion success, I compared ecological and physiological features of native and introduced subspecies of *C. fragile* around the world (Trowbridge 1998); the majority of alleged “weedy” attributes also occurred in native, non-weedy *C. fragile* and, consequently, cannot fully account for the high invasiveness of ssp. *tomentosoides.* The past focus on invasive taxa—in the absence of baseline research on natives—gives potentially misleading impressions about NIS. Comparative, descriptive, and experimental studies are imperative prerequisites to understanding variation in invasiveness among related taxa.

The types of attributes that may vary among *C. fragile* ssp. *tomentosoides* and other subspecies are: mode of reproduction, ploidy level, and salinity tolerance. The parthenogenetic *C. fragile* ssp. *tomentosoides* has enhanced invasive potential compared to related taxa. It would require only one female propagule attached to an oyster shell transplanted to a new bay, or one short-lived planktonic gamete in ballast water discharged into a new port, to inoculate the region with the invasive alga. Parthenogenesis enables the subspecies to avoid the constraints of small population size on population establishment and expansion. Broad salinity tolerance (Malinowski and Ramus 1973; Hanisak 1979; Yang et al. 1997) enables *C. fragile* ssp. *tomentosoides* to inhabit estuaries and bays (in addition to marine habitats). This increases the probability that the alga may attach to shellfish, ship hulls, buoys, nets, or other anthropogenic substrata that could be a vector of regional or global dispersal. The propensity of other subspecies to inhabit low salinity water is not well known although the Australasian subspecies (ssp. *novae-zelandiae* and ssp. *tasmanicum*) often inhabit bays; their salinity tolerance merits future examination.

Among Geographic Regions

Comparison of the population dynamics of NIS in different areas of incursions also yields valuable insight. For *C. fragile* ssp. *tomentosoides*, I am comparing the alga in different regions, which represent different dates of alga incursions: New Zealand (Trowbridge 1995, 1996), Australia (Trowbridge 1999, unpubl. data), Scotland (Trowbridge and Todd 1999, 2001, Trowbridge, submitted ms.), Ireland (Trowbridge 2001, ms. in prep), etc.

Ecological predictions about the role of factors in contributing to invasion success are difficult to assess without rigorous field experiments. Community-level experiments are essential; community-attribute models that should be assessed include (1) species richness or diversity, (2) community naïveté, (3) invasion resistance by natives and prior residents, and (4) top-down/bottom-up control models. Such experiments are being conducted by various research teams on northern Atlantic shores; experimental ecological results will hopefully be soon forthcoming. An analogous community-level approach for investigating *Caulerpa taxifolia* on Mediterranean, Australian, and northern Pacific shores is clearly merited, particularly in areas in which eradication attempts have been abandoned.

Functional Ecology

Morphological Plasticity

Codium and *Caulerpa* are green algal genera belonging to different orders; yet, these orders share many structural and functional similarities that may have important ecological and ecophysiological consequences. Both genera are siphonous in construction: fluid-filled tubes with few internal cross walls. Within both genera, extensive morphological plasticity occurs.

Under certain environmental conditions, *Codium fragile* ssp. *tomentosoides* can persist for years as undifferentiated, branching filaments (Fletcher et al. 1989; Trowbridge 1998). Upon differentiation, these filaments will form a three-dimensional thallus with multiple fronds or axes arising from a basal holdfast. Such thalli can also dedifferentiate, with long chloroplast-filled filaments (not to be confused with the shorter, colorless utricle hairs) extending away from the branches. This phenomenon was common in sea lochs on the west coast of Scotland (Trowbridge 1999, unpubl. data; Trowbridge and Todd 1999). *Codium fragile* ssp. *tomentosoides* also varies geographically in gross macrostructure: maximum length of thalli, extent of branching, width of distal and proximal branches, extent of flattening near nodes, abundance and length of utricle hairs, diameter and shape of utricles, etc.; all of these characters can directly influence herbivore-algal interactions with generalist consumers like urchins and snails but also with specialist consumers like sacoglossan (=ascoglossan) sea slugs (e.g., Trowbridge 1995, 1996, 1998).

Fragmentation and Regeneration

The ecological role of algal thallus fragmentation may be a mechanism of asexual reproduction and/or of thallus reduction due to hydrodynamic or physiological constraints. Similarly, fragmentation may be the consequence of herbivory (Trowbridge 1993, 1998, submitted ms.; Harris and Mathieson 1999; Zuljevic et al. 2001). The complexity of *Codium* and *Caulerpa* spp. thallus fragmentation indicates that the phenomenon is probably multi-causal. Herbivore-induced dispersal of NIS is common in terrestrial systems (Maron and Vilà 2001) and probably marine systems as well.

Branches, utricles, or medullary filaments can all regenerate provided the hydrodynamic conditions are amenable. Pieces of *C. fragile* can reattach in the laboratory (Fralick and Mathieson 1972; Trowbridge, pers. obs.) although field evidence is currently lacking. However, reattachment is not a necessary prerequisite for regeneration. Research is needed on the fate of free-floating, regenerating thalli, particularly whether they can produce gametes.

Sacoglossan Herbivory

Although there is a wealth of information about sacoglossan herbivory on temperate macroalgae (reviewed by Williams and Walker 1999; Trowbridge 2002), comparable work on *Caulerpa*-feeders has only recently been initiated (e.g., Thibaut et al. 2001; Zuljevic et al. 2001, references therein). Sacoglossan herbivory on *Codium* and filamentous green algae can vary from being pivotal to determining macroalgal host distribution for *C. setchellii* to negligible (Trowbridge 1992, submitted ms.). Here I present two cases of extraordinary sacoglossan density on Scottish (Oban, Argyll) and Irish (Lough Hyne, County Cork) rocky shores (Trowbridge, submitted ms.). At such high densities, local elimination or reduction of algal hosts may be possible. Sacoglossan herbivory on *Codium* spp., thus, may be important under certain circumstances; delineating the conditions under which it may be important continues to be a major and elusive challenge.

The degree of sacoglossan feeding specificity varies from extremely rigid at the individual level (Trowbridge 1991) to considerably more polyphagous. Even in the former case, adult specificity can be coupled with morphological, behavioral, and developmental flexibility (e.g., Jensen 1989; Trowbridge and Todd 2001). However, in cases of high specificity, it is not yet known whether feeding preferences are based on slug genotype (Walsh and Trowbridge, in progress) and/or developmental processes. Recent work on the capacity of adult sacoglossans to change hosts and on the capacity of larval sacoglossans to metamorphose and feed on newly available introduced hosts and unfamiliar native hosts (Trowbridge and Todd 2001; Trowbridge, ms. in prep.) has emphasized how little we know about these stenophagous herbivores. Finally, a recent review of northeastern Pacific sacoglossans (Trowbridge 2002) demonstrates that much of the dogma about sacoglossan biology (e.g., extent of functional kleptoplasty, efficacy of anti-predator defenses, reproductive, and dietary details) has been considerably overstated. Thus, any biological control program for *Codium* or *Caulerpa* pests with sacoglossans as control agents should document and demonstrate that all implicit assumptions are valid since many details of the sacoglossan biology are based on inferential or anecdotal information.

In conclusion, past research on *Codium fragile* demonstrates that a comparative approach (taxonomic and geographic) would be productive in future investigations of *Caulerpa taxifolia* incursions. Investigations of species' attributes such as interspecific competition and herbivore-plant interactions are crucial to the evaluation of establishment and invasion success. Finally, experimental field studies on how the attributes of recipient communities may influence invasibility should provide more predictability about where NIS will become established.

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The Availability of Species of *Caulerpa* and "Live Rock" in Retail Aquarium Outlets in Southern California

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Introduction

Hundreds of nonindigenous species have established populations in aquatic habitats in North America (Ricciardi and Rasmussen 1998) and biological invasions are now recognized as a serious threat to marine biodiversity (Lubchenco et al. 1995). There are, however, only a few well-documented introductions of exotic seaweeds and most of these cases involve large, conspicuous taxa such as the invasion of the eastern North Pacific and North Atlantic waters by the Japanese brown alga *Sargassum muticum* (Scagel 1956), the introduction into the western North Atlantic and elsewhere of the Asian green Seaweed *Codium fragile* ssp. *tomentosoides* (Carlton and Scanlon 1985; Goff et al. 1992; Trowbridge 1995), and the incursion of *Grateloupia doryphora* in Rhode Island (Marilyn Harlin, personal communication; Marston and Villalard-Bohnsack 2000). Most exotic seaweeds are probably small, difficult to identify, and easily confused with native species so introductions often go unrecognized.

Recently, three larger and conspicuous seaweeds have invaded Southern California waters. *Undaria pinnatifida*, a kelp native to temperate western Pacific waters, has been found in the ports of Los Angeles, Port Hueneme, Santa Barbara, and Monterey (Cohen et al. 2001; Susan Ellis, Department of Fish and Game, personal communication), and in outer, offshore waters on leeward Santa Catalina Island (Kathy Ann Miller, personal communication). This species has also been reported (Cecere et al. 2000; Forrest et al. 2000; Schaffelke and Campbell 2000) to have invaded Australia, New Zealand, and the central Mediterranean. *Caulacanthus ustulatus*, a red, turf-forming alga is another suspected invader that has appeared in rocky intertidal habitats in Southern California within the last five years. Based on sequence data (Max Hommersand, personal communication), this Southern California strain appears to be closely related to specimens of a French population believed to have been introduced into the eastern North Atlantic from Asian waters (Rueness and Rueness 2000).

Caulerpa taxifolia, the third seaweed species known to have recently invaded Southern California waters, has received much more attention (Kaiser 2000; Dalton 2000; Jousson et al. 2000). This species was first noted as an invader in the Mediterranean Sea in 1984 (Meinesz and Hesse 1991), and is now also believed to have invaded New South Wales, Australia (Grey 2001). *Caulerpa taxifolia* is thought to have altered the structure and changed the natural food webs in Mediterranean Sea ecosystems by displacing native species (Meinesz 1999). *Caulerpa taxifolia* was first reported (Jousson et al. 2000) from Southern California waters in June 2000 in Agua Hedionda Lagoon in San Diego County and Huntington Harbour in Orange County. It appears that inoculation of *C. taxifolia* into these two lagoon habitats was due to the release of material from salt water aquariums. Although the introduction into freshwaters of exotics from the ornamental trade has been known for years to represent a serious problem (Courtenay and Stauffer 1990), most seaweed introductions are believed to have been associated with mariculture efforts or to have occurred via the shipping industry (Ruiz et. al. 2000) by attachment to the hulls of ships or through the release of spores or fragments with ballast water.

During the last decade, there has been an increase in Southern California in the availability of tropical seaweeds in saltwater retail aquarium outlets. Moreover, the purchase of aquarium seaweeds from internet sites is becoming increasingly common. The *C. taxifolia* population found in Southern California is closely related to the invasive Mediterranean strain (Jousson et al. 2000), which can withstand colder temperatures, grow in dense monospecific stands, and produce upright axes up to 2 m tall (Meinesz 1999). During summer 2000, *C. taxifolia* covered approximately 3,500 m^2 in Agua Hedionda, California, and was patchily dispersed over approximately 20,000 m^2 in Huntington Harbour, (Jousson et al. 2000).

Caulerpa taxifolia is not the only species within the genus to display invasive behavior. *Caulerpa racemosa* is also invasive in the Mediterranean Sea (Verlaque et al. 2000) and has greatly changed benthic algal community structure by decreasing species number, diversity, and cover (Piazzi et al. 2001). *Caulerpa brachypus* appears to have recently established populations in Florida (Dennis Hanisak, personal communication), while the Florida native, *C. verticillata*, has exhibited invasive behaviors in Floridian waters (Raloff 2000). Furthermore, the temperate species *C. scalpelliformis* recently appeared in the Mediterranean Sea (Verlaque 1994) and, although native to Southern Australia, has extended its range northward along the eastern Australian coast (Davis et al. 1997).

The establishment of *C. taxifolia* in Southern California embayments presents a warning that other, potentially invasive seaweeds, and particularly *Caulerpa* species, might be capable of establishing populations in local waters. The purpose of this study was to determine the diversity of *Caulerpa* taxa being sold in Southern California by retail saltwater aquarium outlets. We hypothesized that a large number of species are currently being made available to consumers by the retail aquarium trade, and that these species might include some known to have successfully invaded habitats in other parts of the world. We also sought to quantify the availability of “live rock” (hard rocky or coral substrata colonized by multiple species including soft corals, anemones, cryptic tubeworms, and seaweeds) in retail aquarium outlets.

Methods

We sampled retail aquarium stores in Southern California (Los Angeles, Orange, and San Diego counties) listed in the online telephone directories. The completeness of this list was checked with the printed telephone listings for Los Angeles, Orange, and San Diego counties. A total of 50 identified saltwater aquarium outlets were visited between November 2000 and August 2001. We attempted to visit all saltwater aquarium outlets in San Diego and Orange counties, whereas stores in the County of Los Angeles were randomly sampled due to their large number (Table 1). Selected stores that were not sampled were either closed for business on the day of sampling or could not be found. Stores in the County of Los Angeles were assigned to one of 15 geographic sections by the online search engine. Half of these sections were randomly selected and 50% of the stores in each section were also randomly chosen. Species available for sale were purchased upon visitation, and returned to the lab where they were identified, made into herbarium specimens, and fast-dried in silica gel for possible genetic analysis. The frequencies of each species and of "live rock" were then calculated for each Southern California county based on presence or absence within sampled stores.

Results

We observed seaweeds in retail aquarium outlets to either be sold as unattached thallus clumps or affixed to "live rock." "Live rock" included conspicuous seaweeds as well as cryptic pieces of stolon and rhizoids from *Caulerpa* spp. "Live rock" was offered for sale in 95% of all visited stores, whereas seaweeds were sold in 56% of visited aquarium outlets (Fig. 1).

Caulerpa spp. were found in 52% of visited stores indicating that where seaweeds were offered for sale species of *Caulerpa* were usually sold. "Live rock," seaweeds, and *Caulerpa* spp. were each sold at similar frequencies among counties (Fig. 2). Hence, our data reveal that "live rock," and to a lesser extent *Caulerpa* spp., are commonly being sold by saltwater aquarium retailers in Southern California.

A total of 53 specimens belonging to 16 different *Caulerpa* taxa were identified from the visited retail aquarium outlets (Fig. 3). Besides "*C. taxifolia*" (Mediterranean form) which was offered for sale in 10% of the visited stores; *C. serrulata* var. *hummii* (18%), *C. racemosa* (14%), and *C. racemosa* var. *lamourouxii* (14%) were the most commonly sold species. The availability of these and other *Caulerpa* taxa varied greatly by store and by county in the frequency with which they were encountered (Fig. 4). This suggests that there are multiple sources of *Caulerpa* spp. being sold in retail aquarium outlets or that fewer sources provide different species mixes over time.

Discussion

There are over 300 *Caulerpa* taxa (Guiry and Nic Dhonncha 2002) documented worldwide, while approximately 75 species are currently recognized (P.C. Silva, unpublished abstract). However, these numbers are uncertain because morphological variation within the genus is high, thus making accurate species identification difficult. This difficulty is compounded by the fact that interspecific morphological variation in *Caulerpa* can also be great due to responses to environmental conditions such as light (Calvert 1976; Collado-Vides 1999) and temperature (Enomoto and Ohba 1987; Ohba et al. 1992).

In recognition of the documented impacts of the *C. taxifolia* invasion in the Mediterranean Sea, and the recent appearance of the aquarium-strain of this species in Southern California waters, a new California state law was passed (Fish and Game Code 2300, http://www.leginfo.ca.gov/calaw.html). This law, which went into effect September 25, 2001, bans the importation, possession, and sale of nine species of *Caulerpa* (*C. taxifolia*, *C. verticillata*, *C. scalpelliformis*, *C. racemosa*, *C. floridana*, *C. ashmeadii*, *C. mexicana*, *C. sertularioides*, and *C. cupressoides*). Besides banning *C. taxifolia*, this law targets species (*C. ashmeadii*, *C. mexicana*, *C. sertularioides*, and *C. scalpelliformis*) that can easily be confused with *C. taxifolia* because of their feather-like morphology. We found nine taxa (four species) that are currently banned, including "*C. taxifolia*" (Mediterranean form), for sale in retail aquarium stores in Southern California. Seven *Caulerpa* taxa that were not banned by Fish and Game Code 2300 were also identified from our aquarium store collections.

Despite an apparent attempt to simplify enforcement by banning taxa morphologically similar to C. taxifolia, Fish and Game Code 2300 fails to ban two *Caulerpa* species morphologically similar to two other banned species. *Caulerpa microphysa* is morphologically similar to the banned and potentially invasive *C. racemosa* because both species have crowded bead-like branchlets. Additionally, *C. serrualta* var. *hummii* and the banned *C. cupressoides* var. *flabellata* both have flat upright fronds with serrated edges. Morphological plasticity makes enforcing bans on specific species in the genus *Caulerpa* very difficult because most aquarists will not have the expertise to accurately make species level determinations. Moreover, the widespread availability of "live rock," which can support cryptic thalli of *Caulerpa* spp. and other unknown exotic organisms, make rigid enforcement of Fish and Game Code 2300 unlikely.

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Figures . . .

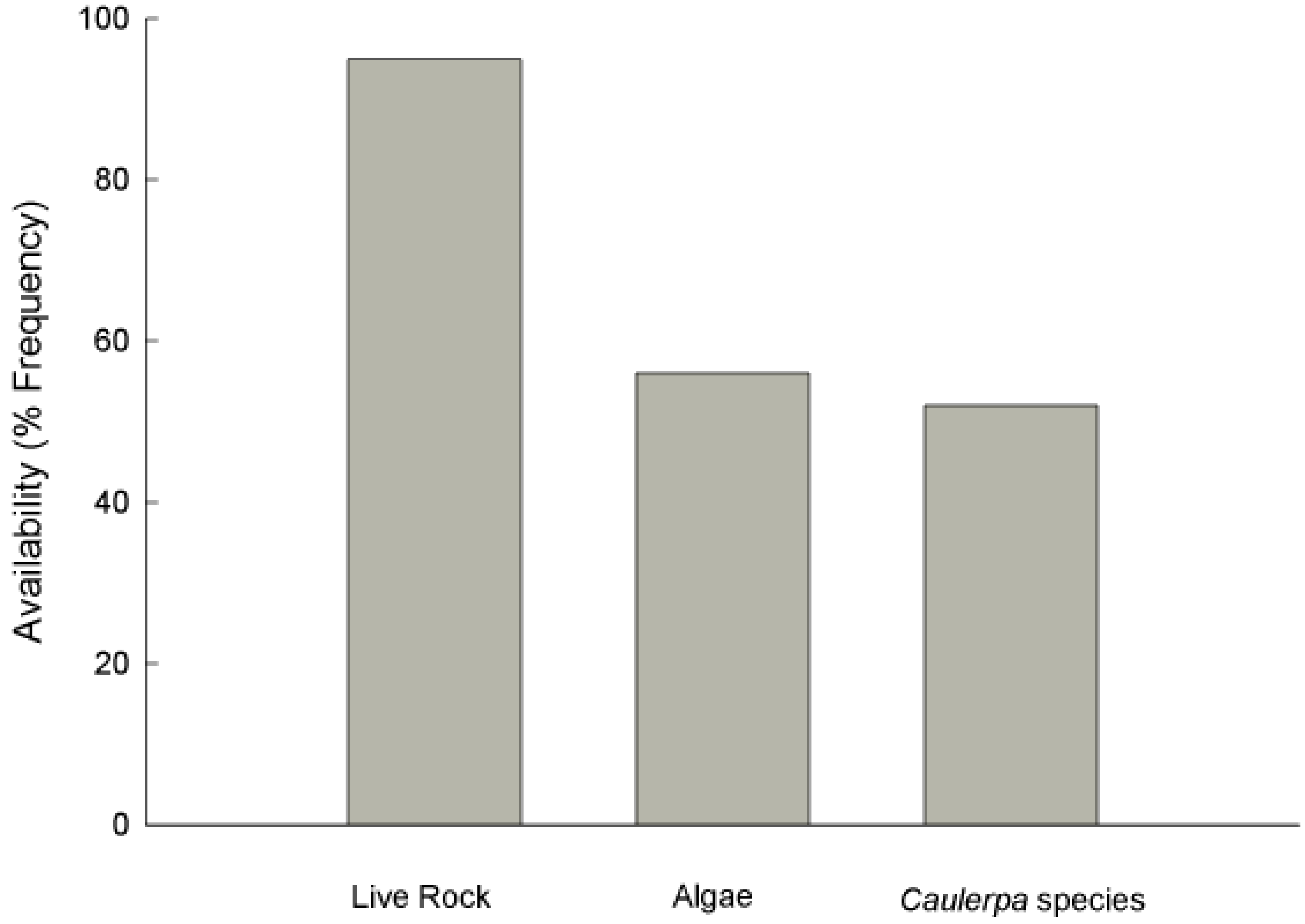

Figure 1. Availability of live rock, algae, and *Caulerpa* species in retail aquarium outlets in Southern California, USA (n=50).

