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PREDICTING RISKS OF INVASION OF *CAULERPA* SPECIES IN FLORIDA

by

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A thesis submitted in partial fulfillment of the requirements
for the degree of Master of Science
in the Department of Biology
in the College of Arts and Sciences
at the University of Central Florida
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ABSTRACT

Invasions of exotic species are one of the primary causes of biodiversity loss on our planet (National Research Council 1995). In the marine environment, all habitat types including estuaries, coral reefs, mud flats, and rocky intertidal shorelines have been impacted (e.g. Bertness et al. 2001). Recently, the topic of invasive species has caught the public's attention. In particular, there is worldwide concern about the aquarium strain of the green alga *Caulerpa taxifolia* (Vahl) C. Agardh that was introduced to the Mediterranean Sea in 1984 from the Monaco Oceanographic Museum. Since that time, it has flourished in thousands of hectares of near-shore waters. More recently, *C. taxifolia* has invaded southern Californian and Australian waters. Since the waters of Florida are similar to the waters of the Mediterranean Sea and other invasive sites my study will focus on determining potential invasion locations in Florida. I will look at the present distribution of *C. taxifolia* - native strain in Florida as well as the distribution of the whole genus around the state. During this study, I address three questions: 1) What is the current distribution of *Caulerpa* spp. in Florida? 2) Can I predict the location of potential *Caulerpa* spp. invasions using a set of environmental parameters and correlate them to the occurrence of the algae with the support of Geographic Information System (GIS) maps? 3) Using the results of part two, is there an ecological preferred environment for one or all *Caulerpa* spp. in Florida? To answer these questions, I surveyed 24 areas in each of 6 zones chosen in a stratified manner along the Floridian coastline to evaluate the association of potential indicators *Caulerpa*. Latitude, presence or absence of seagrass beds, human population density, and proximity to marinas were chosen as the 4 parameters expected to correlate to *Caulerpa* occurrences. A logistic regression model assessing the association of *Caulerpa* occurrence with measured variables has been developed to predict current and future probabilities of *Caulerpa* spp. presence throughout the

state. Fourteen different species of *Caulerpa* spp. were found in 26 of the 132 sites visited. There was a positive correlation between *Caulerpa* spp. and seagrass beds presence and proximity to marinas. There was a negative correlation with latitude and human population density. *C. taxifolia* – aquarium strain wasn't found. Percent correct for our model was of 61.5% for presence and 98.1% for absence. This prediction model will allow us to focus on particular areas for future surveys.

To my wife Gail, to my daughter Jodie
and to my family in Switzerland for their prayers, their love and their support.

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GENERAL INTRODUCTION

Biological invasions

The introduction of alien, or non-indigenous, species into terrestrial and aquatic habitats has been recognized as a major problem for over 100 years (e.g. Bax et al. 2001; Loope & Howarth 2003; Barnard & Waage 2004; Perrings et al. 2005). Scientists around the world have identified alien species as a major threat to biodiversity with dramatic effects on biological diversity, productivity, and habitat structure (Carlton 1999; Wilcove et al. 1998). Besides reducing biodiversity, alien species can act as vectors for new diseases and can alter ecosystem processes; consequently, they can cause major economic losses (Vitousek et al. 1997; Mack et al. 2000). Today, alien invasions are second only to habitat loss as a cause of species endangerment and extinction (ISSG 2000). When species are transported outside their original geographic ranges, many of them become established and spread (Loope 2004). Inhabiting new environments, they are often free of predators, competitors, parasites, and diseases that limit their populations in their native regions (Elton 1958; Debach 1974; Mack et al. 2000; Keane & Crawley 2002).

The ever-increasing transport of species of all kinds is breaking down biogeographical boundaries with profound consequences on indigenous ecosystems worldwide (e.g. Vitousek et al. 1997; Mooney & Hobbs 2000). Globalization has been cited as one of the primary causes of biological invasions (Perrings et al. 2005). The growth and development of the world trade system has resulted in a sharp increase in the number of new species being introduced to ecosystems and the frequency with which such introductions are made (e.g. Jenkins 1996; McNeely 2001; Perrings et al. 2002). The growing volume of transported goods, increasing efficiency and speed, and advancing technologies such as containerization and trade agreements

are key components of the phenomenon and are making detection and interception strategies very difficult to implement and maintain (Bright 1999; Campbell 2001; Loope & Howarth 2003). On top of this, global climate change is likely to exacerbate the problem, favoring invasive nonnative species over native species by shifting the distribution of suitable areas for many species (Mooney & Hobbs 2000; Williams et al. 2004). For example, when an ecosystem's temperature range changes due to the global warming, newly introduced species coming from warmer locations may be better adapted than the native ones and have an evolutionary advantage.

Effective programs to control alien species must be developed, because the invasions threaten the long-term sustainability of native ecosystems and have economic, ecological, recreational, and other associated costs (Bax et al. 2001). Indeed, the direct financial costs alone extend into the billions of dollars (U.S.) each year (Barnard & Waage 2004). Pimentel et al. (2000, 2005) estimated that 50,000 non indigenous species have been introduced into the United States alone, causing annual economic losses totaling up to \$120 billion in agriculture, forestry, and other segments of the economy, including public health.

Introductions of species into new environments have likely been occurring ever since man has moved to new locations (Carlton 2001; Wallentunus et al. 2002). However, the speed of today's transportation increases the chances of survival of accidentally introduced species and makes it easier for both planned and unplanned introductions (Carlton 2001; Wallentunus et al. 2002). History is rich with tales of the disastrous outcomes of some intentional introductions (GISP 2003). Invasive species can be found in all taxonomic groups, and combined they are able to invade any native biota anywhere in the world (McNeely 2001). For instance, in a publication from the World Conservation Union, the Invasive Species Specialist Group (ISSG) lists 100 organisms as the world's worst invasive alien species (Lowe et al. 2000). Among them are terrestrial invaders such as *Anoplolepis gracilipes*, the crazy ant (Lowe et al. 2000). The crazy