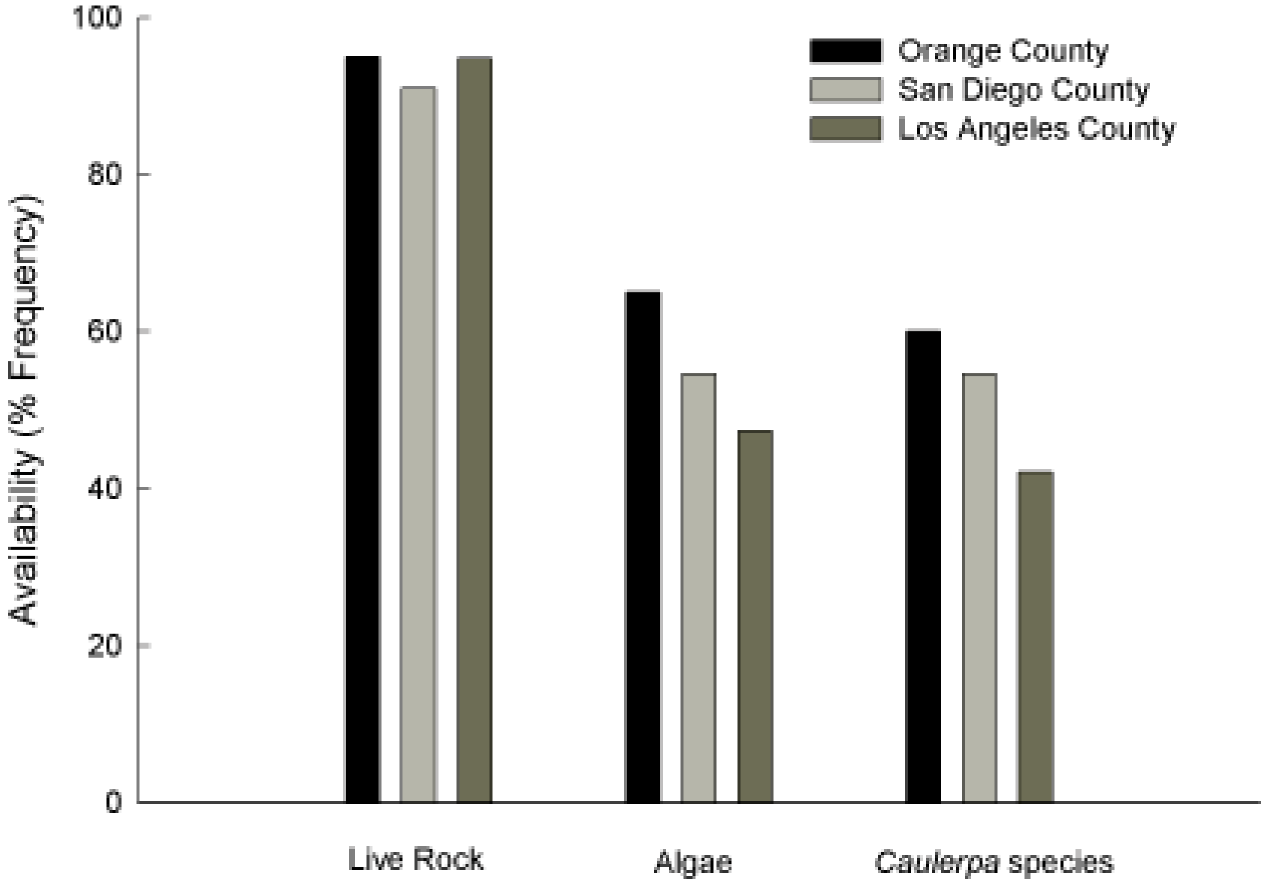

Figure 2. Availability of live rock, algae, and *Caulerpa* species in retail aquarium outlets in three counties {Orange (n=20); San Diego (n=11); Los Angeles (n=19)} in Southern California, USA.

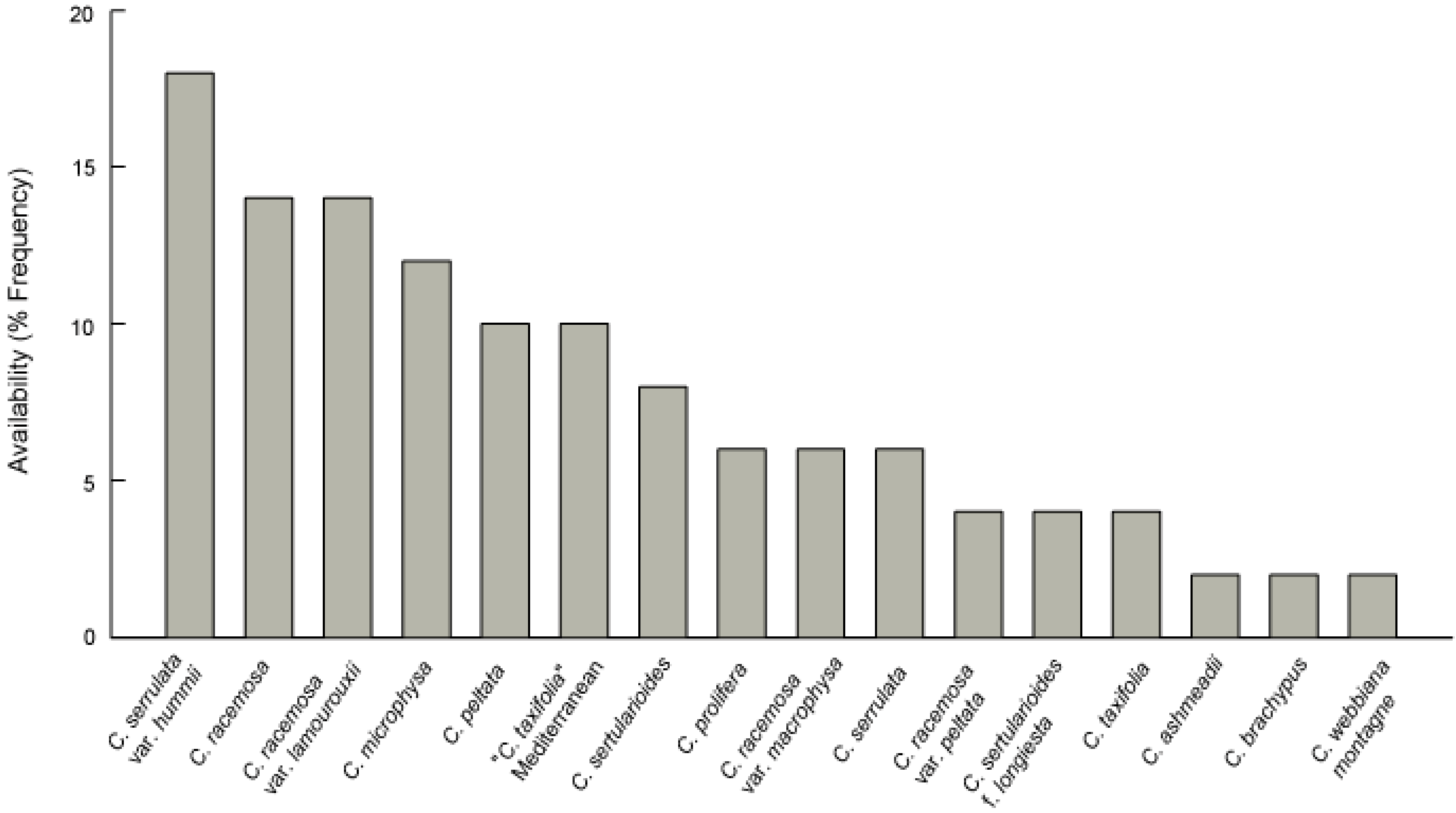

Figure 3. Availability of 16 *Caulerpa* taxa in retail aquarium outlets in Southern California, USA (n=50).

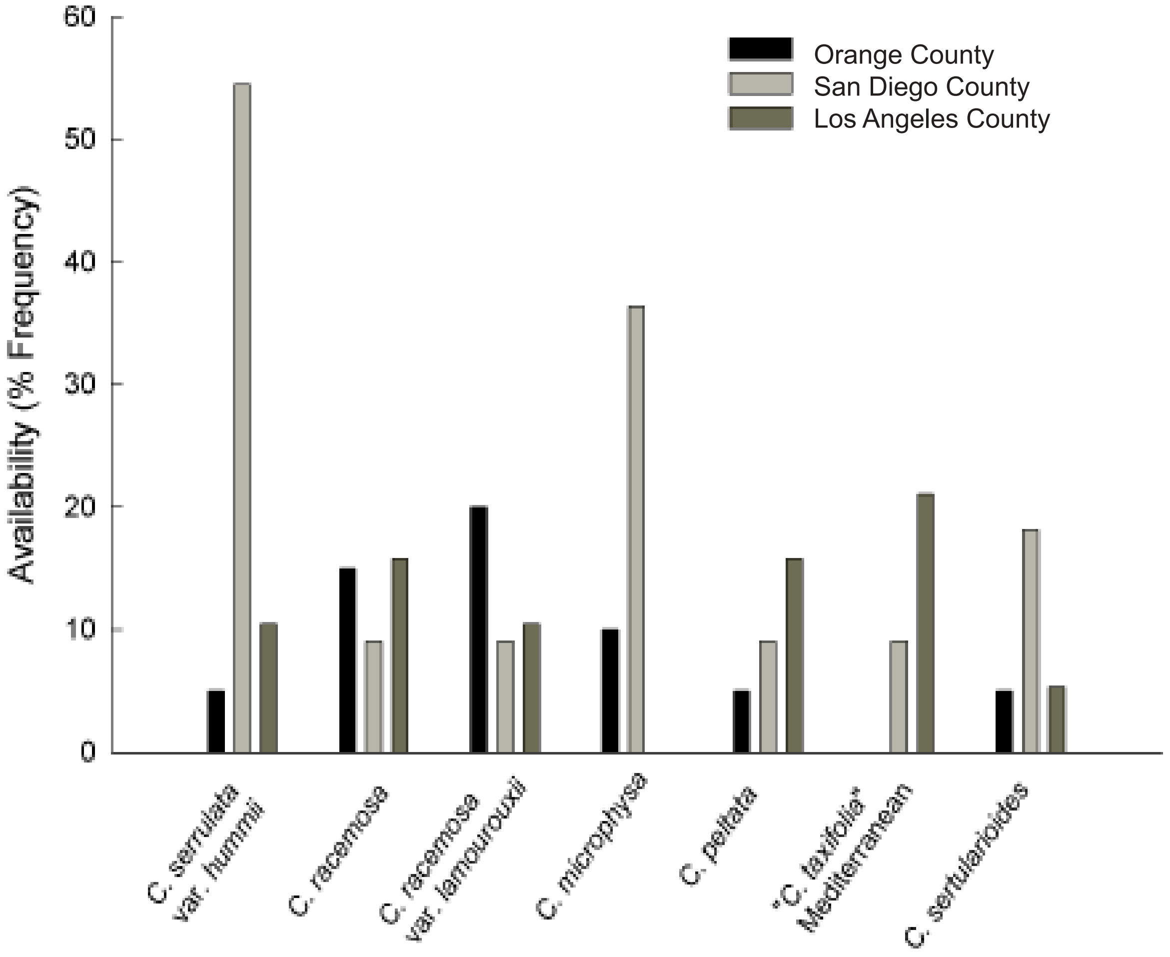

Figure 4. Availability of species of *Caulerpa* that were found at least 10% or more in one of the three counties {Orange (n=20); San Diego (n=11); Los Angeles (n=19)} in Southern California, USA.

Tables . . .

Table 1. **Retail fresh and saltwater aquarium outlets identified from telephone directories in Los Angeles, Orange, and San Diego counties in Southern California, USA. A total of 50 retail saltwater aquarium outlets were visited between November 2000 and August 2001.**

Store Type	Los Angeles County	Orange County	San Diego County
Fresh water only	23	3	4
Salt water	79	23	12
Salt water stores visited	19	20	11

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Caulerpa taxifolia . . .

The Role of Science in Management of *Caulerpa taxifolia* in the United States

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My presentation at this workshop is designed to provide a summary of the role of science in the management of marine life in the United States (U.S.) and in particularly in California.

My perspective is that of an academic scientist involved in marine management, and, in this case, since the beginning of the eradication program on *Caulerpa taxifolia* in Southern California. My perspective is also colored by my experience as a scientific reviewer for management plans and for management programs for major marine environmental problems. In some cases, the scientific review has come when the marine environment had been so thoroughly degraded that it caught the attention of the U.S. president, who then convened a review process (Boesch et al. 1993). At this point, a review is costly, can do little to fix the problem, and serves primarily as a lesson. This is a situation I hope will be avoided in the *Caulerpa* story. The key lesson from these experiences is that management must incorporate science at the earliest stage.

Funding issues aside, the main management challenge I see is how to effect science-based management of *C. taxifolia*. To cite a few examples of why science is important, science is required:

1. To determine the degree to which *Caulerpa* is a threat to our ecosystems
2. To determine how far and fast and by what means it could spread
3. To determine whether eradication or control is effective and how to minimize the costs, both economic and environmental
4. To guide programs to prevention of new introductions and to evaluate program efficacy

Marine scientists and policy makers in the U.S. have reached a consensus that management of marine life and habitats should be science-based and take an ecosystem-level approach (Sherman 1991; Schmidt 1998). In the state of California, this perspective was mandated when the legislature passed landmark legislation called the Marine Life Management Act (MLMA) in 1999 (Weber and Heneman 2000). The MLMA is designed to protect the state's marine plants and animals and habitats for sustainable fisheries. The act mandated that management must be based on scientific information and that the tool to achieve this end would be external scientific peer review. External scientific peer review at an early stage of managing an environmental problem can help insure that the big picture is not lost in the details of daily expediencies and tasks. External scientific peer review provides a measure of reassurance to the public that the actions taken are not arbitrary and have been carefully considered.

The legislative authority to begin immediate management of the *C. taxifolia* invasion in California fell to agriculture, not marine, agencies due to the prescient listing of the seaweed in 1999 as a noxious weed under the Federal Noxious Weed Act. The U.S. Department of Agriculture was the lead agency and in turn, delegated local authority to the California Department of Food and Agriculture. Both agencies were experienced in terrestrial and freshwater weed eradication. In contrast, eradication of marine invasive species in the U.S. has been virtually nonexistent. The agricultural agencies supported immediate eradication and warned that the efforts would have to be sustained for a long period. They also warned of difficulties in sustaining funding for eradication. The experience of these agencies was that research had no place in an eradication scenario because of potential interference with eradication operations, competition for resources, and public perceptions that if research could be afforded, then the invasion must not be as bad as portrayed (L. Anderson and N. Dechoretz, pers. com.).

That *C. taxifolia* is a marine invasion raised new management issues. First, the public has awakened to the sensitivity of marine habitats and their often protected status, e.g., marine wetland species such as eelgrass are protected under the U.S. Clean Water Act. Any eradication effort, no matter how necessary, would be scrutinized by the public for nontarget damage to sensitive marine species. U.S. Fish and Wildlife Service brought this point up during early meetings of the Southern California *Caulerpa* Action Team (SCCAT). Marine habitats in California, although changed over the years as a consequence of natural and human disturbances, are still recognizable as natural habitats in comparison to agricultural fields in the terrestrial environment. Second, eradication techniques developed for aquatic weeds, including algae, had little or no effect on *C. taxifolia* during preliminary trials (R. Woodfield, unpubl. data in report to SCCAT, July 2000).

In recognition that *Caulerpa* represented new territory for eradication of invasive species, the local, state, and federal marine agencies collaborated closely with the agriculture agencies. Eventually the San Diego Regional Water Quality Control Board assumed leadership of SCCAT. The state legislature passed a bill that banned *C. taxifolia* and some similar and other invasive *Caulerpa* species in California, and the California Department of Fish and Game assumed leadership for enforcing this legislation to prevent new invasions.

The Mediterranean invasion of *C. taxifolia* provided the U.S. with a model for the role of science in the *C. taxifolia* invasion. We asked what the role of science was in the Mediterranean invasion and what we could extrapolate from the European experience. Immediately obvious was the polarization of the European scientific community over the origin of *C. taxifolia*, to the detriment of taking action. This polarization proved a disincentive for some scientists to devote their talents to the problem and also throttled the government funding for research. The debate over the origin of the invasive *C. taxifolia* was settled eventually through the genetic research in several European laboratories. The same European labs contributed an early taxonomic identification of the Southern California *C. taxifolia* as the invasive strain, which was the only strain listed as a noxious weed. This listing provided the rationale for immediate action on the part of our governmental agencies.

Of primary concern for the U.S. is the demonstration that *C. taxifolia* causes sufficient ecological damage to merit expensive eradication. Every scientist I have spoken with agrees that the seaweed is one of the most formidable invasive species around, and that native marine communities were displaced by it in Europe. However, the scientific documentation of ecological effects, despite a very extensive literature including peer-reviewed journals and symposium proceedings, is not as strong as we might need in the U.S., where documentation must be increasingly rigorous to stand up in courts for environmental law.

There have been many laboratory studies on the invasive *C. taxifolia*, e.g., effects of the toxins, photosynthetic rates. It is very hard to extrapolate these studies because they were not necessarily performed at natural concentrations or under natural conditions. I have located a single study of stolon propagation rates in the field, which is probably the single most important information for predicting spread rates (Bouderesque 1997).

Because of the difficulty of finding appropriate controls for sites invaded by *C. taxifolia*, studies cited as demonstrating effects on associated organisms, especially animals such as fishes and their prey, are often not replicated. Therefore, there is no quantitative means of assessing whether the result is associated with *C. taxifolia* or by chance with some other environmental factor. A good example is that an extensively cited paper on effects of *C. taxifolia* on fishes was conducted in a marine reserve (no fishing, no *Caulerpa*) and in an infested site with *Caulerpa*. The paucity of juvenile fishes in *Caulerpa* compared to in the reserve could be due to a negative effect of *Caulerpa* or to the effect of fishing. Although the authors were circumspect in their interpretation, the article nevertheless is cited widely as evidence of negative ecological effects of *C. taxifolia*.

Field experimental manipulations by Ceccherelli and Cinelli (1997) of *C. taxifolia* abundance and seagrass abundance were replicated in more than one study. These experiments have been published in peer-reviewed journals and they clearly show that *Caulerpa* can result in a decline in seagrass abundance. They also suggest that the larger, more robust species *Posidonia* is more resistant to *C. taxifolia* than the smaller *Cymodocea* and that degraded beds are more susceptible.

Studies of control/eradication of *C. taxifolia* are difficult to find in the U.S. Most of the information to reach the U.S. has been anecdotal or in difficult-to-obtain symposium volumes. Publication of control and eradication experiments is undoubtedly difficult due to the bias against publishing negative results. An objective of this conference is to allow scientists from other countries to impart their knowledge in this area.