ants, so called because of their frenetic movements, have invaded native ecosystems and caused environmental damages from Hawaiï to the Seychelles and Zanzibar (ISSG 2000). The ants forage in all habitats including the rainforest canopy, decimate land crab *Gecarcoidea natalis* populations and prey on, or interfere in, the reproduction of a variety of arthropods, reptiles, birds and mammals on the forest floor and canopy (ISSG 2000). Scientists are concerned that endangered birds such as the Abbott's booby *Sula abbotti* of the Christmas Islands, which nest nowhere else in the world, could eventually be driven to extinction through habitat alteration and direct attack by the ants (ISSG 2000). Another example of unintentional terrestrial species introduction is the brown snake *Boiga irregularis* in Guam, which was accidentally introduced to snake-free Guam immediately after World War II, via military equipment moved onto Guam (Fritts and Rodda 1995). Soon the snake population reached densities of 100 per ha, and dramatically reduced native bird, mammal, and lizard populations (Pimental et al. 2005). Of the thirteen species of native forest birds originally found on Guam, only three species still exist (Rodda et al. 1997); of the twelve native species of lizards, only three retain the possibility of surviving (Rodda et al. 1997). The snake crawls up trees and utility poles, causing power outages on the island that cost the power utility companies more than \$6 million per year (Coulehan 1987; Pimental et al. 2005). In addition, the brown snake is slightly venomous, and has caused public health problems, especially with children (Pimental et al. 2005). Among other terrestrial invaders are the strawberry guava *Psidium cattleianum* in Florida and the small Indian mongoose *Herpestes auropunctatus* in the Caribbean Islands (Lowe et al. 2000).

In freshwater environments, one of the best-known examples of unanticipated environmental and socioeconomic impact is the infestation of Lake Victoria in Africa by two plants, the water hyacinth *Eichornia crassipes* and giant salvinia *Salvinia molesta* (Lowe et al. 2000). It started when the Nile Perch *Lates niloticus* was introduced to Lake Victoria in 1954 and

contributed to the extinction of more than 200 endemic fish species (Lowe et al. 2000). The Nile perch was introduced to counteract the drastic drop in native fish stocks caused by overfishing (IUCN 2001). The flesh of Nile perch was oilier than that of the local fish; consequently more trees were felled to fuel fires to dry the catch (IUCN 2001). The subsequent erosion and runoff contributed to increased nutrient levels, opening the lake up to invasions by algae and *E. crassipes* (IUCN 2001). These invasions in turn led to oxygen depletion in the lake, which resulted in the death of more fish (IUCN 2001). The far-reaching impacts of these three introductions have been devastating for the environment as well as for communities that depend on the lake for their survival (ISSG 2000). Finally, as examples of invasions in the marine environment, we know the Japanese eelgrass *Zostera japonica* that settled on the Pacific coast of the United States of America and the green alga *Caulerpa taxifolia* (Vahl) C. Agardh (Figs. 1, 2) that invaded the Mediterranean Sea (Lowe et al. 2000).

Fortunately, not all alien species successfully invade new areas. For instance, the green alga, *C. taxifolia*, has entered many waterways worldwide, but did not make it through the cold winter temperatures in the Sea of Japan (Komatsu et al. 2003). The habitats more likely to be invaded are usually vacant or under-utilized niches, have low species richness, have increased human disturbance regimes, or are inherently less competitive than the community from which the invader originated (Elton 1958; Lonsdale 1999; Callaway & Aschehoug 2000; Levine 2000; Daehler 2003).

Invasions in the marine environment

In the aquatic environment, species may enter a community mechanistically in two ways – by natural movements or by human-mediated events (Bertness et al. 2001). Natural movements generally include two dispersal mechanisms (Bertness et al. 2001); the first involves organisms

drifting to new habitats via water currents (e.g. planktonic stages, rafting) while the second mechanism involves marine organisms entering communities by moving along new corridors created by tectonic events or climatic conditions (Bertness et al. 2001). Human-mediated invasions include five important categories: (a) hull fouling and discharges of ballast water and sediments from ships, (b) the aquaculture, bait, and aquarium industries (c) commercial, government, and private endeavors (pleasure boat, biocontrol, ornamental plants and fishes in private aquaria), (d) scientists (moving experimental organisms and scientific equipment), and (e) man-made canals (Bertness et al. 2001).

Marine environments differ from terrestrial ones in several respects concerning successful establishment of non-native species (Wallentunus et al. 2002). They have more benign winters and less extreme summer heat, facilitating survival as well as easier dispersal of propagules, larvae and even adults with currents (Wallentunus et al. 2002). It is extremely difficult to find an efficient method to eradicate an invasive species once it has become established in new waters; furthermore, many methods of eradication used in the terrestrial ecosystems such as mechanical control (harvesting, removal, fencing) or chemical control (pesticides) cannot be used in marine ones (Wallentunus et al. 2002). In the continental U.S., all four coasts—east, west, Gulf and Great Lakes—and the majority of the interior of the United States have been impacted by aquatic invasive species (NSG 2003). Aquatic invasive species may constitute the largest single threat to our coastal ecosystem, our coastal economy, and human health in the coastal region (NSG 2003).

The history, diversity, distribution, and effects of marine invasions are poorly known for most coasts of the world, and invasions that occurred prior to 1850 remain largely ignored (Carlton 1999). Scientists have only recently begun to realize the magnitude of the problem (e.g. Carlton 1999; Ruiz et al. 1999; Perrings et al. 2005; Pimentel et al. 2005). Invasive species are one of the most difficult marine environmental issues we face, with the potential to impose

greater mortality on fish stocks than overharvesting, and greater changes to habitats than any extreme physical disturbance (Bax et al. 2001).

Invasive Caulerpa species

Hundreds of non-indigenous species have established populations in aquatic habitats in North America (e.g. Ricciardi & Rasmussen 1988; Pimentel et al. 2000, 2005). However, it appears that macroalga introductions have received less attention when compared with terrestrial invaders, introduced marine invertebrates and invasive salt marsh plants (Zaleski & Murray, in press). One exception is the aquarium strain of *Caulerpa taxifolia* (Vahl) C. Agardh (Figs. 1, 2). Additionally, other species in the same genus, *C. racemosa* (Fig. 3), *C. brachypus* (Fig. 4) and *C. scalpelliformis* (Fig. 5) have also been reported as invaders in the Mediterranean Sea, southeastern Florida and Australia, respectively (Davis et al. 1997; Schrope 2003; Verlaque et al. 2003).

Historic of Caulerpa species invasions

Caulerpa taxifolia - aquarium strain is known worldwide as the “killer alga” (Figs. 1, 2). This emphasizes its particular invasive ability (Jousson et al. 2000). In the late 1970s, *C. taxifolia* – aquarium strain attracted attention as a fast-growing and decorative for aquariums and was popular in the saltwater aquarium trade (Woodfield 2002). A clone of this species was cultured for display at the Stuttgart Aquarium in Germany and was provided to aquariums in France and Monaco (Woodfield 2002). In 1984, this species was released, probably as waste, from the Monaco Oceanographic Museum into Mediterranean waters (Meinesz & Hesse 1991). It spread from an initial patch of approximately one meter square to over 13,000 ha, bordering six countries by the end of 2000 (Spain, France, Monaco, Italy, Croatia and Tunisia) (Meinesz &

Hesse 1991; Meinesz et al. 2001). In France, in the summer of 2001, more than 30 new independent areas of colonization were discovered (Meinesz 2002) (Fig. 6).

The initial one square meter of area covered by *C. taxifolia* was originally ignored because scientists thought that it would die as the waters cooled down during the winter months (Meinesz 1997). However, we now know that this species had already become adapted to colder waters, having spread throughout the northern Mediterranean (e.g. Relini et al. 2000; Meinesz 2002). Wherever it has established itself, it smothered local flora, including beds of native seagrass *Posidonia oceanica*, that served as a nursery for many commercially important species and has overgrown all native flora and fauna, impacting fisheries and tourism in coastal communities (e.g. Relini et al. 2000; ISSG 2000; Meinesz 2002).

On 12th June 2000, divers in the Agua Hedionda Lagoon near San Diego, California, in the United States discovered a patch of *C. taxifolia* – aquarium strain measuring 20 meters by 10 meters (Jousson et al. 2000). It was thought that the infestation occurred after somebody, probably a resident, emptied a fish tank into a storm-water drain (Raloff 2000). Millions of dollars have been devoted to eradicate this invader in California by bleaching (Woodfield pers. com.), and during their fall 2002 survey, no *Caulerpa* was found for the first time (Merkel and Associates 2002). Nevertheless, the 2003 fact sheet on *Caulerpa* produced by the National Marine Fisheries Service explained that long-term monitoring will be necessary to assure complete eradication, because *Caulerpa* infestations can regenerate from very small fragments (Smith & Walters 1999). Eradication was declared complete in the fall of 2005 at a cost of over 5 million dollars (Walters et al. in press).

Caulerpa taxifolia – aquarium strain was also observed in New South Wales, Australia, in 2000 in the Port Hacking, Careel Bay and Lake Conjola regions (Grey 2001; Wiedenmann et al. 2001; Millar & Talbot 2002; Schaffelke et al. 2002). Once again it is suspected that human

activities, either boating or aquarium releases, or a combination of the two, were responsible for these invasions (Dalgetty 2005). To this day the battle continues to control the spread and hopefully eradicate *C. taxifolia* – aquarium strain in Australian waters (Dalgetty 2005).

Caulerpa racemosa (Forsskål) J. Agardh, has also recently been the object of the scientists' attention. Three taxa occur in the Mediterranean Sea and one of them is invasive (Verlaque et al. 2003). It is currently undergoing a dramatic and continuous expansion throughout most of the Mediterranean (Verlaque et al. 2000). On the basis of morphological and molecular studies, Verlaque et al. (2003) confirmed that this invasion was the result of a recent introduction and identified the invasive variety as *C. cylindracea* (currently known as *C. racemosa* var. *laetevirens* f. *cylindracea* (Sonder) Weber-van Boose). This Mediterranean invasion is even more widespread than that of the highly publicized *C. taxifolia* (Verlaque et al. 2003). Within a few years after its introduction, the first significant signs of a negative impact on some communities and human activities were reported (Balata et al. 2000; Cecere et al. 2000; Ceccherelli et al. 2001; Magri et al. 2001; Piazzini et al. 2001). *Caulerpa racemosa* has been considered a lessepsian migrant (*i.e.* from the Red Sea via the Suez Channel) (Lipkin 1972); it colonized many years ago the eastern Mediterranean Sea (Hamel 1926; Aleem 1948) and has recently spread in the western part of the basin (Piazzini et al. 1994, 1997; Gambi & Terlizzi 1998; Modena et al. 2000), where it is considered a new introduction (Verlaque et al. 2000, 2003).

Both *C. racemosa* and *C. taxifolia* are strong competitors (Piazzini & Ceccherelli 2002). In colonized areas, they tend to eliminate native species and create monospecific beds (Verlaque & Fritayre 1994; Piazzini et al. 2001). Until recently, *C. racemosa* and *C. taxifolia* invasions have only been studied separately because of their different distributions. This changed when the two species of *Caulerpa* came into contact along the Tuscany coast near Leghorn in 1996 (Piazzini &

Ceccherelli 2002). It became evident that where both species co-occur, *C. racemosa* was favored (Piazzini & Ceccherelli 2002).

Caulerpa brachypus is native to the tropical and subtropical Indo-Pacific, ranging from Africa to the Philippines and Australia (Cordero 1977; Sartoni 1978; Sanderson 1997). In its native locations, *C. brachypus* is locally abundant and is occasionally growing in seagrass beds or attached to scattered rocks on deep sand plains (Littler & Littler 2000). It is found up to 30 meters deep (Littler & Littler 2000). The invasive *C. brachypus* was first reported in the West Palm Beach area of Florida in 2001, where it was already abundant (Schrope 2003; SFER 2005). Previously, it had been discovered in the Caribbean Basin (Littler & Littler 2003). In Florida it was widespread in waters 20 to 40 meters deep and overgrew and displaced other macroalgae, sponges, and corals (SFER 2005). The vectors of introduction in both the Caribbean and Florida are unknown; aquarium releases, hull fouling, and ballast water have all been suggested (Schrope 2003). In Florida this species spread north into the Indian River Lagoon system (Schrope 2003), which was consistent with prevailing coastal currents, but it has not yet been reported in the Florida Keys or on the west coast of Florida (L.J. Walters pers.com.). However, this invasive species was stopped or at least limited by Hurricanes Frances and Jeanne that battered Florida in August and September 2004 (B. LaPointe pers. com.).