What is well-known is that all species of *Caulerpa* grow exceedingly fast and have a remarkable capacity to outgrow a disturbance, be it fragmentation or burial. We know that *Caulerpa* morphology is notoriously plastic and under environmental control. This plasticity makes it very difficult to enforce attempts to prevent future introductions except at the level of the genus. The original listing of *C. taxifolia* as a noxious weed (Federal Register, Vol. 64, No. 50, 3/16/99) dismissed the public comment that other species or even the whole genus be listed, because of difficulties with species identification, on the grounds that "unnecessarily rigid trade restrictions" would be imposed. To date, despite the federal noxious weed listing and the state bill (AB1334, http://www.leginfo.ca.gov/pub/bill/asm/ab_1301-1350/ab_1334_bill_20010925_chaptered.pdf) banning 9 species of *Caulerpa*, recent shipments of *Caulerpa* spp. have slipped through customs in the San Francisco area (S. Ellis, California Dept. of Fish and Game, pers. com.). Other *Caulerpa* species have become invasive. Examples include *C. racemosa* in the Mediterranean (Ceccherelli et al. 2000, Piazzi et al. 2001), *C. scapelliformis* (Davies et al. 1997), and *C. verticillata* in the Florida Keys (Science News, Vol. 157:373, 6/10/00). *Caulerpa racemosa* and *C. verticillata* are grown in aquariums and risk being released. It seems there is sufficient scientific evidence to support a ban on the genus *Caulerpa* as a precautionary approach to marine resource management.

We also know that it is difficult to predict how an invasive species will perform in a new ecological setting. Europeans were surprised that *Caulerpa* survives in cool waters off Croatia. The first discoverers of *C. taxifolia* in Huntington Harbour in Southern California were surprised it overwintered there. Thus, even if we gain exhaustive knowledge of the ecological effects of *C. taxifolia* in Europe, we will benefit from doing scientific research on the local invasion. We cannot afford to just "study it all we want in Europe" as has been suggested to avoid interfering with the eradication efforts.

What scientific information is needed immediately to manage the invasion effectively?

- What is the [Cl^-] and exposure time needed to kill *Caulerpa* in the field? There are some anecdotal reports that a buried fragment might take several months to regenerate. How do we know it is dead? Will it regrow in a treated area?

- What is the collateral (nontarget) damage from eradication? Documenting this provides the public with a show of good faith that, although we had to proceed with eradication, we know what else was lost in the process. This information is also useful to calculate economic losses due to the invasion, beyond the known eradication costs. A complete economic analysis would provide support for increasing efforts to prevent new introductions and to eradicate quickly, before costs increase as the invasion spreads. The information is also critical to set restoration targets, particularly for eelgrass, widgeon grass (*Ruppia maritima* in Huntington Harbour), and any other protected species that was impacted.

- Where might we expect *C. taxifolia* to spread? Given the temperature tolerance data from Europe, *C. taxifolia* could survive in Northern California and in Oregon. What are the environmental limits to its distribution and spread? Information on this is required to target field survey efforts and to enlist the support of other states in preventing introductions.

- Is the eradication effective? Survey data have been accumulating since July 2000. These data can be modeled in some manner by a qualified scientist to estimate when eradication efforts might be expected to end, or what level of continuing control is necessary. This information would help anticipate future funding needs.

While the above questions are critical for management, there are other pressing scientific gaps:

- What are the ecological effects of *C. taxifolia*? I discussed the need for this knowledge previously. To answer this question, carefully designed field experiments in the invasion sites are required. There is no compelling reason why they could not have been pursued given that it took over 6 months to treat all known patches initially and patches still remain.

- What is the response of *Caulerpa* to environmental factors in the field? Deployment of environmental sensors together with periodic, replicated, and simple measures of growth or abundance would greatly increase knowledge of growth dynamics and environmental limitations of growth. The information is likely to be useful in strategizing when eradication efforts are most likely to be effective.

- What is the probability that *C. taxifolia* can establish on the open coasts of North America? The hydrodynamic regime and community structure are very different from the more enclosed Mediterranean and Adriatic Seas. Before a major investment is made in engineering open coast eradication technology, a minor investment in determining settlement/attachment dynamics in simulated open coast flows seems advisable.

- Is there a correlation between habitat 'health' and *Caulerpa* invasiveness? This has been a debate in Europe and the relationship between environmental health and invasibility is a pressing issue in invasive species ecology and management in general. There have been very few marine analyses. However, one (Stachowicz et al. 1999) suggests that species diversity is correlated with resistance to invasions. Some terrestrial studies, however, have shown the reverse.

If a relationship between environmental quality and invasibility exists, there is further incentive to improve and protect marine environmental quality. There is some indirect evidence that degraded marine habitats are susceptible to invasive species. Chisholm et al. (1997) and Fernex et al. (2001) contend that *C. taxifolia* is most successful in degraded or polluted Mediterranean habitats. Ceccherelli and Cinelli (1997) demonstrated that healthy seagrass is less susceptible to invasion by *Caulerpa*. Reusch and Williams (1999) demonstrated that intact dense eelgrass beds are resistant to invasion by the Asian mussel. In my experience, eelgrass beds in Southern California are degraded in many attributes compared to those I have observed in other parts of the U.S., Mexico, and Japan (Table 1), and that this might have made them susceptible to a *Caulerpa taxifolia* invasion. I need to point out that *Caulerpa* joins two other nonnative species experimentally demonstrated to have negative effects on eelgrass in San Diego (Reusch and Williams 1999; Williams and Heck 2000). I have also observed a fourth nonnative species, *Zoobotryon* sp., overtopping eelgrass and causing summer die-offs, but have not documented the effect experimentally.

In closing, I will present some management challenges for which scientific information, such as I have outlined, would be useful:

1. Are we employing the best cost-effective eradication method that causes the least collateral damage to sensitive marine ecosystems?

2. Is eradication working and how should this be defined in a scientific-based management program?

3. What defines the decision-making process for changing eradication technique?

4. Can a rapid, inexpensive, unequivocal technique for identifying *C. taxifolia* be developed that agencies could use?

5. Is there something we can do now that will facilitate planning for future restoration of eradication sites?

Science-based management requires that research and eradication efforts be combined in carefully considered, creative ways that do not interfere with the eradication program. The end result will provide a more powerful means to prevent and treat new invasions and to make eradication efforts cost-effective with minimum damage to the native communities. Myers et al. (2000), in a review article outlining the decision process for determining whether to recommend an eradication program for invasive species, recommends that, “Where possible, eradication projects should be viewed as ecological experiments.”

Tables . . .

Table 1. Eelgrass Habitat Quality in San Diego

1. Over 90% of original seagrass habitat has been lost.

2. *Caulerpa taxifolia* is not the only invasive species:

    - Asian mussel (*Musculista senhousia*)
        - Reduces vegetative propagation rates as a linear function of mussel density

    - Stinging anemone (*Bunodeopsis* sp.)
        - Causes local die-offs
        - Reduces leaf growth rates by 70%

3. Genetic diversity is reduced due to disturbance and mitigation: Eelgrass in Agua Hedionda has no detectable genetic (allozyme) diversity.

    - Reduced genetic diversity is correlated with:
        - lower vegetative growth
        - reduced seed germination
        - reduced production of flowering shoots

4. Eelgrass epifauna are few in number and small in size:

Herbivorous gastropods	**#/m^2**
Mission Bay, San Diego	0–400
Chesapeake Bay	10–400
False Bay, Washington	526
Nova Scotia, Canada	1000–3000
Isopod (*Idotea*)	
Mission Bay, San Diego	0–60
Chesapeake Bay	0–400
Padilla Bay, Washington	90–2000
The Netherlands	1000
Amphipod (*Caprella*)	
Mission & San Diego Bays	0–7
Padilla Bay, Washington	90–2000
Amphipod (gammarid)	
Mission and San Diego Bays	0–400
Chesapeake Bay	100–1800
Japan	900–2400

5. Eelgrass has lower leaf shoot densities:

	Range in mean #/m^2
San Diego County (4 sites)	141–255
North Carolina (2 sites)	1157–2045
Washington (2 sites)	98–323
Rhode Island (2 sites)	275–356

6. Bays are closed for up to 90 days/year due to contamination from run-off.

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Caulerpa taxifolia . . .

Caulerpa taxifolia in the United States:

Rapid Response and Eradication Program

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Introduction

The discovery of *Caulerpa taxifolia* on June 12, 2000, in a small area within the 350-acre Agua Hedionda Lagoon near San Diego, California initiated one of the most remarkable responses to an exotic invasive species in the United States. Through a set of serendipitous and fortuitous circumstances, the response to the first find of this invasive marine alga in the Northern Hemisphere was decisive, extraordinarily quick, and appears to be effective. The eradication program underway—now approaching its second year—attests to the ability of divergent groups of scientists, key regulatory and action-agency government staff, and affected stakeholders to focus on containing and treating the infestation even when all the answers and options could not possibly be exhaustively evaluated. In short, the response relied on assessing the best science- based information (not speculation) in the context of urgency to protect California coastal waters and acting on the most likely avenues for success. The result has been a hands-on lesson in deployment of "Rapid Response" strategies and methodologies analogous to a real "fire drill."

I will summarize how this transpired and try to provide some understanding about the decision-making processes; what has worked, what did not, and what is still unknown. Lastly, I will provide some preliminary data on the assessment of the effectiveness of the eradication program as of this conference.

Awareness of *Caulerpa taxifolia* in the United States

Two years before the discovery of *C. taxifolia* in Agua Hedionda Lagoon, the potential threat from introduction of this alga was recognized on at least on two fronts. In 1998, the Aquatic Nuisance Species Task Force reviewed known spread and impacts from the plant and *C. taxifolia* was placed on the Federal Noxious Weed List. This resulted from the persistence and diligence of a number of key scientists and other professionals involved with other aquatic and terrestrial invasive species.

These were important steps in establishing both federal-agency, and to some extent, state-agency awareness of the threat, as well as beginning a basic level of restrictions on the ***inter*****state** movement of the plant. However, this did not address issues of ***intra*****state** movement, possession or sale of *C. taxifolia*, nor did it include any taxa other than the "Mediterranean Strain." The lack of intrastate regulation and the general widespread use of the genus in the aquarium trade explain why many aquarium dealers were found to be selling *C. taxifolia* in California when preliminary surveys were made after the discovery here. Regardless of this, the importance of the regulatory status of *C. taxifolia* (inclusion on the Federal Noxious Weed List) and the level of awareness within the invasive species scientific community cannot be overstated.

Fortuitous Circumstances Enabled a Rapid Response

These circumstances, coupled with highly fortunate early detection of *C. taxifolia* in the relatively small, protected infested site in Agua Hedionda Lagoon, combined to facilitate a remarkably fast reaction. The site was under fairly frequent monitoring by Merkel and Associates as part of a contracted eelgrass restoration project. Divers were on the general site, and most importantly, were alarmed by the presence of the alga. To her credit, Rachel Woodfield (biologist for Merkel and Associates), immediately notified California state and federal research and regulatory agencies, and had specimens sent to University of California, Berkeley to confirm the identification.

What followed the discovery and confirmation of *C. taxifolia* exemplifies both the strengths in California's regulatory and action-agency experience with invasive species, and some weaknesses in dealing with a previously unreported exotic aquatic marine plant.

Fig. 1 provides an aerial view of the two sites. Agua Hedionda Lagoon actually has three subsections: an outer lagoon (immediately adjacent to the open ocean); a middle lagoon with little public use; and the inner lagoon, which is used for many recreational purposes, including a jet-ski rental business. It is in the inner lagoon where *C. taxifolia* was discovered. The sections are separated by slightly constricted openings, but all are open to the diurnal tidal pattern of this latitude. There is also some freshwater input to the inner lagoon during the winter. The presence of an electrical generating plant (which uses lagoon water for cooling) adds further complexity to the "uses" of the site.

The Huntington Harbour site is about 5 acres in area and is both distant and relatively isolated from the ocean. It is surrounded by homes and delineated by cement bulkheads. Water is pumped into the system periodically. The site does not have the types of wave-producing recreational activities (i.e., high speed vessels) that are common in Agua Hedionda. Regardless of these differences, the general hurdles to eradication soon became evident are summarized as follows:

Challenges to Eradication of *C. taxifolia*

- No experience eradicating exotic marine algae
- Unclear agency authority and responsibility
- Unclear and multiple "ownership" of site (water, substrate, and uses)
- No documented successful *C. taxifolia* eradication programs
- No public awareness of threat from *C. taxifolia*
- No eradication protocols in place

Yet, despite these hurdles, a series of meetings held in the first weeks and months after the discovery of *C. taxifolia* in Agua Hedionda produced much animated, but constructive dialogue. The brainstorming by a variety of scientists within state, federal, academic, and private organizations, resulted in the development of a consensus-driven eradication plan. Progress was made for several reasons, summarized in Table 1. More importantly, however, it was the dedication and persistence of the group as a whole to maintain a focus on eradication, and to find solutions to overcoming difficult roadblocks. The complementary strengths, experience, and expertise of each member resulted in formation of the "Southern California *Caulerpa* Action Team" (SCCAT), and culminated in decisive actions spanning such issues as the technologies for treatments, regulatory constraints, "authority to act," public outreach and education, and funding.

Perhaps one of the most critically important early decisions was the stance taken by the San Diego Regional Water Quality Control Board (SDRWQCB) to define *C. taxifolia* a "pollutant." This forward-thinking approach not only made emergency funds available (as they would in the case of an "oil spill"), but it also recognized the parallel between chemical pollutants and exotic "biological pollutants" in impairing water quality and interfering with the beneficial uses of the water. However, the parallel diverges when one considers that these types of biological pollutants replicate rapidly, and can disperse both in the water as well as leapfrogging to other sites through boating-related activities.

Choice of Containment and Treatment Methods

There was no "off the shelf" *C. taxifolia* eradication protocol available. Experience gained from other California eradication programs, especially the Hydrilla program, was applied. The following steps and components were considered essential to a successful *C. taxifolia* eradication program:

- Delineate boundaries of the infestation (how much, where)
- Contain all plants and prevent immediate spread
- Kill and/or remove all living target plants and propagules
- Evaluate effectiveness of treatments and containment
- Prevent reintroductions
- Monitor for spread and reestablishment
- Mount an effective public awareness/education program
- Initiate new, appropriate, and enforceable regulations
- Declare successful eradication only when no living parts are detected for three to five years following the last treatments
- Conduct appropriate, relevant and timely research

The realities of available resources and other constraints necessarily drive the relative allocation of time and the phasing for each of the above components. However, it was clear to all participants that immediate containment and treatments were top priority.

The continued spread of this alga in the Mediterranean and Australia attested to lack of adequate methods, even though a variety had been attempted. In addition, conditions and circumstances surrounding the California infestation differ in several ways: generally poor visibility, loose, unconsolidated substrate compared to most of the Mediterranean and Australian sites. Thus mechanical methods that were tested tended to immediately create low-to-nil visibility and the danger of spreading fragments was high.

Other options were considered including dredging or containing the entire inner lagoon and treating with a biocide or algicide. When first discovered, the extent of the known infestation was a few hundred square-feet consisting of a main colony and some smaller colonies. Thus, considering all the pros and cons of different methods, the most expedient and effective containment was to cover the colonies in 60 mil PVC, and seal the edges with sand bags. Within a week of the discovery, some preliminary trials were conducted using known, registered aquatic herbicides at maximum or higher label-rates. These included diquat, copper (copper-chelates), endothal, and fluridone. None of these produced significant results within 10–14 days, even though they typically would in susceptible plants.

It is important to recognize that these products were developed for use in fresh water. A variety of potential interferences might occur in saline conditions. Only bleach (liquid hypochlorite) and vinegar (5% acetic acid) appeared to kill the alga within a few days. Since hypochlorite produced rapid, visible symptoms, was relative inexpensive and short-lived, it was chosen as the best treatment available. Liquid hypochlorite (30% by wt.)

was pumped into ports (fitted with caps) in the PVC tarps after these had been secured in place. Tarps were left in place for a period of several months to over one year before sediment core samples were removed to assess the efficacy (see discussion on assessment following). Fig. 2 shows diagrammatically how tarping and treating was done.

When an additional find was made in Huntington Harbour, the small sizes of colonies afforded an opportunity to use solid forms of chlorine-producing tablets, typically used to maintain chlorine levels in swimming pools. Each colony was contained with PVC underneath which one or more tablets were placed. These treatments were left in place until the year following the initial treatments. The assessment of this approach is underway now.

Restriction of Public Use

Agua Hedionda serves as a recreational site for a wide range of public uses including fishing, jet skiing, waveboarding, waterskiing, and kayaking. In addition, normal tidal exchanges at six hour intervals create variable flow velocities and directions, though these obviously cannot be controlled without complete physical isolation of the entire inner-lagoon. Because of the high wave energies generated from powered vessels plus the high potential for movement of *C. taxifolia* fragments, and concerns for the safety of divers implementing the eradication program, infested areas were immediately excluded from public access. Subsequently, further restrictions were imposed to facilitate surveillance and monitoring which, due to low visibility, required SCUBA divers to search rather finegrid transects.

The most recent approach employs a 1-meter-square grid pattern to ensure that small plants are not overlooked. These restrictions and greater ones, including complete closure of the inner lagoon, have generated a great deal of debate and discussion. At present, a significantly modified use policy has been adopted, but the continued threat to disturbance and potential dispersal of undetected plants may necessitate full closure in the future. The current approach resulted from a series of stakeholder meetings and small working sessions with the goal to produce a tentative working plan.

Outreach and Education

Within two weeks of the discovery of *C. taxifolia*, initial public information materials were gathered. Through the combined efforts of the San Diego Regional Water Quality Control Board, National Marine Fisheries Service, Merkel and Associates, California Department of Fish and Game, and stakeholder groups, the sphere of awareness gradually enlarged from a small group of SCCAT participants, to more and more public at large. Tandem efforts were made to notify and inform key state and local elected officials to support regulatory action and for funding efforts. Again, through serendipitous events, in June and July, the BBC was filming a follow-up story on the *C. taxifolia* invasions in the Mediterranean and sent a crew to San Diego to document the U.S. effort. The program was ultimately broadcast on PBS stations, providing excellent coverage of the new U.S. problem and eradication program.

Regulatory Responses

Though *C. taxifolia* was already included on the Federal Noxious Weed list, it could still be used, sold and transported within California. Furthermore, the listing included only the “Mediterranean strain.” Notwithstanding the listing, it became quite clear to SCCAT that much more stringent limits on the movement of the species was crucial to prevent further introductions. In addition, restricting a regulatory exclusion to a single species seemed untenable due not only to the wide variation in morphology within that species, but more importantly due to the great difficulty in correctly identifying similar species within the *Caulerpa* genus. With remarkable speed, and strong support within the scientific community, the City of San Diego banned the entire genus from possession, transport, and sale within the first year of the discovery. Shortly thereafter, a statewide ban was imposed on *C. taxifolia* and eight other species (though not the entire genus). In effect, these statutes placed a legal prohibition on possession of *C. taxifolia* and several other problematic *Caulerpa* species. The breadth of these city and state quarantines have simplified enforcement and go a long way toward prevention of additional introductions—at least in California. Eventually, the statewide ban may reach the genus level as more information is obtained on the ability to identify and interdict shipments within and into the state.

Assessment of Eradication

Since the first objective in the program was containment and treatment, SCCAT members decided to leave tarps in place for several months. In addition, following the initial treatments of the largest colonies, smaller scattered plants were observed throughout the following year’s monitoring period. Some had probably been missed due to difficulties in visibility; some may have been derived from colonies that had been covered. In the late fall of 2001, plans developed by USDA-ARS to sample sediment from several treated colonies.

After review by SCCAT's Technical Advisory Committee, the consensus was to remove intact sediment cores (10.2 cm wide by 20 cm deep) (Fig. 3) from sites representing the following treatments and conditions:

1. Tarped + liquid chlorine
2. Tarped + tablets
3. Tarped only
4. "Control"— untarped sites that had never had *C. taxifolia*

Four repeated core samples were taken from what was originally densely populated areas in tarped + treated sites. Four sites were sampled. Additionally, control cores were taken from four different sites.