Finally, we also know of the rapid spread of the green alga *Caulerpa scalpelliformis* (R. Brown ex Turner) C. Agardh that follows its establishment in Botany Bay (Australia) (Davis et al. 1997). In February 1996, this alga occupied at least 0.35 hectares of the substratum within the Bay (Davis et al. 1997). Within twelve months of the appearance of the alga at Inscription Point, it had reached an average cover of $56 \pm 11\%$ with an estimated average fresh biomass of $5.2 \pm 1.1 \text{ kg m}^{-2}$. Over the same time period, the average cover of sessile invertebrates declined from 48 to 23% (Davis et al. 1997).

Biology of Caulerpa

In order to better understand the ecology of this species, a closer examination of its biological characteristics is needed. *Caulerpa* species are coenocytic, multinucleate green algae, native to the Caribbean and other tropical oceans and seas of the world, including Australia, Brazil, Ceylon, Indonesia, Philippines, Tanzania and Vietnam (Ramey 2001). Some members of the genus *Caulerpa* are also native to Hawaii, the Philippines, Tahiti, south Florida and the Gulf of Mexico (e.g. Littler et al. 1989; Littler & Littler 2002). In native habitats, individuals grow in small patches and do not cause problems (Ramey 2001). *Caulerpa* spp. protect themselves by producing chemicals that are toxic to potential predators such as the two main macro-herbivores in the Mediterranean Sea, the sea urchin *Paracentrotus lividus* and the snail *Sarpa salpa* (Lemee et al. 1993).

Little is known about the nutrient dynamics of *C. taxifolia* and other *Caulerpa* species (Chisholm et al. 1996). It appears that they can utilize nutrients and carbon sources from the sediment by uptake through the rhizoids and associated bacteria (Chisholm et al. 1996), even in eutrophicated, anoxic sediments (Chisholm & Jaubert 1997). Some species in the genus are tolerant to shading conditions ($27 \mu\text{mol m}^{-2}\text{s}^{-1}$ at a photoperiod cycle of 14h light and 10h dark) (Komatsu et al. 1997), enabling growth in areas where photosynthesis is light-limited for most macroalgae as a result of greater depths.

Caulerpa taxifolia (Figs. 1, 2) has branches that are feather-like, flattened, and rise from creeping stolons anchored by rhizoids to the substrate (Littler et al. 1989). This species was found in sand on reef flats or in fine sediments adjacent to mangroves in sheltered or moderately wave-exposed areas to 15 m deep (Littler et al. 1989). In its native waters, individuals are small (blade height: 3-15 cm), isolated, and generally uncommon (Littler et al. 1989). Average densities of its invasive counterpart are reported to have much greater biomass, exceeding 4,700 stolons and

9,000 fronds/m² and as high as 27,000 stolons and 95,000 fronds/m² which are the highest reported for *C. taxifolia* anywhere (Wright 2005). Like many other siphonous algae, sexual reproduction is limited in this species and the majority of propagation is via asexual vegetative fragmentation (e.g. Walters & Smith 1994; Ceccherelli & Cinelli 1999; Smith & Walters 1999). When cut, wounded or punctured, fragmented blades of Hawaiian *C. taxifolia* as small as 10 mm in length were successful at vegetative fragmentation (Smith & Walters 1999).

The invasive, aquarium strain of *C. taxifolia* can grow on many kinds of substrates, including rocks, sand, mud and dead rhizomes of seagrasses (Meinesz et al. 1993; de Vaugelas et al. 1999). This clone can grow larger, and in deeper and colder waters than the tropical populations of the species, and the clone forms continuous meadows from the surface to more than 30 m deep (Meinesz 1997). Isolated individuals have been found in water to 100 m deep (Boudouresque et al. 1995). Unstable substrates such as ripple-marked sediments and shallow rocky shores exposed to strong wave action seem to be some of the rare exceptions where *C. taxifolia* cannot become established (de Vaugelas et al. 1999). It frequently co-occurs with seagrasses (Smith & Walters 1999; Williams 1984, 1990). *C. taxifolia* – aquarium strain is also known for being concentrated to zones where heavy development took place or in the vicinity of poorly-treated wastewater (Chisholm et al. 1997).

Caulerpa racemosa is one of the most ubiquitous species in this genus (Littler et al. 1989). It forms intertwined mats of whitish-yellow rhizomes with upright branches bearing distinctive, grass green, swollen of beadlike (spherical) tips on the branchlets, resembling clusters of grapes (Littler et al. 1989). Plants are attached by rootlike rhizoids that cling tightly to the rocks in heavy surf areas, spread by cylindrical rhizomes in the intertidal, and are encountered down to 20 m deep. It is highly variable in morphology, with a dozen varieties and forms (Littler et al. 1989).

The invasive strain of *C. racemosa* is regarded as close to *C. racemosa* var. *occidentalis* J. Agardh, and is currently spreading very rapidly throughout the Mediterranean (Verlaque et al. 2003). New morphological and molecular studies identified the invasive variety as *Caulerpa cylindracea* Sonder, endemic to south-west Australia, and currently known as *C. racemosa* var. *laetevirens* f. *cylindracea* (Sonder) Weber-van Bosse (Verlaque et al. 2003). The new name *C. racemosa* var. *cylindracea* (Sonder) Verlaque, Huisman et Boudouresque has been proposed for this highly invasive strain (Verlaque et al. 2003). It seems destined for extensive invasion in the Mediterranean Sea (Balata et al. 2000). Only a few years after its introduction, the first significant signs of a negative impact on some communities and on human activities, such as changes in benthic community structure and decrease of biodiversity impacting fisheries, have been reported (Balata et al. 2000; Cecere et al. 2000; Ceccherelli et al. 2001; Magri et al. 2001; Piazzini et al. 2001).