All cores were removed in December 2001 and transported by van to the USDA-ARS Exotic and Invasive Weed Research Laboratory on the UC Davis campus. Twenty-four hours after removal, cores were immersed in aerated 20 liter containers filled with "Instant Ocean" (30 ppt) and maintained at 19.5 °C (+/-.8 °C) under cool-white fluorescent lamps supplemented with incandescent light (total ca. 200 µmols /m2/sec) in and LD: 14:12 photoperiod. In order to confirm that these conditions and the sampling methods would facilitate and support growth of *C. taxifolia*, 8 control cores were inoculated with explants having a short piece of stolon plus a single frond; and 8 cores were inoculated with a short piece of stolon only (no frond) (Fig. 4). Explants were inserted 2 to 4 cm into the top of the cores. All cores were observed weekly for 76 days and 50% of the "Instant Ocean" was refreshed biweekly. Observations included: number of fronds, lengths of fronds, emergence of other plants and invertebrates.

The results of this initial assessment are extremely encouraging: no *C. taxifolia* was observed in any of the cores from any of the treatments. The cores inoculated with stolons plus single fronds grew with a doubling rate of about 10 to 12 days (i.e., doubled lengths and number of fronds). Only one control core that had been inoculated with a single stolon (no frond) had produced a new frond. A few coelenterates and mollusks were observed in the control cores as well as several annelid worms. Most surprising, however, were seedlings of eelgrass that emerged from several cores taken from treated sites. Many cores had two to three eelgrass seedlings. This observation, though certainly preliminary, suggests that not only were the chlorine treatments effective, there was also a viable seed-bank of native eelgrass released. More core assessment and field assessment will be required to verify this phenomenon, but it does provide hope and incentive to persist with the eradication protocol. Figs. 5 to 8 provide examples of the plants 76 days after inoculating the control cores and after immersion of the cores from treated sites. The complete results will be published elsewhere.

Summary and Conclusions (Strengths and Weaknesses)

In all pest control and eradication programs, there is an inherent need to balance the objectives of the project with the realities of working in a complex biological and sociological environment. One such reality is that there is a difference in skills, experience, and coordination needed for successful implementation of eradication (programmatically and biologically) and the biological knowledge base of the targeted species. For example, the physics and chemistry of fire is crucial to understanding of fire, but is not sufficient to develop a fire department with rapid response capabilities. The latter is a different order of complexity since it must incorporate a wide range of human behavior, human perceptions, human experience, human expectations, and available control technology. We live in a society where “scientific literacy” is generally abysmal. There is, unfortunately, even less “invasive species literacy.” Accordingly, we can expect that with most aquatic invasions, there will be moderate to strong reactions and questions about:

1. The need to eradicate
2. The methods used to eradicate
3. The “authority” to act

From the public’s vantage point, besides air and food, water is the next most important resource—one that evokes emotional responses based upon both reality and perceptions. The *C. taxifolia* infestation fits this pattern well, as do many invasions of freshwater sites, particularly potable water systems. In light of all the circumstances surrounding the Agua Hedionda and Huntington Harbour infestations, how did this program get launched so quickly? I have briefly recapped the essential components below.

Components of the *Caulerpa taxifolia* Rapid Response:

- Scientific and political awareness in place two years before discovery
- Political will followed scientific input (collective SCCAT action)
- Fortuitous finding and location (surveillance and ID)

- Essential components of eradication program assembled through multi-agency consensus (collective SCCAT action)
- Field team was in place
- Technology inputs quickly evaluated and priorities assigned
- Dedicated people
- Rapid access to funds and other resources

Why was an “ad hoc” group (SCCAT) formed? This development illustrates the one major weakness in responding to invasive species invasions in general: lack of a clearly defined, lead agency with authority to act quickly. SCCAT filled that breach by driving the program out of the necessity for environmental stewardship and shear will to succeed. Importantly, this experience can serve as a model for developing a “rapid response” paradigm that can be adapted to other likely invaders so that lag-time to response is minimized and critical funding problems can be solved before an infestation is discovered. Similar models can best be developed by serious “fire drill” exercises for known, likely invaders and with a sufficient range of scenarios to account for several likely sites of invasion. These exercises should be supported jointly with federal and state resources since we are, in effect, trying to protect “the Commons.”

Figures . . .

Figure 1. Sites of first *Caulerpa taxifolia* infestations in California. Top: Agua Hedionda (Carlsbad – 30 miles north of San Diego). Bottom: Huntington Harbour (near Seal Beach). *Photo by Merkel and Associates.*

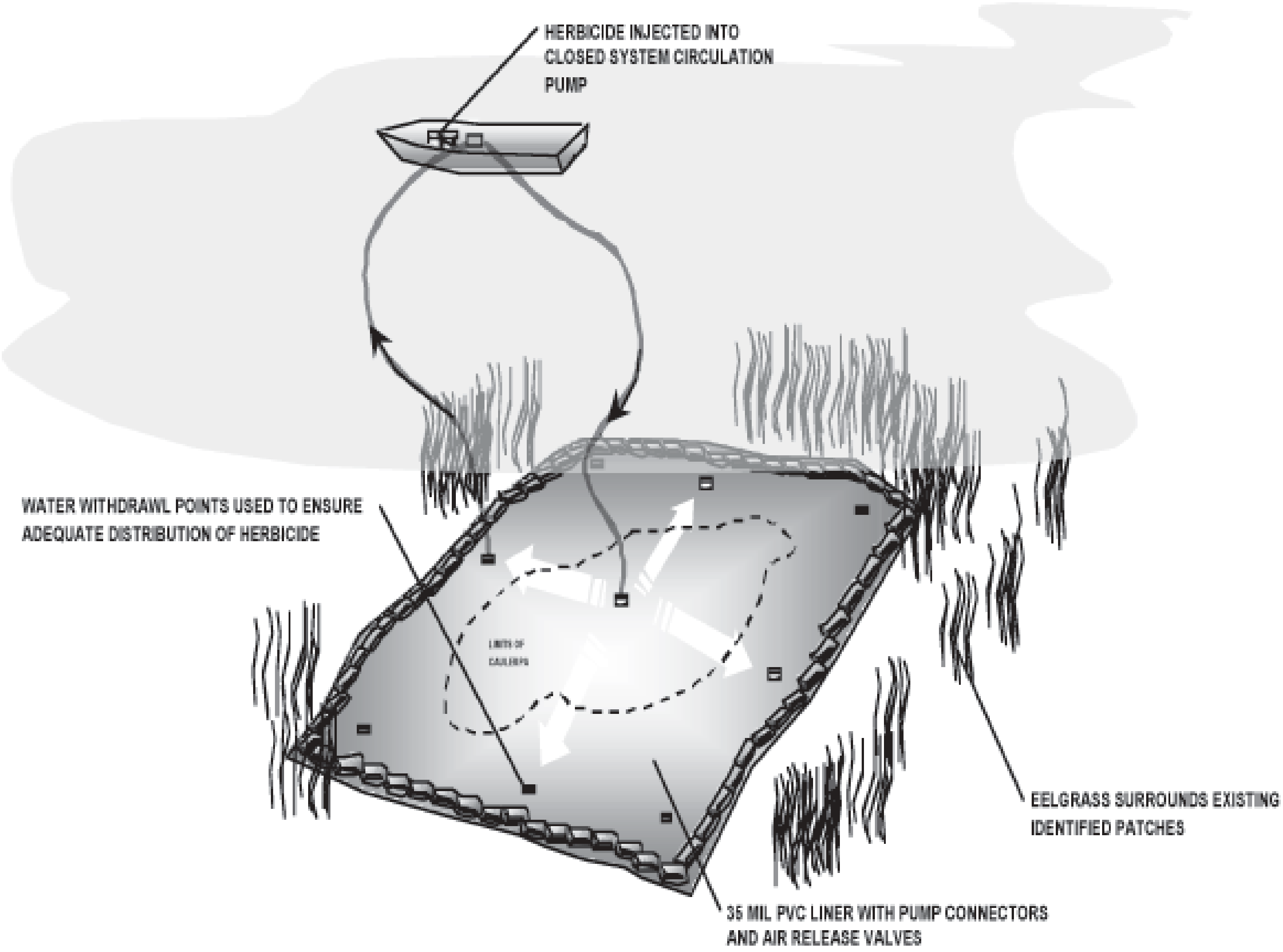

Figure 2. Diagram depicting typical tarping of *Caulerpa* colonies for containment and treatment with chlorine in California. *Drawing by Merkel and Associates.*

Figure 3. PVC core sampler used for removal and transport of sediment from *C. taxifolia* infested sites after treatment with chlorine.

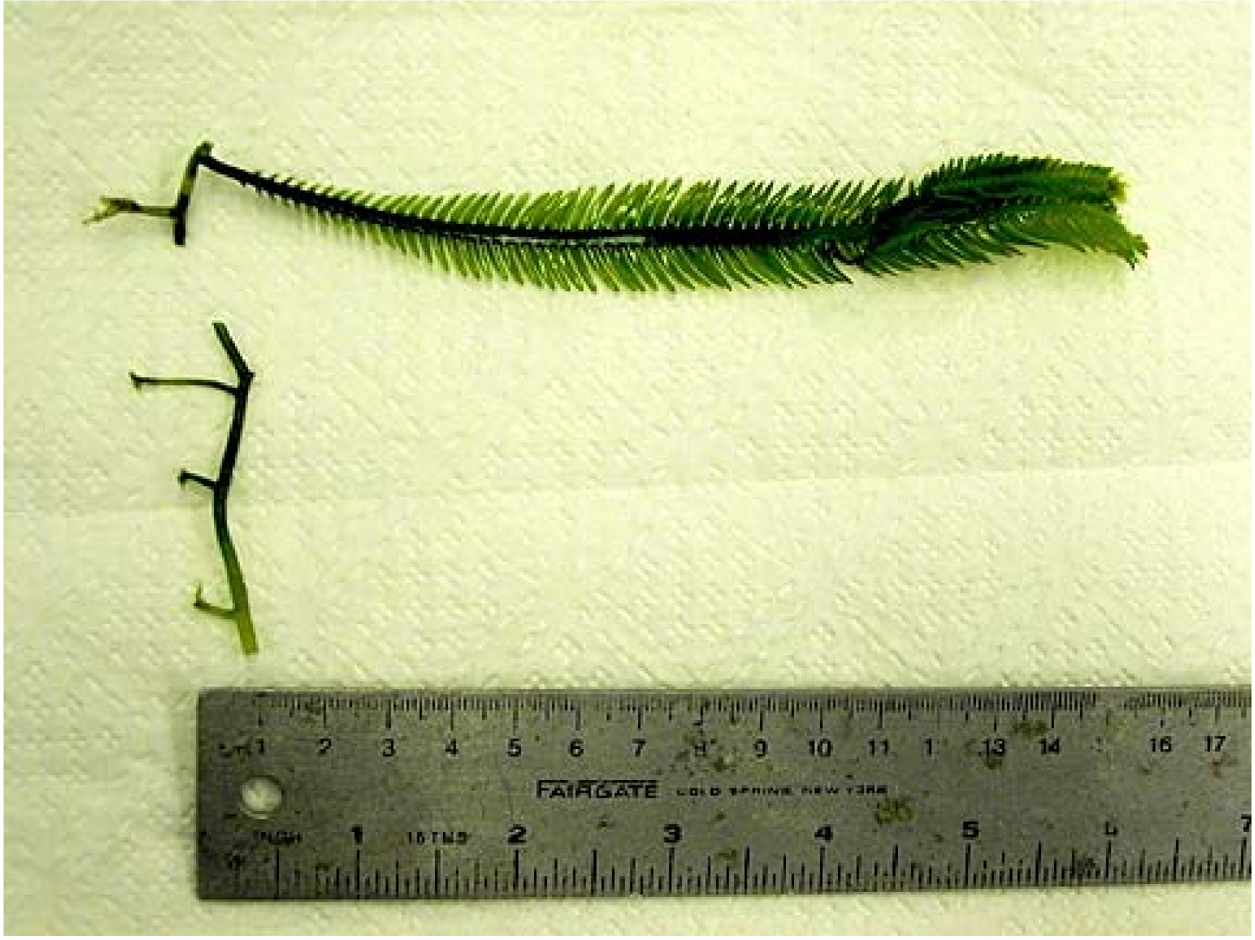

Figure 4. Two types of *Caulerpa taxifolia* explants used to inoculate “control” (untreated) sediment cores to verify adequate grow-out conditions.

Figure 5. Examples of *Caulerpa taxifolia* growth in “control” (untreated) sediment cores 76 days after inoculation with single frond explants.

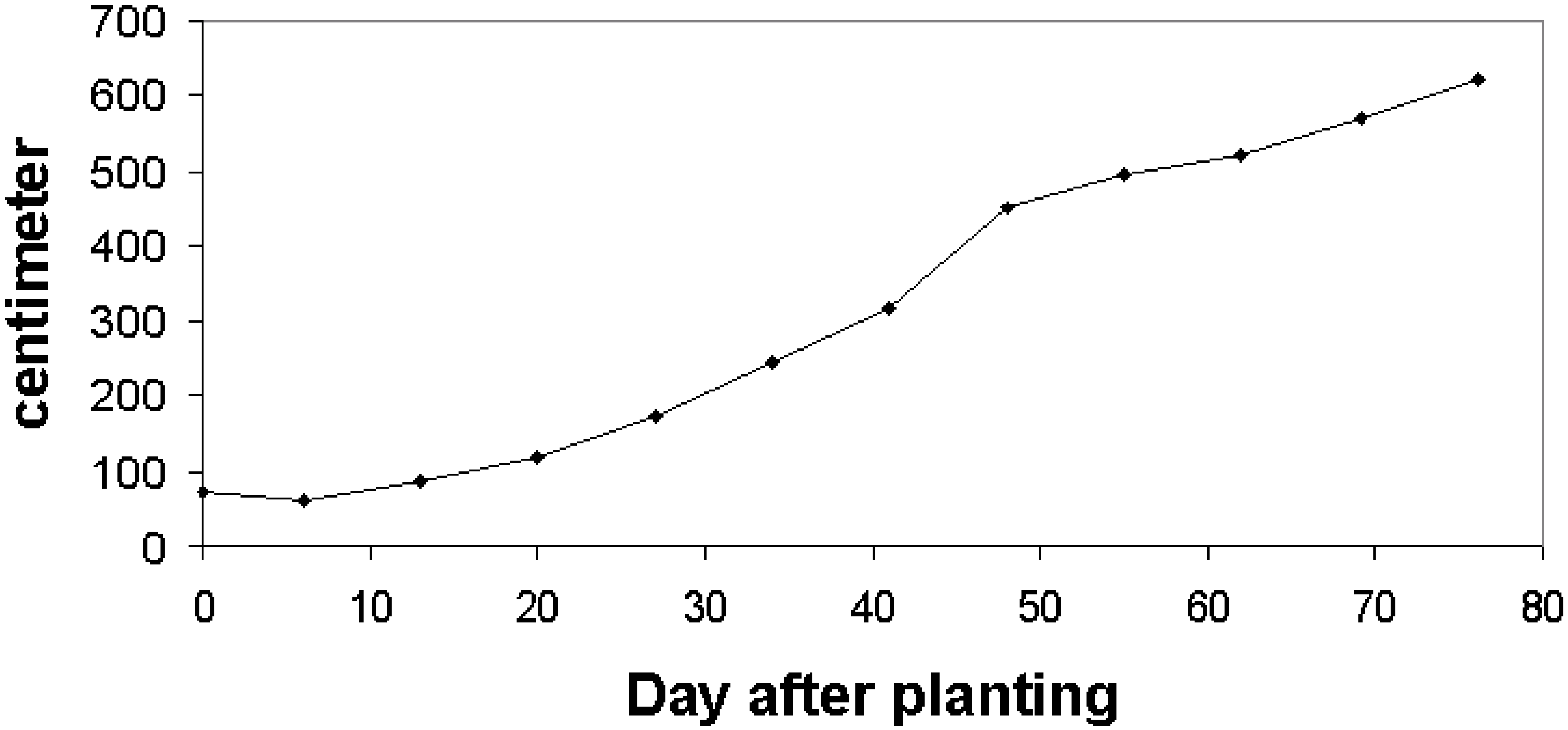

Figure 6. Cumulative length of *Caulerpa taxifolia* fronds in control cores 76 days after inoculation.

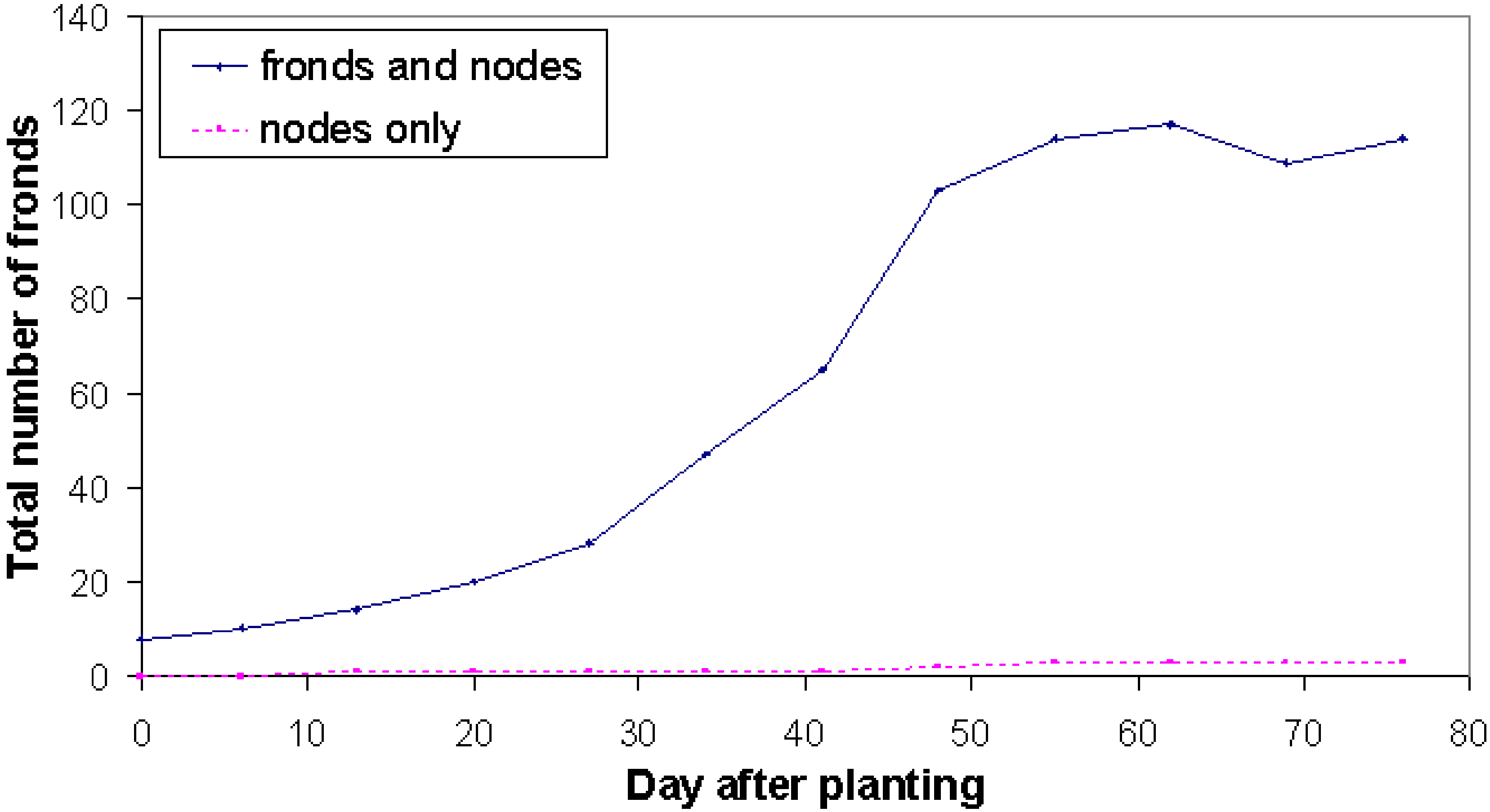

Figure 7. Total number of *Caulerpa taxifolia* fronds in control cores (frond and nodes versus nodes only) 76 days after inoculation.

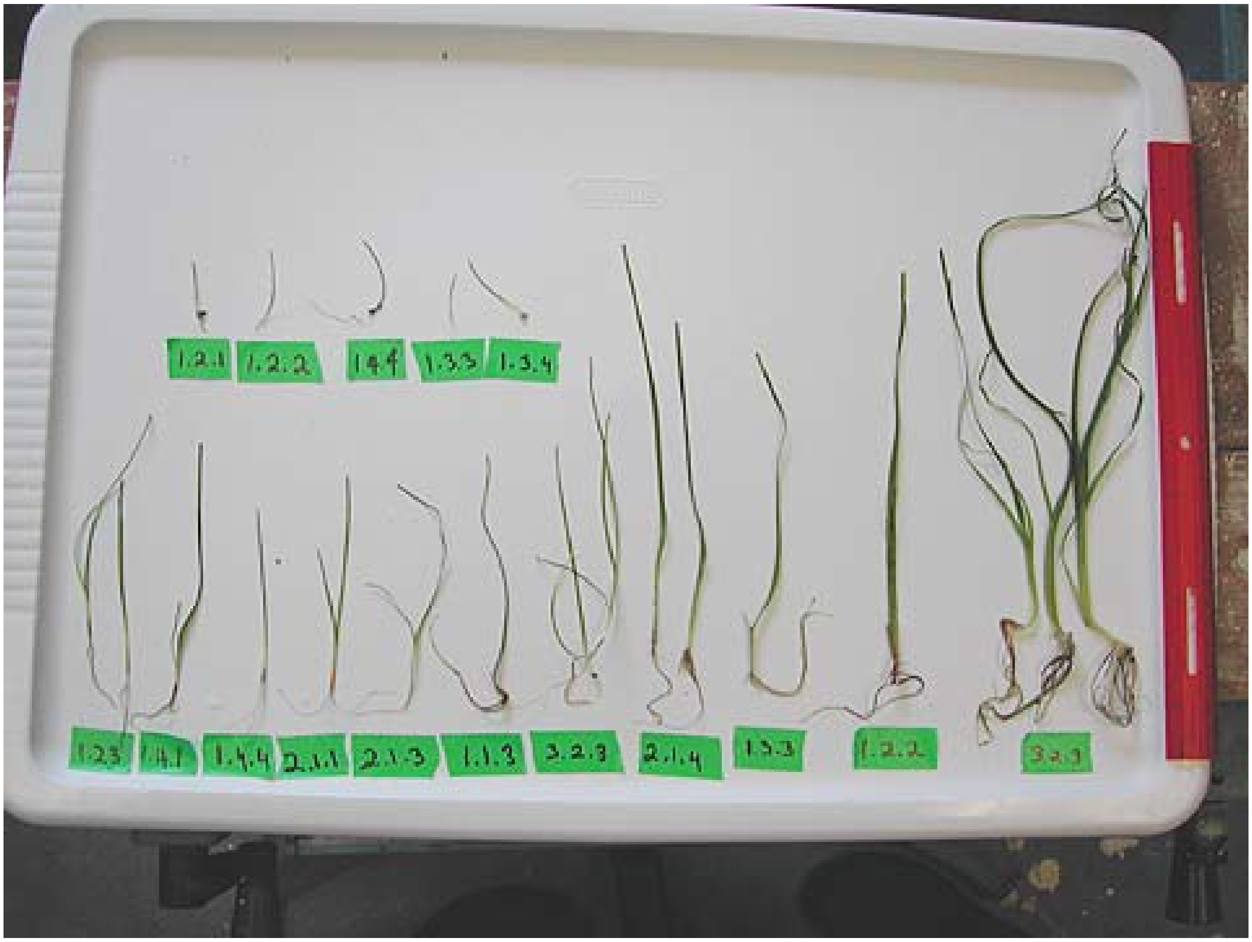

Figure 8. Eelgrass seedling from sediment cores 76 days after removal from sites treated to eradicate *Caulerpa taxifolia* in Agua Hedionda Lagoon.

Tables . . .

Table 1. Key Contributors to the Development of *C. taxifolia* Eradication Plan

Group	Role
San Diego Regional Water Quality Control Board	Designated *C. taxifolia* as “pollutant.” Provided emergency “cleanup” funding support; outreach and education
California Department of Fish and Game	Enforcement authority–restriction of access to eradication site(s).
California Department of Food and Agriculture	Experience in eradication of exotic freshwater flowering plants (e.g. *Hydrilla verticillata*).
University of California, Davis	Phycological expertise–scientific support for improved regulatory restrictions; outreach and education (UC Extension).
U.S. Department of Agriculture–Agricultural Research Service	Scientific expertise–control and eradication of higher aquatic plants and algae; in-kind support for early assessment of algicides and assessment of treatment efficacy.
National Marine Fisheries Service (NOAA)	Federal marine waters regulatory authority; funding support.
Cabrillo Power, LLC	Early, rapid funding to help support eradication and surveillance.
Merkel and Associates	First detection and notification; hand-on eradication field team; outreach and education.
Stakeholder/Citizens	Public liaison and awareness; support for obtaining regulatory changes and funding; adjusted lagoon uses.

Caulerpa taxifolia . . .

Summary of *Caulerpa taxifolia* Invasion and Management in the

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Situation and Strategies in the Concerned Mediterranean Countries

The tropical green alga, *Caulerpa taxifolia*, has spread steadily since its introduction into the northern Mediterranean Sea at Monaco in 1984. Centralized monitoring efforts, within the framework of two European programs (Life and DGXI), led to the regular surveying of the *C. taxifolia* invasion until 1997. Since then, the spread of the alga has been monitored independently using methods developed by several international groups involved in the cooperative monitoring efforts. These observations, generated by countries concerned with the *C. taxifolia* invasion, have been brought together in an effort to assess current invasion status. Consequently, standardized methods have since been established to measure the spread of this alga consistently on both spatial and temporal scales. Thus, regional or global status of the invasion can be described and compared from one year to the next among different invaded sites.

At the end of 2000, six countries were affected by the invasion of *C. taxifolia*: Spain, France, Monaco, Italy, Croatia, and Tunisia. The main characteristic situation in each country is summarized briefly.

Spain

Caulerpa taxifolia was first discovered in the summer of 1992 in an area 50 m^2 at Cala d'Or Majorca, Balearic Islands. An eradication plan was initiated in 1992–1993 and a control plan was thereafter instituted in 1994–2000. The group in charge of this is the Comunidad Autonomia de las Islas Baleares. Surveys were conducted in both the Valencia and Cataluynia regions. Additionally, 12 scientists cooperated with two international European DGXI research and management programs. In the spring of 2001, more than 64 hectares were infested at Mallorca in three sites: Porto Pedro, Cala d'Or -Cala Grande, and Porto Colom. Some natural dieback was observed in the summer of 2001 in very dense beds of *C. taxifolia*.

France

The first infestation was discovered in July 1990 in an area approximately 50 m^2 at Cap Martin. In 1992–1993, a coordinating committee was formed involving 50 representatives of various government agencies and nongovernmental organizations. A total of 11 meetings were held to coordinate scientific research, surveys, public education, and control experiments. From 1993–1999, more than 100 scientists cooperated with two international European DGXI research, management, and education programs. Since 1994, the national park of Port–Cros has been managed with an annual survey and an eradication program to contain the spread of *C. taxifolia*. Since 1998, a new coordination committee held four meetings to coordinate scientific research and surveys. In spring 2001, *Caulerpa* infested more than 3,184 hectares in three regions and 76 zones. By December 2001, there were 30 additional zones invaded.

Monaco

The initial invasion was first discovered in 1984 in an area 1 m^2. By 1998, a limited eradication effort using hand removal was conducted in a protected area. In spring 2001, all littoral habitat in the entire country was infested (more than 75 hectares) with large colonies in the two protected areas. A survey in autumn 2001 found that *C. taxifolia* is the dominant marine plant of this country.

Italy

Caulerpa taxifolia was first discovered in June 1992 in an area approximately 200 m^2. An eradication effort using hand removal was conducted in 1992, 1993, and again in 1998 by local scientists at Messina, Elba, and Chiavari, but was unsuccessful. From 1993–1999, 25 scientists cooperated with the two international European DGXI research, management, and education programs. By spring 2001, more than 9415 hectares were infested in four regions (Liguria, Toscania, Sicilia, and Calabria).

Croatia

The first infestation was discovered in 1994 in a large area approximately 3000 m^2. Eradication or control efforts were begun in 1996, with a control program organized by the federal government in 1998. By spring 2001, at least 41 hectares were infested in three regions (Krk-Malinska near Rijeka, Barbat Canal, and Hvar–Starigrad near Split).

Tunisia

In this recent invasion, *C. taxifolia* was first discovered in January 2000 in an area of approximately 350 hectares. An information campaign was organized by the government in 1998 and a map of the invaded zone was produced by the Institute of Sciences and Technology of the Sea. By spring 2001, approximately 1000 hectares were infested in area approximately one mile offshore from Sousse Harbor (an area frequented by large ships awaiting entry into the harbor).

Research and Public Information

The research on the Mediterranean invasion has resulted in more than 80 peer-reviewed publications as well as an additional 179 papers published in the proceedings of four workshops. A total of 420 people in 115 laboratories or institutions participated in this work. As a result, the data available for *C. taxifolia* are greater than for any other introduced marine species.

Information distributed to the public includes more than 300,000 brochures that have been dispensed to divers, fishers, and sailors in several languages including English, Spanish, Catalan, French, Italian, Croatian, and Arabic (Tunisia and Turkey). In addition, there have been more than 1,000 press releases and over 100 television programs on the *Caulerpa* invasion.

Management

Several methods have been used for control or local eradication of *C. taxifolia*. These include:

1. Manually removing more than 20 individual patches (covering less than 3 m^2). These were destroyed with success.

2. Physically removing; suction dredging (water or air); covering with plastic sheeting; or using warm or cold water have been applied with some success.

3. Chemically eradicating with copper or salt has been effective in some areas.

4. Biologically controlling in an aquarium and the open sea with Mediterranean sea slugs *Oxynoe olivacea* and *Lobiger seradifalc.* In addition, the tropical sea slugs *Elysia subornata* and *Oxynoe azuropunctata* have been studied in aquaria as possible control agents.

Legislation to Limit the Spread of *Caulerpa taxifolia* in the Aquarium Trade in Mediterranean Countries

All concerned nations have signed international legislation and recommendations for the control of introduced species that threaten ecosystems, habitats, or species. Several examples of legislation include:

1992	(October 26) Spain, Generalitat de Catalunya (Decreto)
1993	(March 4) France, Ministry of Environment and State Secretariat of the Sea (Arrêté)
1994	(May 10) Spain, Comunidad of Valencia
1996	(March 20) Spain, Comunidad Autonomia de las Islas Baleares (Orden)

Existing Treaties and International Instruments Against Introduced Species

1. Convention on Biological Diversity 1992 (article 8 (h))
   " Contracting Parties must prevent the introduction of, control or eradicate those alien species which threaten ecosystem, habitats, or species..."

2. Law of the Sea Convention 1982 (article 196)
   "States shall take all measures to prevent, reduce, and control the international or accidental introduction of species, alien or new, to a particular part of the marine environment, which may cause significant and harmful changes thereto."

3. Berne Convention (for Europe) 1979 (article 11)
   "Each contracting Party undertakes to strictly control the introduction of non native species."

4. Protocol of the Barcelona convention (for Mediterranean countries)
   "The Parties shall: take all appropriate measures to regulate the intentional or accidental introduction of non-indigenous or genetically modified species and prohibit those that may have harmful impacts on the ecosystems or species and endeavor to implement all possible measures to eradicate species that have already been introduced when, after scientific assessment, it appears that such species cause or are likely to cause damage to ecosystems, habitats, or species in the area to which this Protocol applies."

Conclusion

The invasion of the Mediterranean Sea by the introduced invasive strain of *C. taxifolia* is continuing to expand. By the end of 2000, approximately 131 km^2 of benthos had been infested in 103 sites along 191 km of coastline in six countries. Over 30 new invasion sites were identified in France in the summer 2001.

We conclude that eradication has not been possible since 1992. Therefore, efforts should be on control techniques that can slow down the pace of invasion or local eradication measures that focus on areas of particular concern less than 1 ha in area, such as specific marine protected areas. There is some hope that future reduction of *C. taxifolia* in the invaded region can be achieved using biological control with tropical slugs (Sacoglossan). However, more immediate gains may result from information distributed to fishers who may be able to reduce the spread by anchors or nets. Additional controls for the sale *C. taxifolia* in the aquarium trade could prevent new introductions from aquariums. Unfortunately, 18 years after the first discovery of the invasive *C. taxifolia,* there is no global strategy to control this invasion in the Mediterranean Sea.

Caulerpa taxifolia . . .

Discussion of *Caulerpa taxifolia* Management in the Mediterranean

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Despite the intense focus on the invasion of *Caulerpa taxifolia* in the Mediterranean since 1992, the invasion has expanded beyond the point where eradication is possible. However, several management actions have been successful, including extensive public education and coordinated surveys documenting the progress of the invasion.

Public Awareness

One of the primary successes in the management of *C. taxifolia* in the Mediterranean has been the public awareness campaign initially undertaken since 1991 by the French Laboratoire Environnement Marin Littoral of the University of Nice-Sophia Antipolis and later followed by other countries. This public awareness campaign delivered the following messages:

- Notify scientists of new invasions
- Avoid the spread of *Caulerpa* to new areas by anchors or fishing gear

Invasion Monitoring

Mapping each new site invaded by *Caulerpa taxifolia* provided important information on the invasion dynamics in the Mediterranean. By standardizing survey methods, scientists have been able to compare year-to-year and zone-to-zone differences in the invasion (Vaugelas et al. 1999).

Modelling the Spread of *Caulerpa taxifolia*

Models of the *C. taxifolia* invasion can be used as a predictive tool to define a general management strategy. Most of the work dealing with models of invasive species has focused on species interactions. These models are often derived from Lokta-Volterra prey-predator theory, which focuses on the relationship between community stability and the number of species in the system. Substantial knowledge of the system is required and these models can only be applied to simplified systems (Williamson 1996).

In aquatic systems, the only studies modelling the dynamics of invasions are in freshwater ecosystems. Most models use differential equations to simulate the population dynamics of an invasive species and/or its control agent (Godfray and Waage 1991; Ramchara et al. 1992; Fisher and Grant 1994). Modelling an invasive species requires background knowledge of the ecology of the invader. In marine ecosystems, studies of invasive species do not have the same rich history, and to our knowledge, no modelling work in this system has dealt with invasive species.

Modelling the spread of *C. taxifolia* in the Mediterranean began in 1994. The basic model was developed by Hill et al. (1996, 1997, 1998), but these studies lacked data for some important parameters for the biology of this alga. More recent studies and model development have now succeeded in making this model operational as a predictive tool.

The aim of the modelling is to evaluate and predict the spread of *C. taxifolia* anywhere in the Mediterranean. The main objectives are:

1. To simulate the range expansion of the alga in a few sites where data are available from field studies, aquarium experiments, or from the literature.
2. To predict *C. taxifolia* expansion by taking into account the environmental parameters such as bathymetry, substrate type, etc.
3. To present the results as maps of recent colonization events in order to compare them with the field maps.
4. To develop a model of colonization in order to assess eradication effort, assist alga surveys, and guide management.

These objectives apply generally to the scale of the entire *C. taxifolia* population. A more detailed model will be developed for the fate of individual *C. taxifolia* fragments.

Modelling Techniques

The necessity of including spatial parameters in the model determines the choice of the modelling methods. We used a stochastic, discrete events simulation with software that can use maps of any Mediterranean site by coupling the model with a GIS (Geographical Information System) database. Because of stochastic events, for each simulation experiment, numerous replications are required. Quantitative results are given as a mean value and the standard deviation. The map of colonization shows the probability of colonization of *C. taxifolia.*

Spatial Parameters

The spatial parameters are the depths and the substrate (Fig. 1). The currents at the study site, if known, can be also integrated in the model.

Lateral Expansion of the Colony

The lateral expansion of the *C. taxifolia* meadows is defined by the growth of the stolons, which are available in Komatsu et al. (1994), Hill et al. (1998), and Thibaut (2001). The expansion rate depends upon the substrate, the depth, and the season.

Changing Biomass

According to Thibaut (2001), the biomass of *C. taxifolia* in one cell of the model changes in two steps:

1. A transitory phase where the biomass does not reach an asymptote.
2. An equilibrium phase where the biomass oscillates around the maximum biomass (carrying capacity).

In the model, the maximum biomass depends on the substrate, depth, and localization of the site (cape, bay).

The biological parameters of *C. taxifolia* (growth and death rates) are considered as deterministic and are influenced by depth, season (temperature), and substrate. The optimal growth season is from May to September.

Dispersal of Fragments

The spread of *C. taxifolia* depends upon the production of fragments and the resulting vegetative reproduction. Experiments and observations show that the fragments produced sink rapidly and do not float (Thibaut 2001). Local currents are the main influence affecting fragment dispersal. Thus Hill et al. (1998) found that the dispersal of *C. taxifolia* fragments was best represented by a uniform circular distribution. Two distances of dispersal were used (Fig. 2):

1. A low distance that includes most of the fragments (90%).
2. A high distance (few hundred meters) that includes a few fragments (10%).

Therefore, in the model the alga can disperse by production of fragments whose number, distance, and direction of dispersal are randomly chosen from an interval depending on substrate and local depth. Because of this stochastic feature, each simulation experiment is replicated 1024 times in order to obtain an average “image” of *C. taxifolia* spreading. This “synthetic image” is obtained by spectral analysis that gives the probability of occurrence of *C. taxifolia* at the study site. Time is treated as discrete with a time step of one month.

Simulation Field

The study site is given as a grid divided into cells, where for each cell the depth and substrate are determined. For each cell affected by *C. taxifolia*, the colonization level and the biomass are available. The size of a cell varies from a few cm^2 to several kilometers (Fig. 3).

The probability that *C. taxifolia* colonizes and grows in a cell obeys a set of rules depending on the depth, the substrate, and the number of algal fragments colonizing this cell.

Applications

In order to demonstrate the usefulness of this approach two experiments are presented. The first one is a comparison of a simulated and a natural spreading in a non-controlled area. The second is a prediction of what would occur if no control had been engaged at Port-Cros, a French marine national park.

Saint-Jean Cap Ferrat (Alpes-Maritimes), Bay of Les Fosses

The Bay of Les Fosses is a relatively narrow, shallow water site. A fragmented seagrass bed of *Posidonia oceanica* with a large, dead mat in the middle had colonized this tiny bay. The initial observations noted a 16 m^2 colony in October 1993 on a dead mat of *P. oceanica* at 3 m deep (Meinesz et al. 2000; Fig. 4). Yearly surveys occurred from October 1993 to October 1996, and therefore, the simulations covered the same time frame.

The comparison of field observations of *C. taxifolia* in this bay and the results of the simulations shows the model fits the field observations well (Table 1).

Fields observations show that the spread of *C. taxifolia* mainly occurred on the dead mat of *P. oceanica* and very little on the sand. The seagrass bed of *P. oceanica,* considered dense at this depth, started to be colonized by the alga only in the second year. The results of two years of simulation (1995–1995) match the field observations and the colonies on the dead mat are denser. After the third year of simulation, we can see that the dense seagrass bed is only affected by sparse colonies of *C. taxifolia*. No large patch of the alga developed. At one end of the bay, some edges of the sea grass bed are invaded (Fig. 5).

Hyères (Var), National Park of Port-Cros

The national park of Port-Cros is the only French site where an official eradication program was undertaken. The result of annual eradication efforts since 1994 was complete eradication of all *C. taxifolia* in this area. The aim of the simulation at this site was to predict what would happen if no control was undertaken.

During the different surveys in the Bay of Port-Man, *C. taxifolia* was often observed as isolated fragments or small colonies (<1 m^2), located between 12 and 25 m depth on dead mats of *Posidonia* seagrass beds. Therefore, the initial situation accounted for in the model is a 0.8 m^2 *C. taxifolia* colony on a dead mat of *Posidonia* occurring between 10- and 20-m depth (Fig. 6). The simulation covered a period of four years.

The first year of simulation (1994) is not illustrated because it is not distinguishable from the initial conditions. Spreading of *C. taxifolia* after the second year (1995) would have been restricted around the initial point, with 19.7 m^2 densely covered. Most colonies would be growing on the dead mat of *Posidonia* with the dense bed of *Posidonia* not yet being colonized. By the end of the third year of the simulation (1996), 1340 m^2 are heavily colonized.