Another invasive *Caulerpa* that has created problem in the state of Florida is *C. brachypus*. *Caulerpa brachypus* has a creeping stolon from which arise erect, paddle-like blades that are 2-3 cm in length (Cordero 1977; Sartoni 1978; Silva 2002; Lott 2003). These blades are normally simple, but some forms in the Philippines have bifurcated or trifurcated blades (Cordero 1977; Sartoni 1978; Silva 2002; Lott 2003). It superficially resembles some small native seagrasses, but is distinguished from those by the lack of a central leaf vein. *Caulerpa brachypus* appears to be limited to high salinity reefs in subtropical to tropical waters (Sartoni 1978).

Finally, *Caulerpa scalpelliformis* (R. Brown ex Turner) C. Agardh, which continues its establishment in Botany Bay (Australia), is epilithic, medium to dark green, with extensive stoloniferous prostrate axes bearing upright fronds to 20 cm in height and 3 cm broad (FloraBase 2005). Its terete and naked stolons, 1-3 mm in diameter are attached to the substratum by fine rhizoidal branches (Davis et al. 1997; FloraBase 2005).

What can be done to eradicate Caulerpa species?

Many methods to control *Caulerpa* have been tested throughout the Mediterranean (Makowka 2000). Some have tried to manually uproot the alga. Unfortunately one torn frond that gets away can generate a new outbreak (Smith & Walters 1999; Makowka 2000). Divers have used pumps to uproot the alga, but unless the rhizomes are completely removed, individuals may regenerate in the same place at a rate quicker than its original growth rate (Makowka 2000). Other eradication methods discussed at the January 2002 International *Caulerpa taxifolia* Meeting (San Diego, CA), included poisoning *Caulerpa* with substances like copper, potassium, sodium or chlorine bleach (e.g. Uchimura et al. 2000; Williams & Schroeder 2004), smothering the algae with a heavy plastic tarpaulin cover which prevents light exposition, and using underwater welding devices to boil the plant (Madl & Yip 2005). Lately, in Australia, experimental use of salt to control the invasion by *Caulerpa taxifolia* in New South Wales gave mixed results (Gabsy et al. 2005). Success was significantly greater during colder months (Gabsy et al. 2005). Also, the West Lakes in Australia were sealed off and filled with freshwater from the River Torrens. This worked very well, and, as of May 2005, the lake was clear of the weed (Dalgetty 2005).

Two species of marine snails, *Aplysia depilans* and *Elysia subornata*, Verrill, 1901 (Mollusca: Opisthobranchia), represent potential biological controls (Makowka 2000). Dr. Kerry B. Clark, a malacologist from the Florida Institute of Technology in Melbourne, presented his findings to Dr. Alexandre Meinesz (University of Nice, France) about these sea slugs that preferentially forage on *Caulerpa*. Meinesz didn't pursue the idea until he encountered first-hand evidence of the animals' selective foraging on *Caulerpa* spp. Since then, he has been studying the biology and dietary preferences of *Elysia subornata*, a tropical species that is a specialist grazer on many species of *Caulerpa*. Three other slugs, *Oxynoe azuropunctata* (Jensen 1980), *Oxynoe*

olivacea (Rafinesque 1814), and *Lobiger serradifalci* (Calcara 1840) are also specialist predators on *Caulerpa* (Coquillard et al. 2000). Only the unshelled species, *E. subornata*, is able to store the algal chloroplasts and to keep them functional (Clark et al. 1990). This phenomenon, called kleptoplasty, allows the sea slugs to forage over long distances (Clark 1995).

Ascoglossan species of a division of Nudibranchiata, in which the mantle itself serves as a gill—are also able to concentrate secondary metabolites of *Caulerpa* species (e.g. caulerpenin) as repellent toxins against predators (Paul & Van Alstyne 1988; Jensen 1994). Among the four species listed above, the tropical / subtropical *E. subornata* seems to be the best candidate as an agent of biological control of *C. taxifolia* because this species has direct benthic development (Clark et al. 1979), allowing it to quickly establish in locally dense populations, and it has the highest feeding rate on *C. taxifolia*, corresponding to the destruction of 5-6 cm frond per day at 21°C and a 8-9 cm frond per day at 25°C (Thibaut et al. 1998, 2001). Lastly, *E. subornata* dies at temperatures lower than 15° C (Meinesz et al. 1996). *Elysia subornata* is found from the southern Caribbean to Jacksonville, Florida in grassy shallow habitats (Clark & De Freese 1987). However, neither of identified two strains of *E. subornata* fed when placed with *C. taxifolia* - aquarium strain (A. Meinesz pers.com.).

Prediction models as another tool of prevention and management

Recently, researchers in several areas of ecology and evolution have begun to change the way in which data are analyzed and biological inferences are made (Johnson & Omland 2004). Rather than the traditional null hypothesis testing approach, they have adopted an approach called model selection, in which several competing hypotheses are simultaneously tested against the data (Johnson & Omland 2004). Models can then be ranked and assigned weights, providing a quantitative measure of relative support for each hypothesis (Johnson & Omland 2004).

My goal is to use the model selection approach to create a prediction model first by choosing variables that correspond directly to causal factors of absence/presence of *Caulerpa* spp. When trying to produce geo-referenced ecological information about the habitat requirements for species like *Caulerpa* spp., Geographic Information System (GIS) can be used to produce the data needed in the models (Store & Jokimäki 2003). These predictive habitat distribution models, derived by combining multivariate statistical analyses with GIS technology, have been recognized for their utility for conservation planning (Gibson et al. 2004). For example, habitat suitability maps of the swamp antechinus *Antechinus minimus maritimus* (a mammal from Tasmania), created by this same method, not only provided baseline information about the spatial arrangement of potentially suitable habitat for this endangered species, but also helped to refine the search for other populations, making the model an essential conservation tool (Gibson et al. 2004). Brotons et al. 2004 used presence-absence modeling methods to predict bird habitat suitability. They created maps of the bird's distribution, a tool that is key in understanding the ecology and conservation in particular when stating hypothesis, which rely on accurate knowledge of where species occur (Brotons et al. 2004). Joy and Death (2004) showed the many potentials of their map created from predictive modeling of freshwater fish and decapod assemblages, using GIS and neural networks such as: monitoring and predicting temporal changes in fishes communities caused by human activities and shifts in climate, identifying areas in need of protection, biodiversity hotspots, and areas suitable for the reintroduction of endangered or rare species. GIS-based prediction models are the most adapted, suitable and adequate tool to address my research question.