After four years (1997), the densely covered area sharply increased to 1.9 ha and the affected area reached 40 ha, still located mainly on the dead mat and on the edge of the *Posidonia* bed. After four years of simulation, spectral analysis showed a high probability of *C. taxifolia* settlement in the middle part of the dead mat and a very low recruitment within the seagrass bed (Fig. 7).

The model shows that the Bay of Port-Man is a good site for *C. taxifolia* recruitment. The fast colonization of the dead mat of *P. oceanica* in the simulation results is real. Indeed, during all annual surveys in this bay, *C. taxifolia* was always found on the dead mat substrate in spite of active research in the surrounding seagrass bed of *P. oceanica*. Similar study sites (dead mat surrounded by a dense seagrass bed between 10- and 20-m deep) also exhibit the same pattern of colonization. The simulated increase in affected area between 1994 and 1995, a few square meters, matches the area eradicated every year since 1994. The model shows that after 2.5 years, it is very difficult to control the *C. taxifolia* expansion. After three years, it will not be possible to eradicate the algae using the classical methods of eradication (chemical and manual control). Colonization of this bay will also endanger other sites in the park. This prediction highlights the efficiency of controlling *C. taxifolia* as soon as the alga is discovered and has helped guide the control strategy for the park.

Biological Control

Since 1992, different eradication tools were developed in order to control the spread of *C. taxifolia* in the Mediterranean. These methods (physical and chemical) are efficient only in small patches and it appears that they are inappropriate for global control of the algae. According to Lafferty and Kuris (1996), when these classical control methods are inefficient, biological control techniques can provide a solution. Some different types of biological control (Simberloff and Stiling 1996) are:

- Enhancement of local predators to control the alien
- Classical biocontrol (use of nonnative predators to control the alien)
- Neoclassical biocontrol (use of nonnative predators to control an indigenous species)

Until now, no attempt of neoclassical biocontrol was done in marine ecosystems, although it is common in terrestrial systems. Throughout the world, four projects concerning biological control in marine systems are under consideration:

1. The control of the North American comb jelly *Mnemiopsis leidyi* in the Black Sea and in the Azov Sea with salmon, butterfly fish, or another ctenophora *Beroe* sp. (ICES 1997).
2. The control of the European green crab *Carcinus maenas* in Australia, Tasmania, or in the U.S. with the endoparasite *Sacculina carcini* (Tresher et al. 2000; Goddard et al. 2001; Tresher and Bax 2001).
3. The control of the North Pacific seastar *Asterias amurensis* with the castrator ciliate *Orchitophyra stellarum* or the copepod *Scottomyson gibberum* (Kuris et al. 1996; Tresher and Bax 2001).
4. The control of *Caulerpa taxifolia* with a sacoglossan mollusc (Meinesz et al. 1996; Thibaut et al. 1998; Thibaut and Meinesz 2000; Thibaut et al. 2001; Zuljevic et al. 2001).

We evaluated the potential of the possible enhancement of Mediterranean sacoglossan species *Oxynoe olivacea* and *Lobiger serradifalci*, the only species able to feed only on *C. taxifolia* (Thibaut and Meinesz 2001). Evaluation of these species shows that (Thibaut and Meinesz 2000; Zuljevic et al. 2001):

1. *Oxynoe olivacea* is a poor competitor.
2. They are both rare on the *C. taxifolia* meadow, even after 18 years of colonization and 13,000 ha of sea bottom affected as well as the appearance of a second invasive species, *C. racemosa* var. *occidentali*s.
3. No natural regression of *C. taxifolia* due to *O. olivacea* has been observed.
4. They have a pelagic larval development, which may result in low recruitment making it impossible to maintain dense perennial populations.
5. Cultivation is difficult and costly.
6. *Lobiger serradifalci* fragments *C. taxifolia* thallus and contributes to its dispersal.

Thus, it appears that natural control of *C. taxifolia* invasion in the Mediterranean is unlikely and that the enhancement of the populations of these Mediterranean species is useless. Thus, we looked at the possibility of using nonnative species in the classical biocontrol tradition. The Caribbean sacoglossan species *Elysia subornata* was evaluated (Coquillard et al. 2000; Thibaut et al. 2001). The main advantages of this species are:

1. Strong specificity for the *Caulerpa* genus
2. Benthic larval development
3. High recruitment
4. High predation efficiency

A risk analysis was conducted following the ICES's guidelines (ICES 1997) . It appears that (Thibaut et al. 2001):

1. *Elysia subornata* is only able to survive with *C. taxifolia* or *C. racemosa* as the exclusive diet. A complete depletion of Mediterranean *Caulerpa* is ecologically impossible.
2. Possible pathogen introduction is reduced by a long quarantine period and aquarium experiment of cohabitation with the Mediterranean sacoglossan species.
3. Possible competition with indigenous *Caulerpa* herbivores is unlikely.

4. Dispersal over the release region is reduced due to the absence of a pelagic larval stage.

The main drawback of this species is that *E. subornata* does not withstand temperatures below 13ºC. A computer model was developed to evaluate the potential of this species (see Coquillard et al. 2000 for details). This model used a "multi-modelling" technique to simulate the population dynamics of *E. subornata* and its impact on a *C. taxifolia* meadow. This model appeared to be a useful tool for the evaluation of the release protocol of *E. subornata*.

In conclusion, natural control of *C. taxifolia* invasion by Mediterranean sacoglossan species is unlikely, but biological control appears to be the most appropriate solution with other introduced sacoglossan molluscs. We now have to find a cold-resistant temperature species, such as *E. subornata*, from northern Florida.

Conclusions

The main failure in the management of *C. taxifolia* is that, since 1992, the invasion has progressed too far to permit eradication of this alga in the Mediterranean. But public education seems to have contributed to a slower rate of spread and regular surveys have provided valuable information on the dynamic of this invasion. Modelling techniques appear to be useful predictive tools in the management of this alga and have helped decision makers control its expansion in some marine sanctuaries. Finally, biological control should be carefully considered with introduced sacoglossan molluscs as a possible hope for global control.

Figures . . .

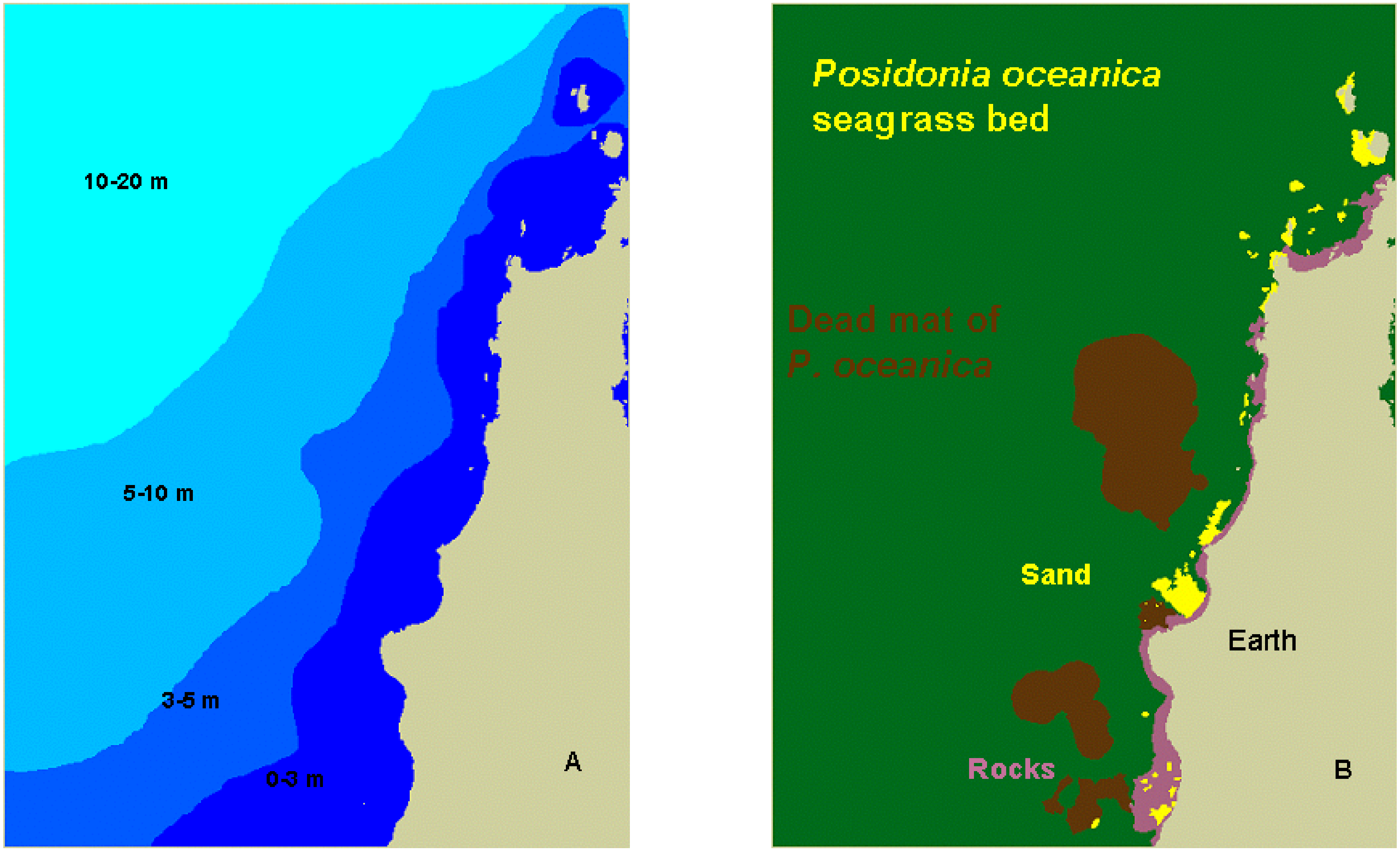


Figure 1. Example of map of the bathymetry (A) and substrates (B) integrated in the model.

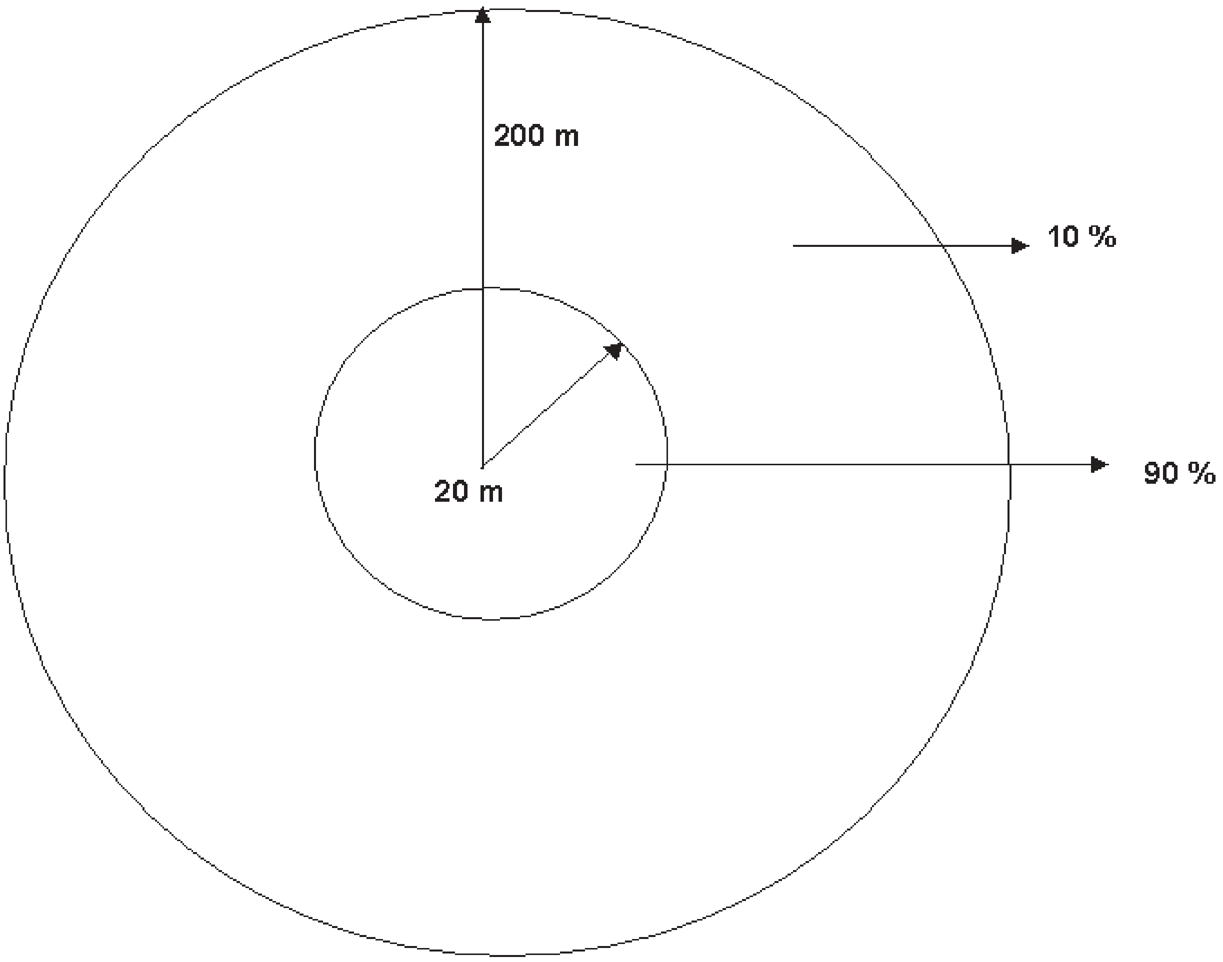


Figure 2. Example of dispersal distance and the probabilities of dispersal used in the model.

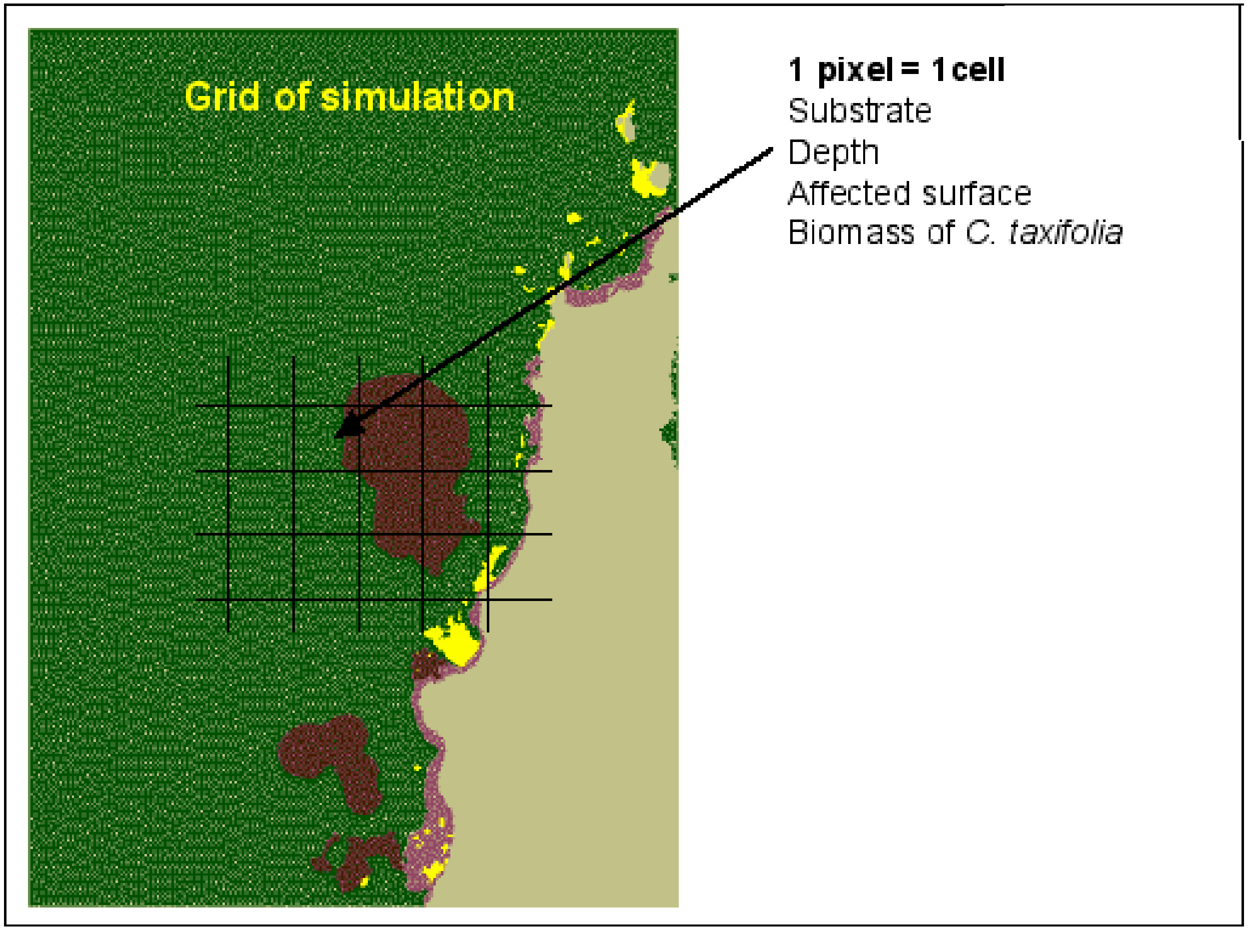


Figure 3. Information available on a cell of the simulation field.

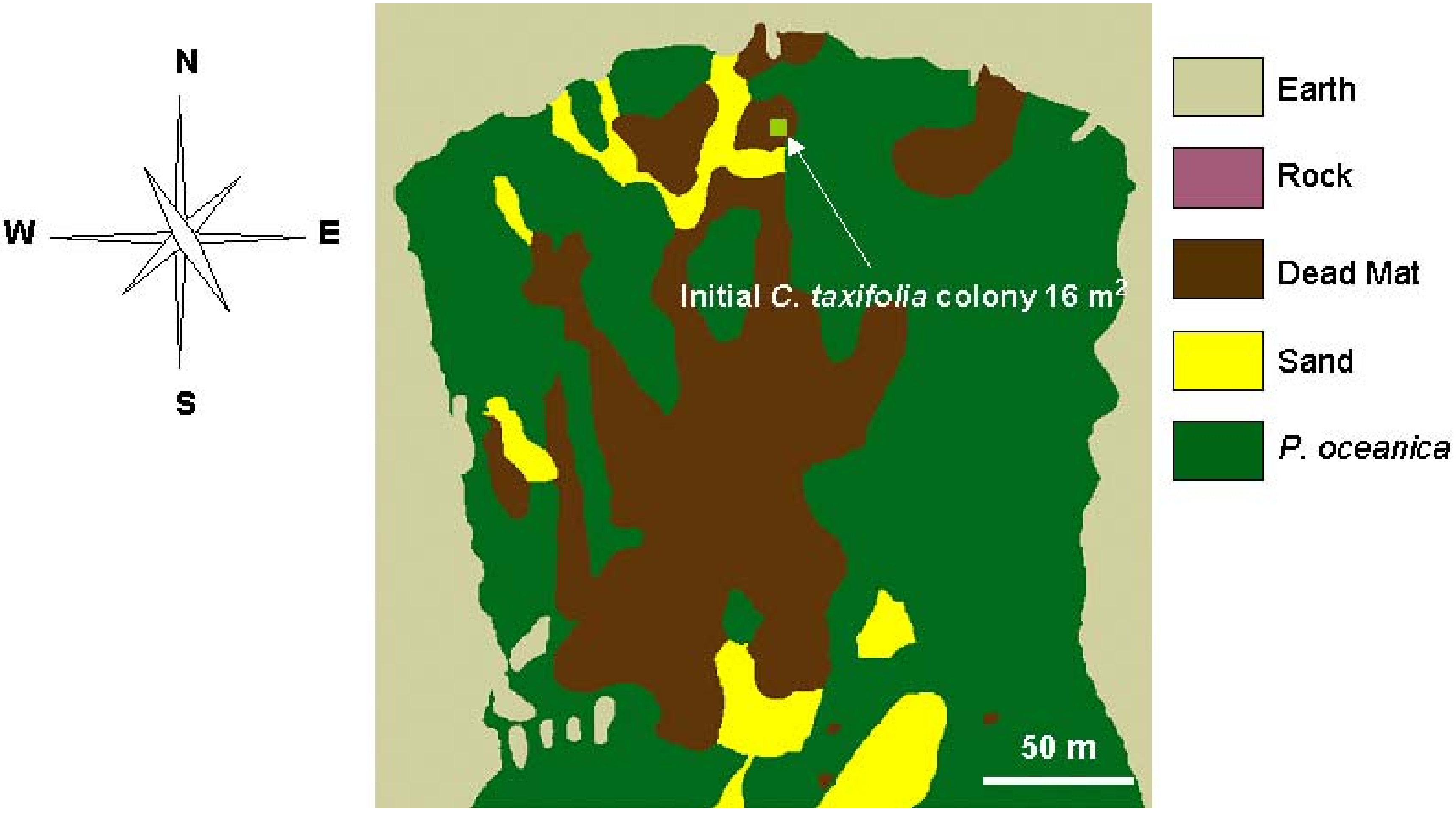


Figure 4. Initial invasion of *Caulerpa taxifolia* in the Bay of Les Fosses used for the simulations (October 1993).