Research Objectives

1. To determine the current distribution of *Caulerpa* species in Florida.
2. To determine potential future invasion locations of *Caulerpa* by building a prediction model using four parameters hypothesized to be important for determining distribution patterns – i.e. latitude (temperature), seagrass, human population density and proximity to marinas.

Research Questions

1. What is the present observed distribution of *Caulerpa* species around Florida?
2. Are there invasive species present in Florida other than the declared *C. brachypus*?
3. Is there a correlation between the occurrence of *Caulerpa* species and latitude (temperature)?
4. Is there a correlation between the occurrence of *Caulerpa* species and seagrass beds?
5. Is there a correlation between the occurrence of *Caulerpa* species and population density?
6. Is there a correlation between the occurrence of *Caulerpa* species and proximity to marinas?
7. Using the four parameters cited above, is it possible to calculate the probability of presence of *Caulerpa* species in all nearshore waters areas around Florida?
8. Using the four parameters cited above, is it possible to estimate locations where *Caulerpa* invasions would most likely occur?

CHAPTER ONE: INTRODUCTION

The introduction of alien, or non-indigenous, species into land and freshwater habitats has been recognized as a major problem for over 100 years (e.g. Bax et al. 2001; Loope & Howarth 2003; Barnard & Waage 2004; Perrings et al. 2005). Scientists around the world have identified alien species as a major threat to biodiversity with dramatic effects on biological diversity, productivity and habitat structure (Wilcove et al. 1998; Carlton 1999). In the marine environment, the genus *Caulerpa* is a genus of particular concern. *Caulerpa taxifolia* – aquarium strain (Vahl) C. Agardh, is known worldwide as the “killer alga” (Jousson et al. 2000) (Figs. 1, 2). In 1984, this species apparently escaped or was released, probably as a waste, from the Monaco Oceanographic Museum into Mediterranean waters (Meinesz & Hesse 1991). It spread from an initial patch of approximately one square meter to over 13,000 ha bordering six countries (Spain, France, Monaco, Italy, Croatia, and Tunisia) by the end of 2000 (Meinesz & Hesse 1991; Meinesz et al. 2001). It spread throughout the northern Mediterranean, where it has overgrown all native flora and fauna, impacting fisheries and tourism in coastal communities (e.g. Relini et al. 2000; Meinesz 2002). In France alone, more than 30 new independent areas of colonization were discovered in the summer of 2001 (Meinesz 2002) (Fig. 6). The initial one square meter of area covered by *C. taxifolia* was originally ignored because it was thought that the species would die as the waters cooled down during the winter months (Meinesz 1997). However, we now know that this species adapted to colder waters (Meinesz & Hesse 1991; Meinesz 1997; Meinesz et al. 2001). Wherever *C. taxifolia* became established, it smothered local flora, including beds of native seagrass *Posidonia oceanica* that served as a nursery for many commercially important fishes (ISSG 2000).

In 2000, divers in the Agua Hedionda Lagoon near San Diego, California, discovered a patch of *C. taxifolia* – aquarium strain measuring 20 by 10 meters (Jousson et al. 2000). It is thought that the infestation occurred after somebody emptied a fish tank into a local storm-water drain (Raloff 2000). *Caulerpa taxifolia* was also observed in New South Wales, Australia in 2000 in the Port Hacking, Careel Bay and Lake Conjola regions (Grey 2001; Wiedenmann et al. 2001; Millar & Talbot 2002; Schaffelke et al. 2002). Once again it is suspected that human activities, either boating or aquarium releases, were responsible for these invasions (Millar & Talbot 2002). To this day the battle continues to control the spread and hopefully eradicate *C. taxifolia* – aquarium strain in Australian waters (Dalgetty 2005).

Another invasive species of this genus is *Caulerpa racemosa* (Forsskål) J. Agardh. It is currently undergoing a dramatic and rapid expansion throughout most of the Mediterranean Sea (Verlaque et al. 2000); this invasion is even more widespread than that of the highly publicized *C. taxifolia* (Verlaque et al. 2003). Both species of *Caulerpa* are strong competitors (Piazzi & Ceccherelli 2002). They tend to eliminate native species in colonized areas and create monospecific beds (Verlaque & Fritayre 1994; Piazzi et al. 2001). For many years, *C. racemosa* and *C. taxifolia* invasions were studied separately because of their different distributions. The two species of *Caulerpa* came into contact along the Tuscany coast near Leghorn in 1996 (Piazzi & Ceccherelli 2002). Where both species co-occur, *C. racemosa* was favored (Piazzi & Ceccherelli 2002). A third species of this genus, *Caulerpa brachypus*, created concern on the east coast of Florida, U.S. It was first reported in the West Palm Beach area of Florida in 2001, where it was already locally abundant (Schrope 2003; SFER 2005). Previous reports from other habitats in the Caribbean Sea exist (Littler & Littler 2003; Schrope 2003; SFER 2005). This species spread north in Florida into the Indian River Lagoon system, which was consistent with prevailing coastal currents, but it has not yet been reported in west Florida (Schrope 2003). However, it

seems that *C. brachypus* did not make it through Hurricanes Frances and Jeanne that battered Florida in the late summer of 2004 (B. LaPointe pers. com.). The vector of this introduction is unknown; aquarium releases, hull fouling, and ballast water have all been suggested as possible sources of origin (Schrope 2003).

Florida, the location of my research, is one of the states leading the nation in problems caused by non-native species (Simberloff et al. 1997). The Mediterranean fruit fly, citrus canker, West Nile Virus, Brazilian pepper trees and water hyacinth are all regularly featured in local and statewide news reports (Simberloff et al. 1997). Most of its coastline closely matches the environmental conditions of other areas invaded by *Caulerpa taxifolia* – Mediterranean strain and thus, is very likely to be invaded in the near future (L.J. Walters, unpublished data). Considering the length of Florida's shoreline and the importance of these waters to the state's economy, it is urgent to prepare for such an event. A task force was started to mobilize the government and public attention in an attempt to prevent Florida to be the next invasion site of this green alga.

The goal of my research was to determine locations that are most susceptible to *Caulerpa* invasion by aquarium dumping, or that would be more suitable for the settlement of invasive species of the genus *Caulerpa*. Being able to concentrate on areas that are more at risk would greatly help our prevention and eradication efforts. Two questions are fundamental to this goal: 1) Where is the habitat most suitable for *Caulerpa* species? 2) What areas are most likely to be invaded, especially if aquarium dumping is involved?

CHAPTER TWO: MATERIALS AND METHODS

Sampling strategy and choice of parameters

Vegetation surveys of large areas (e.g. > 2100 km of coastline for the state of Florida) are expensive and time consuming (Olsen et al. 1999). My limited time-frame and logistics, as well as the large scale for this research (the entire Floridian coastline), demanded a sampling plan that would give meaningful results. Four main sampling strategies exist: 1) random, 2) regular, 3) proportional-stratified and 4) equal-stratified (Hirzel & Guisan 2002). “Random sampling” draws points completely at random. Although the “random technique” is the easiest to implement because it needs few skills and little apriori knowledge of the environment, it would certainly have minimized the variability of the type of environment found all along the coastline of Florida. A “regular sampling” strategy draws upon points sampled at each node of a regular grid, whose cell size is adjusted so as to generate a number of points as close as possible to the desired number (Hirzel & Guisan 2002). Such a sampling strategy is also equally easy to implement, requires no particular knowledge of the environment and has a better representation of the environment than the “random technique”. However, because of the dimensions of the survey area, it would very likely underestimate the variance of conditions around Florida. Simple random or systematic (i.e. “regular”) arrangement of sampling units of the study area do not achieve sampling maximum variation, which is the focus of habitat typification (Knollová et al. 2005). Such sampling strategies tend to yield high numbers of replicates of common habitats whilst rare habitats are under-represented, or even missing (Gillison & Brewer 1985; Kenkel et al. 1989; Bunce et al. 1996).

Modern biological surveys of large areas increasingly use environmentally “stratified sampling” designs (Patton 1990; Goedickemeier et al. 1997; Gimaret-Carpentier et al. 1998;

Olsen et al. 1999; Yoccoz et al. 2001). In “stratified sampling”, the population is divided into levels or strata that represent clearly defined groups of units within the population and are sampled independently (and randomly) from each of the groups (Quinn & Keough 2002). Strata are defined on the basis of environmental variables that have been shown in previous studies to have a correlation with the occurrence of a species (Knollová et al. 2005). If there is sufficient information on the spatial pattern of such variables (e.g. digital climatic or geological maps), appropriate strata for sampling can be created by overlaying these maps in GIS (Knollová et al. 2005).

Sampling designs that use random arrangements of sample points within strata are assumed to maximize the between-sample point variation and to give the same chance of common and rare habitat types being sampled (Knollová et al. 2005). Also, stratified sampling (i.e. proportional or equal-stratified) is likely to be more representative on a large scale than a simple random sampling because it ensures that all major habitat types are included in the sample (Quinn & Keough 2002). A “proportional-stratified” sampling strategy assigns to each strata a number of sample points proportional to its area (Hirzel & Guisan 2002). Compared to an “equal-stratified sampling” strategy, it would inadvertently skew the prediction by increasing the possibility to find a positive correlation to the object of the research in larger strata. In the “equal-stratified sampling” strategy, each stratum contains the same amount of sample points thus giving the best representation of each strata and habitat type (Hirzel & Guisan 2002). The literature shows that an “equal-stratified sampling” strategy is among the most accurate and most robust methods (Hirzel & Guisan 2002). Therefore, I chose the “equal-stratified sampling” strategy and created a set of variables that would be suitable to predict the habitat preference for *Caulerpa* spp.

I choose parameters that were available on public GIS databases. To find the “best” regression model for my research, I had to find the smallest subset of predictors that provided the

“best fit” to the observed data (Quinn & Keough 2002). There are two reasons for this. First, the “best” subset includes the predictors that are most important in explaining the variation in the response variable. Second, other things being equal, the precision of predictions from our fitted model will be greater with fewer predictor variables in the model (Mac Nally 2000). Among potential parameters available on the public domain, some were excluded based on lack of appropriateness for my planned sampling methodology. For example, bathymetry was not chosen because my sampling was restricted to depths of less than 10 meter. However, this should not pose a problem since most of *Caulerpa* spp. occur above 20 meters (Littler et al. 1989). Also, Thibaut et al. (2004) reported higher biomasses of *C. taxifolia* between 6 and 10 meter deep compared to other depths where it is also found. Maps showing the presence of aquatic preserves, coral reef, mangrove forests and salinity were also considered, but none of these parameters were accurately represented on a continuous basis around Florida’s peninsula. Another reason for excluding these was that they were correlated with other variables. Substrate type and vegetation shoreline were not chosen because of the lack of support from the literature that would give an eventual correlation with marine species occurrence. Water chemistry data was not used because it was limited to certain stations and did not cover the entire coastline.

The first parameter I selected was temperature, knowing that most *Caulerpa* species inhabit warmer waters (Silva 2002). For example, the lethal lower temperature for *C. taxifolia* in the Mediterranean is 7°C for the aquarium strain, and its lethal maximum temperature is 32°C (Komatsu et al. 1994; Ramey 2001). Elsewhere, the non-invasive *C. taxifolia* has a lethal temperature of 14°C (Komatsu et al. 1994; Ramey 2001). Since Florida’s temperature varies from east coast to the west coast as well as from north to south, I chose it to be the initial parameter that I would use to stratify the state (Fig. 7).