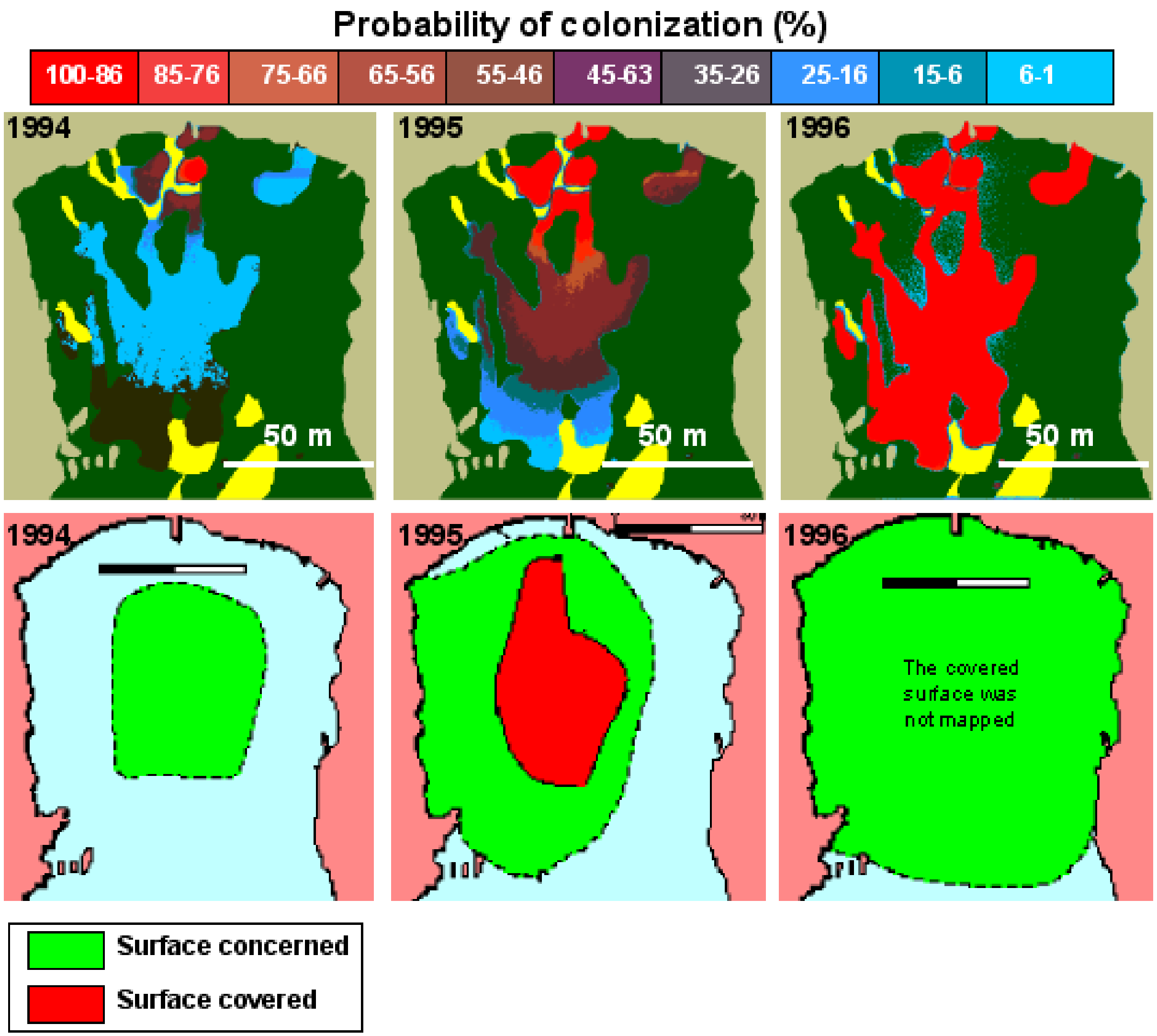


Figure 5. Comparison of simulated (upper) and observed (lower, Meinesz et al. 2000) changes of *Caulerpa taxifolia* in the Bay of Les Fosses.

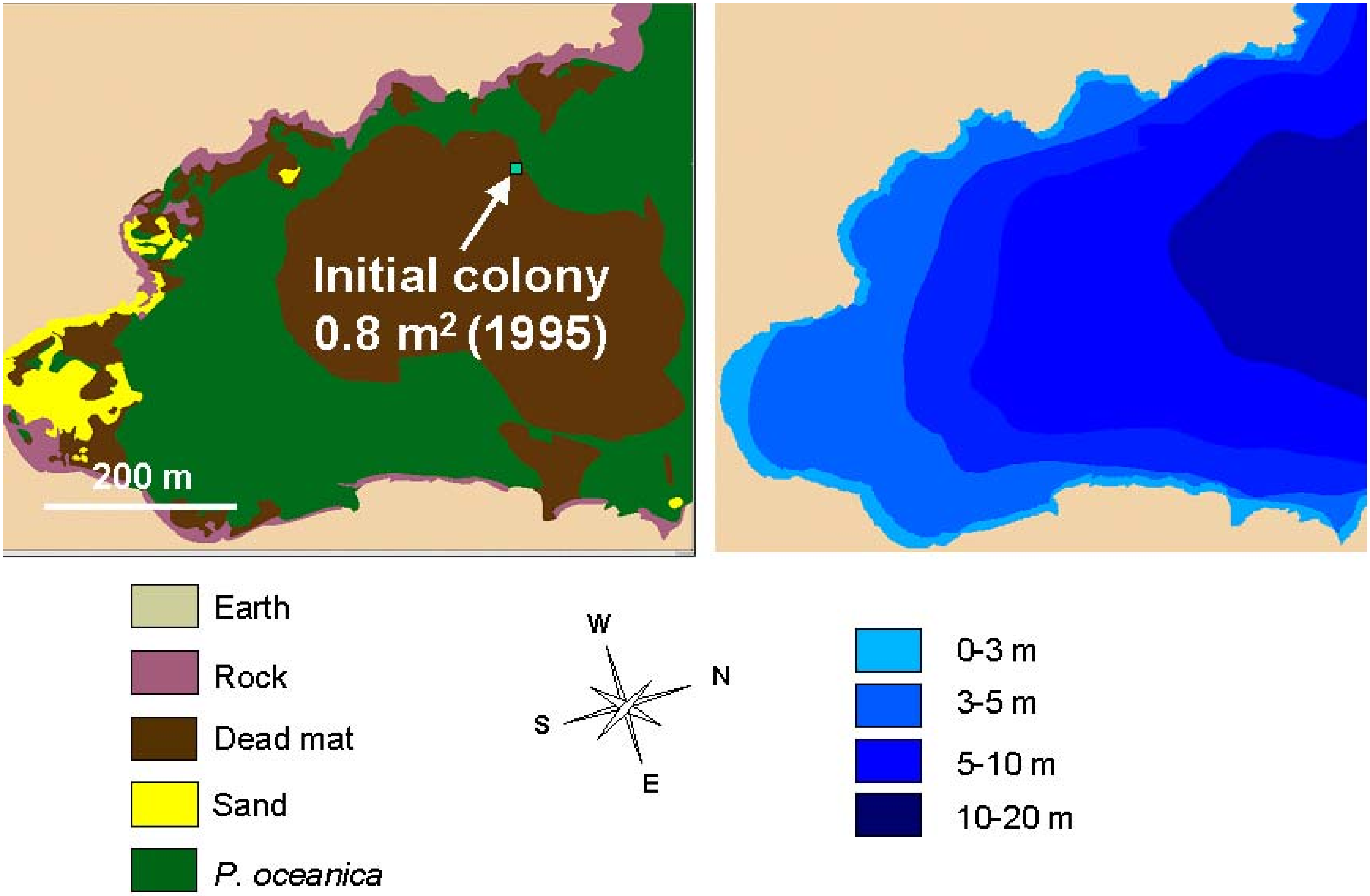


Figure 6. Maps of substrates (A) and depths (B) of the Bay of Port-Man (National Park of Port-Cros).

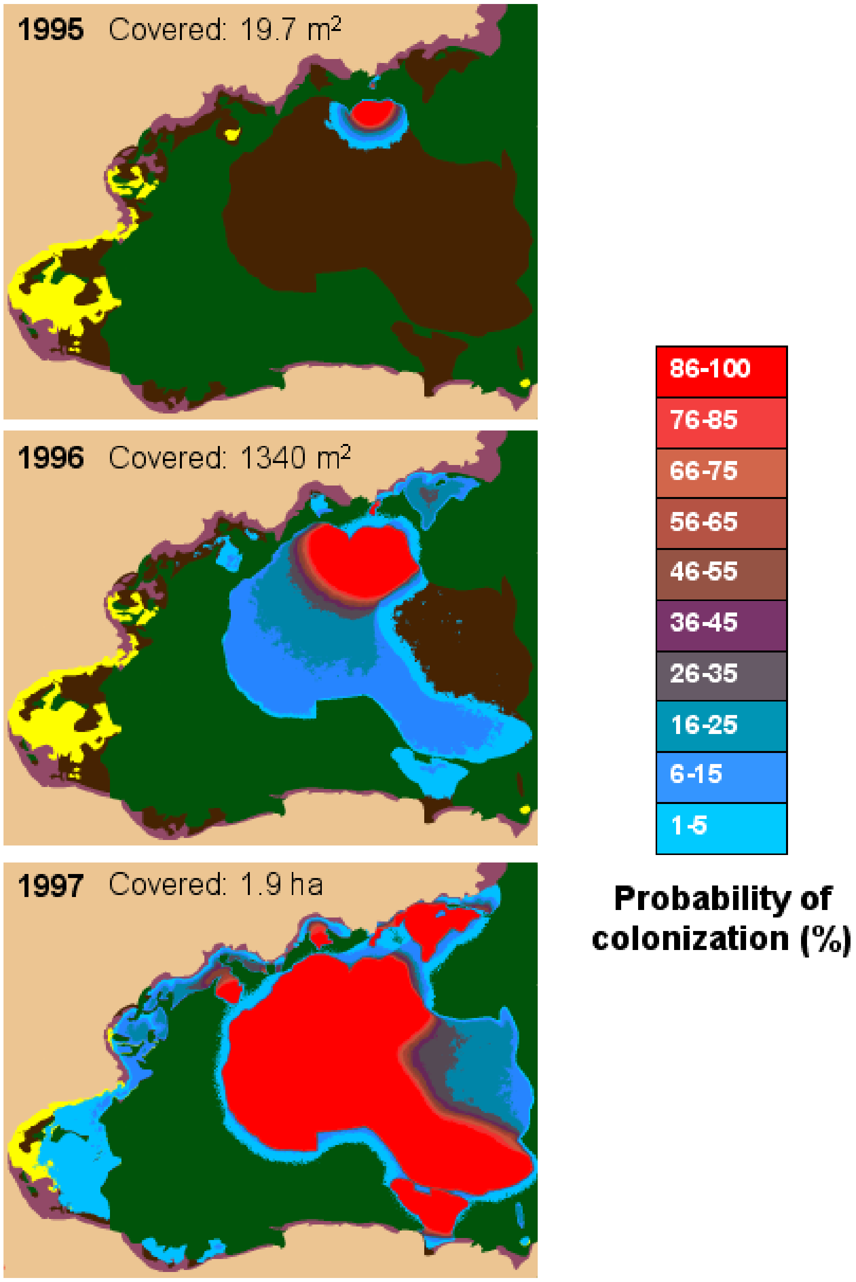
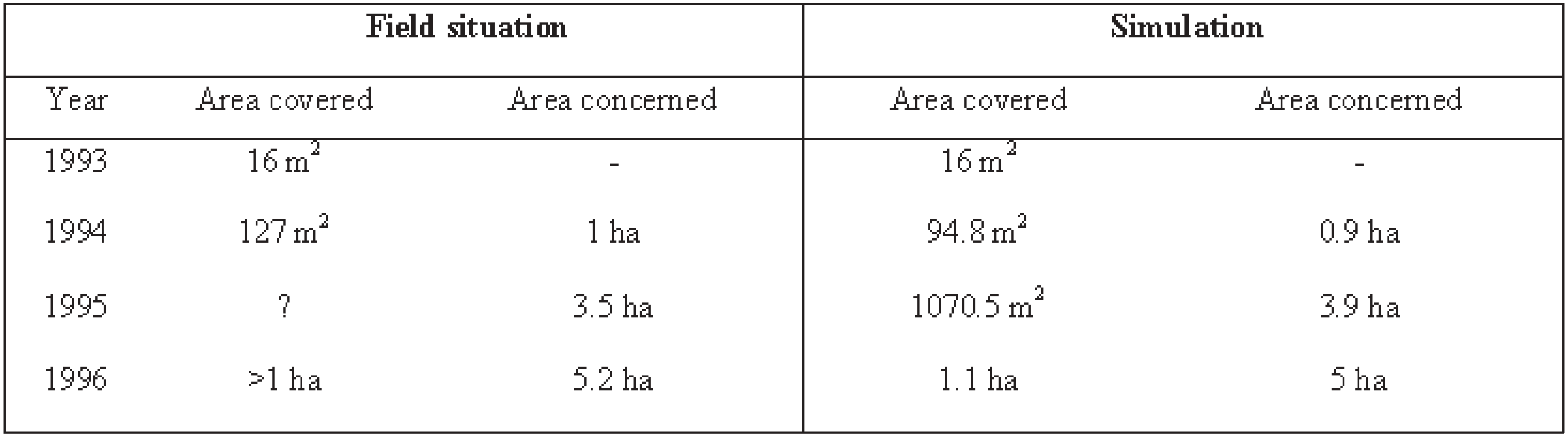


Figure 7. Simulated changes in the distribution of *C. taxifolia* in the bay of Port-Man (National Park of Port-Cros).

Tables . . .

Table 1. **Comparison of the field observations with the simulation results.**



Field situation			Simulation	
Year	Area covered	Area concerned	Area covered	Area concerned
1993	16 m^2	-	16 m^2	-
1994	127 m^2	1 ha	94.8 m^2	0.9 ha
1995	?	3.5 ha	1070.5 m^2	3.9 ha
1996	>1 ha	5.2 ha	1.1 ha	5 ha

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Reproduction of *Caulerpa taxifolia* in the Mediterranean Sea

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The introduced tropical alga, *Caulerpa taxifolia* (Vahl) C. Agardh, has been rapidly spreading since the mid-1980s throughout the Mediterranean Sea (Meinesz and Hesse 1991). This expansion has been the result of many factors including its tolerance of a broad range of substrate, light, temperature, and nutrient conditions as well as a lack of predatory species and extremely successful vegetative reproduction (Boudouresque et al. 1995). Complete regeneration is possible from each part of the thallus: fronds, pinnules, and stolon or hairlike tiny rhizoids. In nature, most of the vegetative reproduction occurs due to frond damage. Storm generated waves can produce numerous fragments, each of them capable of regeneration into a new plant.

At 25ºC, formation of an entire plant including fronds, stolon, and rhizoids from a single frond occurred within 10 days (Fig. 1). At two days, the fragment develops a root cluster near the bottom of the fragment. After four days, a new creeping stolon appears just above the rhizoid clusters. A six-day-old fragment develops a new rhizoid stem on the small creeping stolon. After eight days a new frond will form on the stolon. After ten days of regeneration, a fragment has become a new plant with all morphological elements.

Regeneration is possible also from tiny rhizoids, which are rooted in the sediment. In one experiment, algae growing on a stone was eradicated, but the rhizoids were left in the sediment. Three weeks later, new fronds started to grow directly from the sediment as a result of regeneration from the rhizoids. Regeneration from the rhizoids becomes a great problem during manual eradication of the algae. It is possible that after manual extraction of the algae, tiny rhizoids remain in the sediment and become a source for re-colonization.

During the winter in the Mediterranean Sea, the algae can be damaged due to low seawater temperature. First, a necrosis of the fronds occurs, then all fronds senesce and only a network of creeping stolons remain. By the end, the stolons have disappeared entirely. In that area during the summer, new fronds grow directly from the substrate as a result of regeneration from rhizoids overwintered in the sediment.

Sexual reproduction is quite common for tropical *Caulerpa* populations in their native range. With the introduced strain in the Mediterranean Sea, incomplete sexual reproduction occurs during the summer period where some *C. taxifolia* thalli become fertile (Zuljevic and Antolic 2000). Fertile thalli are easy to detect in the field as a result of reticulate depigmentation of the frond. This is accompanied by the development of papillae usually on the frond axes. The visible changes of pigmentation and appearance of papillae occur about 36 hours before gamete release (Fig. 2), which occurs in the early morning. All fertile plants release their gametes in a short period of 10 minutes, approximately 27 minutes before sunrise. Heavy, overcast skies delayed gamete release for a few minutes. Obviously, release of the gametes is a synchronized event coordinated by the light intensity. The released gametes form a green cloud around the plant, which is dispersed within 5–10 minutes, depending on hydrodynamics. Algae released their entire protoplasmic contents during spawning and died. The empty thalli then disintegrate completely within 2–3 days.

The analysis of gamete samples showed no evidence of successful sexual reproduction: only male gametes without eyespots were observed (the eyespots are a diagnostic feature of *Caulerpa* female gametes). The absence of female gametes with red eyespots is a reason why the fertile thalli are green. If there are female gametes, the fertile thalli become partially brownish. Despite prolific release of male gametes, sexual reproduction does not occur because female gametes are absent. The reason for the absence of female gametes remains unknown.

These unusual features could theoretically be utilized for *C. taxifolia* control. If we could artificially trigger gametogenesis in the field, because of absence of female gametes and death of the parental plants, we could eradicate the algae.

Figures . . .

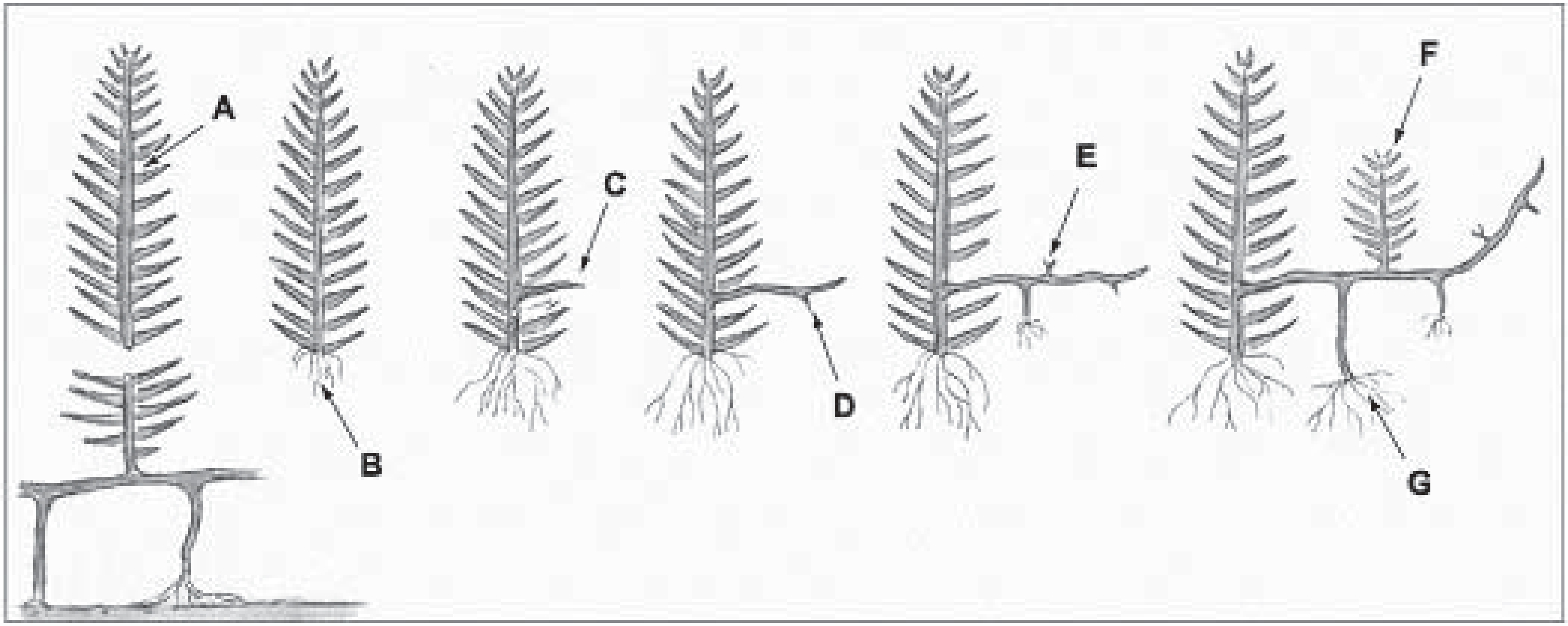

Figure 1. Regeneration of the *Caulerpa taxifolia* from a fragment of frond. (A) fragment, (B) rhizoid cluster, (C) a new stolon, (D) a new rhizoid stem, (E) appearance of a new frond, (F) a new frond, (G) rhizoid cluster.

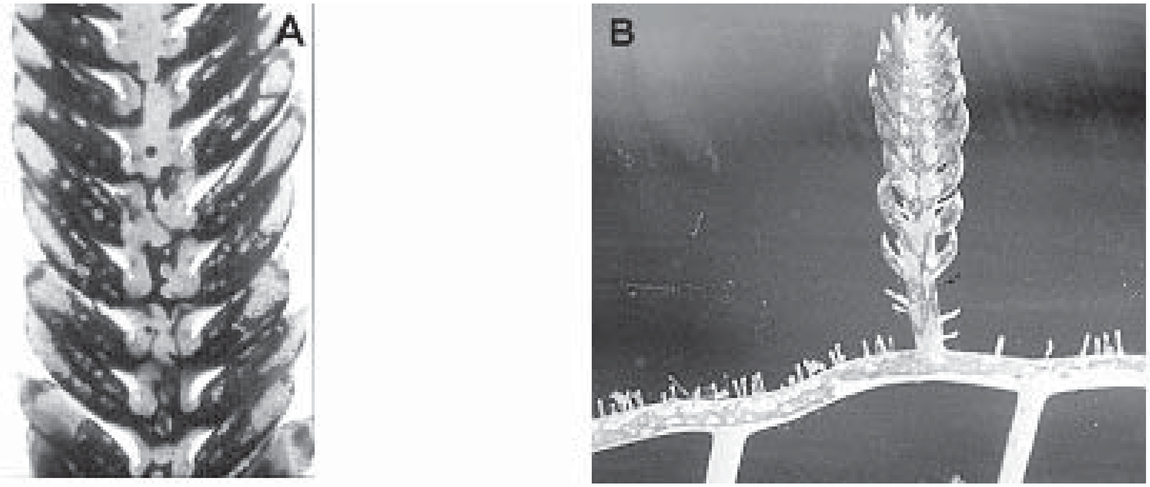

Figure 2. Changes in the thalli of *Caulerpa taxifolia* during gametogenesis around 24 h before gamete release. (A) detail of frond with reticulate depigmentation, (B) reticulate depigmented thalli with papillae.

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Caulerpa taxifolia . . .

Appendix:

Summary of Discussions
Address Information
Additional Photos

Summary of Discussions

I. International Consortium for *Caulerpa* Research

Objectives:

1. Conduct field and mesocosm research on *Caulerpa* in native and invaded habitats
2. Obtain sufficient funds to support international research teams and biannual conference
3. Provide science-based recommendations on methods for control, surveillance, and prevention of introductions and establishment in nonnative habitats.

Research Needs

A. Evaluate eradication methods
B. Define dispersal mechanisms
C. Quantify ecosystem impacts
D. Understand physiology and population genetics
E. Investigate potential biocontrol agents
F. Evaluate recovery/restoration
G. Monitoring existing invasions and detecting new invasions

A. Evaluate Eradication Methods

1. Treatment duration
2. Toxicant concentration
3. Monitoring requirements
4. Minimize environmental costs
5. Minimize economic costs
6. Collateral treatment damage
7. Impact zone
8. Residual toxins
9. Substrate specificity
10. Lab & field data collection on eradication efforts
11. Influence of depth
12. Seasonality & year-to-year variations
13. Need to integrate the above components
14. Investigate influence of currents on treatment efficacy
15. Substrate requirements

B. Dispersal Mechanisms

1. How far, how fast, and by what vectors is *Caulerpa* transported
2. Fragment viability & sexual reproduction
3. Potential of storm, wind, current dispersal
4. Potential animal vectors
5. Human mediated: recreational/marine activity – highest impact; new aquarium introductions
6. Commercial/industrial users/uses
7. Northern limits of temperature range
8. Potential for bio-terrorism with nonnatives

C. Ecosystem Impacts

1. Fish and fisheries, catch data, and surveys
2. Invertebrates communities
3. Seagrasses and other plants (community energetics & function)
4. Vulnerability of communities to invasions
5. Sensitive, rare and threatened & endangered species
6. Habitat modification
7. Physical ecosystem impacts/disturbance
8. Waterfowl & migratory shorebirds
9. Compilation of background information for invaded sites
10. Organism interactions in invaded versus natural areas
11. Water quality & sediment variables

D. Physiology and Genetics

1. Effects of chlorine, salt, herbicides, shading on survival
2. Temperature, salinity, and turbidity influence on growth
3. Genetics of invasive *Caulerpa* and invasiveness
4. Investigate factors controlling sexual reproduction
5. Nitrogen levels and chemical variability
6. Nutrient requirements and influence on growth
7. Contaminant & nutrient load when *Caulerpa* dies
8. Ecosystem magnification of contaminants
9. Bacterial associates & nutrients needed
10. Genetically specific/viral pathogens
11. Survivorship & dormancy cues

E. Biocontrol

1. Herbivore specificity and genetic or environmental basis
2. Herbivore environmental tolerances
3. Herbivore life history characteristics
4. Pathogen survey
5. Potential for antibiotics
6. Focus on slug research due to specificity
7. Herbivore management and grazing

F. Recovery/Restoration

1. Evaluate collateral damage resulting from eradication
2. Monitor recovery over time

G. Looking for New Infestations

1. Side-scan sonar- moderate resolution, ground truthing required
2. Laser- moderate resolution, ground truthing required
3. Aerial Photo- moderate resolution, ground truthing required
4. Diver transects- highest resolution, no ground truthing
5. Towed video- high resolution, occasional ground truthing
6. Single-beam sonar- moderate resolution, ground truthing required
7. Marking of patches for resight- pingers, buoys
8. Manned & unmanned submersibles- fragmentation possible
9. Spectral radiometry- visibility limited, substantial ground truthing required
10. Sonar triangulation
11. Multi-beam sonar
12. Chemical indicators
13. Predictive modeling

II. Management Options for *Caulerpa taxifolia* Invasions in Southern California

1. Need to attach expected recovery time to each category and percent of area treated in given water body
2. Longer it takes to restore habitat, the longer the social/economic impacts on the community
3. Social, economic, and ecological impacts are dependent on size and use of harbors
4. Need to examine consequences of *Caulerpa taxifolia* infestation versus treatments (no action alternative)

A. Physical Management Options

1. Manual removal
    a. Ecological impacts- very few
    b. Social impacts: continued surveillance needed

2. Suction Dredge
    a. Air lift versus water lift
        1. air pump a problem
        2. air lift is more feasible, but less effective
        3. water keeps pieces more intact, less fragmentation
    b. Limited by visibility
    c. Limited by seasonal growth patterns
    d. Limited by type of substrate
    e. Moderately successful in small patches
    f. Ecological impacts: dependent upon area size; likely greater than manual; toxic, unicellular algal blooms may follow; resuspension of toxins
    g. Social impacts: interference with other uses, odors, disposal of dredge spoils

3. Barricade and Treat
    a. Most likely for success in AHL depending upon treatment chosen
    b. Create wall between lagoons (inner and outer) with rock or sheet and treat entire lagoon
    c. Use filter fabric or perforated barrier
    d. Need two miles of fabric, may get fouled
    e. Limited by visibility, flow
    f. Better used in low-lying, smaller development area

- g. Ecological impacts: severe, but expected shorter term, perceived greater impact in lagoons with Endangered Species; migratory species recruitment or colonization
- h. Social impacts: cultural, traditional concerns; visual impact; safety; property values, odor; health concerns; alternate housing may be needed during treatment

4. Drain and Excavate
    - a. Likely to be successful in Huntington Harbour; closed environment
    - b. Consider for inner basin, specific to particular harbor
    - c. Depth of sediment a limitation, dredge to 0.5 meter
    - d. Dredge spoil disposal a consideration
    - e. May need to be repeated at some frequency
    - f. Ecological impacts: severe, but expected shorter term, perceived greater impact in lagoons with endangered species; migratory species recruitment or colonization;
    - g. Social impacts: cultural, traditional concerns; visual impact; safety; property values, odor

5. Cover with Tarp
    - a. Likely to be successful in lagoons
    - b. Safety margin is possible
    - c. Advantages: safety margin is possible; growth through tarp unlikely
    - d. Limited by wave and tidal action
    - e. Flat environment is best, but some success with vertical tarping with a higher density foil
    - f. Ecological impacts: likely to be less than other methods, but dependent on area tarped
    - g. Social impacts: some disruption during installation, surveillance will be needed

6. Sand
    - a. Not likely to be successful on open coast
    - b. Water displacement and fragmentation possible
    - *c. Caulerpa* may be able to grow in it; needs to be thick
    - d. Energy limited, not recommended by Mediterranean workers
    - e. California: some patches have 5 inches of sand cover and have not regrown
    - f. Likely to be more expensive than tarping

g. Ecological impacts: likely to be less than other methods, but effects of additional sand unknown, area dependent
h. Social impacts: some disruption during installation, surveillance will be needed

7. Detection and Monitoring
    a. Critical methodology needed for long-term
    b. Ecological impacts: none
    c. Social impacts: monitoring interferes with recreational uses

B. Chemical Management Options

1. Chlorine and tarp
    a. Likely to be highly successful
    b. Liquid is cheap and reduces biomass quickly, bleaches from bottom up
    c. Liquid is more effective than pucks, faster gas release
    d. Treat with high saline water and Rodamine to monitor and keep chlorine in place
    e. Chlorine gel may be an option though expensive
    f. Chlorine is temperature sensitive
    g. Chlorine is less effective in anoxic conditions or high turbidity
    h. Ecological impacts: kills everything
    i. Short-term effects: degrades habitat

2. Copper Sulfate
    a. Machine application- low dose applied, expensive, boat required, increases fragmentation
    b. Soaked cloth- easy to use in aquatic systems, no boat needed for small patches, useful in deeper areas
    c. Kills rapidly, but likelihood of long-term success unknown
    d. Ecological impacts: unknown, may have long-term toxicity

3. Salt
    a. Dissolves quickly, easy to deploy
    b. Labor intensive, boat support needed
    c. Effective in some situations
    d. May not work well on below ground growth in soft sediments

4. Acetic acid
    a. May be promising, but difficult to see kill

5. Lime
    - a. Effectiveness unknown; not effective with *Codium*

C. Thermal Management Options

1. Dry Ice
    - a. Not applicable
2. Hot Water
    - a. Not feasible in most cases
3. Cold Water
    - a. Not feasible in most cases

D. Biological Management Options (only for long-term control)

1. *Oxynoe* species
    - a. May not be effective
2. *Elysia* species
    - a. May not reproduce and be effective
3. Other species
    - a. South Florida species that are more resistant to temperate conditions
    - b. Others that could be transported with El Niño
4. Induce sexual reproduction
    - a. Potentially useful, but no mechanism for induction yet

III. Outreach and Education Efforts and Needs for *Caulerpa taxifolia*

There were numerous discussions regarding outreach efforts to increase *Caulerpa taxifolia* awareness. The ideas resulting from the final session of the conference, as well as suggestions made specifically by Ted Grosholz, Alan Millar, and Alex Meinesz, are listed below. The order of topics is not meant to reflect priorities.

Strategic Plan Approach

A. Identify issues
B. Establish goals
C. Articulate objectives
D. Delegate tasks
E. Implement plan
F. Measure of success

A. Issues

1. The eradication effort needs broad public support for continued viability
2. Honesty and education about non-eradication possibility & time frame of efforts
3. Prevention of new introductions (mechanical and source)
4. Engage industry & educational institutions to help with solution to prevent new introductions of invasive species by developing collaboration & cooperation
5. Identification guides for public
6. Visible consensus regarding the problem & solution among academic & regulatory groups
7. Importance of central location for information, reporting & local contacts available (avoid duplication)
8. Gather ideas from birders re: organization
9. Audience identification; venue id; educational medium for communication of info (seasonality of education; school/summer holidays)
10. Know what message you want to communicate

B. Goal: To educate the public and key individuals/ decision makers on the need to eradicate *Caulerpa* from California.

C. Objectives

1. Increase awareness, commitment, leadership in recreational public
2. Educate and involve aquarium industry regarding alternatives to *Caulerpa spp*.
3. Develop new management practices to minimize future introductions
4. Educate agencies, wardens, and customs staff about regulations and findings of *Caulerpa spp*.

D. Tasks: Identify outreach audiences, educational techniques, and venues.

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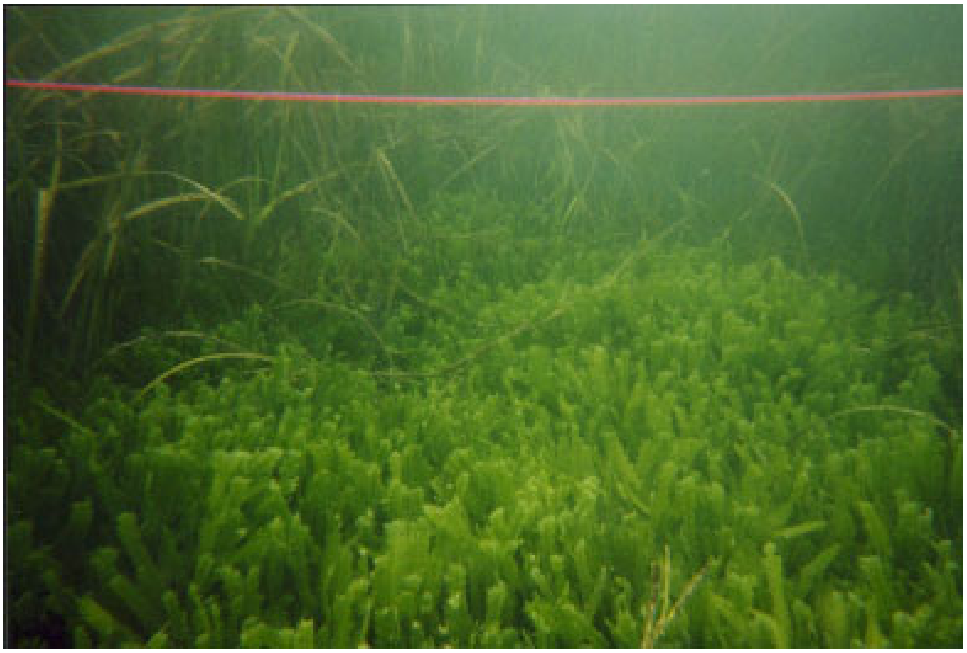
Additional Photos

California



Large patch of *Caulerpa taxifolia* found within an eelgrass bed in Agua Hedionda Lagoon, California. *Photo by Merkel and Associates.*

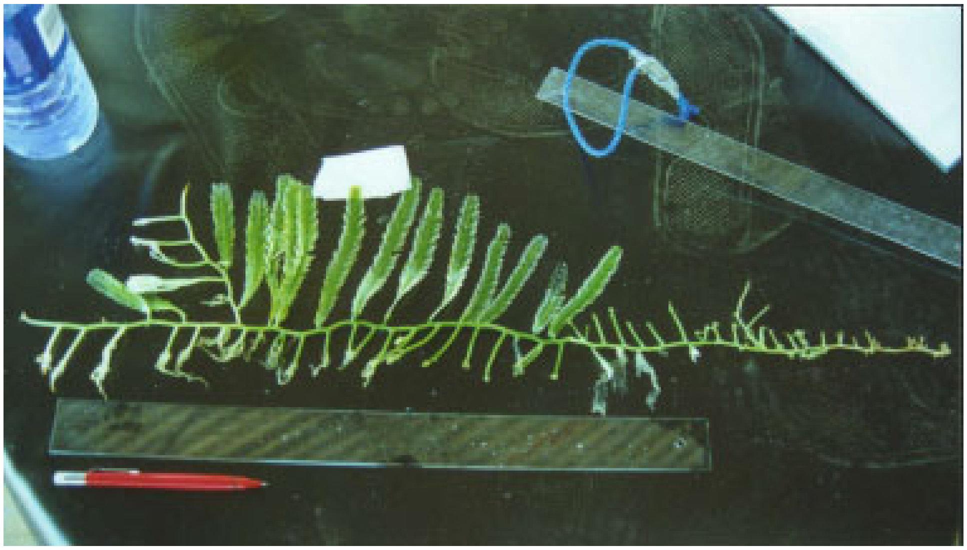
Chlorine pucks being placed on *Caulerpa taxifolia* before a black containment tarp was placed over the area. *Photo by Merkel and Associates.*

Decorator crab with *Caulerpa taxifolia* fragments on it. *Photo by Merkel and Associates.*

Caulerpa taxifolia patch found in Huntington Harbour, California. *Photo by Merkel and Associates.*

Site of *Caulerpa taxifolia* infestation in Huntington Harbour, California. *Photo by Lars Anderson.*

Huntington Harbour, California. *Photo by Lars Anderson.*



Caulerpa taxifolia plant. *Photo by Merkel and Associates.*

Sandbags surrounding an eelgrass bed in a *C. taxifolia* infested area. *Photo by Merkel and Associates.*

Snug Harbor (part of Agua Hedionda Lagoon) overview. Bright green patches are areas of *Caulerpa taxifolia*. *Photo by Merkel and Associates.*

Diver preparing to inject chlorine under a tarped patch of *Caulerpa taxifolia*. *Photo by Merkel and Associates.*

Tarped patch of *Caulerpa taxifolia*. *Photo by Merkel and Associates.*

Transect lines swum by divers at Snug Harbor in Agua Hedionda Lagoon to survey for *Caulerpa taxifolia*. *Photo by Merkel and Associates.*

Mediterranean

All photos by Alex Meinesz.

Boat anchor on *Caulerpa taxifolia* bed.

Caulerpa taxifolia growth on algae.

Caulerpa taxifolia growth on invertebrate in the Mediterranean.

Caulerpa taxifolia in the Mediterranean.

Caulerpa taxifolia growth on invertebrate in the Mediterranean.

Caulerpa taxifolia in the Mediterranean.

Caulerpa taxifolia in the Mediterranean.

First patch of *Caulerpa taxifolia* (invasive strain) was discovered outside of the Monaco Aquarium in 1984.