The second parameter chosen was the presence of any seagrass, including *Halodule wrightii*, *Syringodium filiforme*, *Thalassia testudinum*, *Halophila johnsonii*, *Halophila decipiens*, *Halophila engelmannii* and *Ruppia maritima*. All seven listed species naturally occur in Florida (Virnstein & Morris 1996). Seagrass density and distribution, is currently being monitored around the coastline of Florida by direct observation and satellite imagery (by Florida Fish and Wildlife Conservation Commission (FWC), Florida Marine Research Institute (FMRI), Coastal and Marine Resource Assessment (CAMRA)). Thus, seagrass presence fits the requirement for this study. These data were used to determine the location of all Floridian seagrass beds (Fig. 8). The presence of seagrass has frequently been found in areas where conditions were favorable for *Caulerpa* establishment. *Caulerpa* species are known to be the first colonizers of areas that later are colonized by seagrass beds (William 1984, 1990). For example, *C. prolifera* is known to grow around seagrass beds (Smith & Walters 1999), *C. cupressoides* var. *lycopodium* occurs in meadows of *Halodule wrightii* (Magalhaes et al. 2003) and, in the Mediterranean Sea, *C. taxifolia* outcompeted the seagrass *Posidonia oceanica* (Chisholm et al. 1997). In fact *C. taxifolia* has taken over many areas historically covered by *P. oceanica*, and killed 45% of *Posidonia* shoots in one year (Villele & Verlaque 1994). Relini et al. (1998a, b, c) found that *C. taxifolia* replaced *Cymodocea nodosa* (Ucria) Ascherson in a coastal area near Imperia, Italy. However, Ceccherelli et al. (2002) suggested that, over the long term, the two species were likely to coexist and that nutrient supplies from the sediment would not enhance the probability of success of the seagrass or the alga.

The third parameter I included in my model is the local human population density. I arbitrarily chose 25,000 inhabitants to be the limit between low human-impacted and high human-impacted areas. The coastline of Florida hosts many small communities with less than 25,000 inhabitants. Thus, it is a suitable and useful variable because of the presence of major

cities of more than 25,000 inhabitants present all around the coastline. Thus, they would appear in each of my strata. Increasing anthropogenic pressure on coastal environment can have severe consequences to ecosystems (State of the Environment 2003). In the Mediterranean Sea, *Caulerpa taxifolia* – aquarium strain was concentrated in zones with extensive development (Madl & Yip 2005). However, this parameter may have different consequences, since high population density means more opportunity to find exotic species in waste water, aquarium dumping or boat traffic, but also more pollution, potentially preventing or increasing the growth of alga.

The fourth parameter included in this research is the presence / absence of boat marinas. Marinas were well represented around the state on a GIS layer (FGDL: www.fgdl.org). The likelihood of boat traffic transporting exotic species from one area to another, makes marinas prone to becoming primary invasion sites (Boudouresque et al. 1995; Loope 2004). Docks are frequently areas where people have easy access to marine environment, making them logical locations for aquarium dumping as well. All the GIS data were downloaded from the Florida Geographic Data Library (FGDL: www.fgdl.org).

To optimize my sampling effort, I stratified the Florida shoreline into six different temperature zones. I used temperature information found on the NOAA website under the Comprehensive Large Array-Data Stewardship System (CLASS: www.class.noaa.gov). Bi-monthly sea surface temperature from the Floridian coastline, covering a period of four years (2001-2004), was downloaded. This data was available as a grid of 14 km per side (Fig. 7). I transferred the temperature data of each pixel along the coastline to an Excel spreadsheet (207 color-coded pixels) and performed ordinations for each summary temperature (monthly, seasonal and annual) variable using PC-ord (MjM Software Design). The winter months of January showed the most contrasting patterns and January temperatures sorted into six distinct groups

(Figs. 7, 11). Thus, the Florida coastline was stratified into six different temperature zones (Fig. 12). From the western extreme of the Floridian coastline, the first zone ended at a longitude of 85°W; the second zone ended near Tampa at 28°N; the third zone went down to Key West in the Keys (north portion of the Keys); the fourth went from Key West (south portion of the Keys) up on the east coast to the longitude 27°N; the fifth up to the longitude 29°N; and the sixth up to the north-eastern point of Florida at the Georgia border (Fig. 13A-D).

Using ArcMap 9.1, I created a union of the four parameters. The data layers were gathered and modified as needed to be usable for this study. A line data layer of the Florida coastline was buffered by 3 km in order to integrate lagoons and estuaries, and was clipped at the points determined to be the boundaries between zones. A data layer for marinas was obtained and a buffer of 2 km was created around each marina since modeling of the spreading of *Caulerpa* fragments (Hill et al. 1988) showed that there is a gradient of natural fragment dispersal for short distances (several hundred meters). Thus, within this buffered zone of 2 km of radius, I concentrated only on the growth that might have happened due to a release in the marina itself. A greater zone of influence would overlap with other parameters of the research. City/town (with city limits) and seagrass presence/absence data layers were obtained and merged with the marinas data layer. The marina/seagrass/city data layer was merged with the temperature zones data layer and the zones data layer was used to clip the other data layers to the extent of the Florida coastline. The final layer consisted of data in a 3 km buffer around the entire coastline of Florida cut into six zones that provided information on the presence/absence of seagrass, cities, and marinas, and the extent of each zone.

This map was essential for choosing my survey locations. For each location survey, I selected a zone (e.g. Zone 5) in ArcMap, and then had the computer indicate the areas where seagrass was present, in a low populated area and where there was a marina in the vicinity.

ArcMap gave me a choice of all the areas that corresponded to this combination of parameters (Figs. 13A-D). Within each area, every point shown was equally probable. I noted all possible areas and eliminated the ones that were inaccessible (i.e. US Air Force Base). Among all the areas remaining, I used a random number generator and randomly chose three areas to survey. I did this operation for the 48 different associations of parameters (Fig. 14) and randomly chose three zones per association of parameter to survey. This gave a total of 144 locations to survey around the state of Florida. The exact GPS coordinates was used to access each location using a handheld Garmin eTrex GPS receiver (accuracy < 14 m). Once on site, I measured a line of 100 m along the shore equally distributed on each side of the GPS point and snorkeled along this line, back and forth up until I was 20 meters far from shore. This way, an area of 2000 m² at each location was surveyed and I recorded the presence of each species of *Caulerpa* in every location.

Building the model and the probability map

Of the 144 points anticipated, 132 points were located, evaluated and the data was entered on an Excel sheet; twelve were not considered because the 6th temperature zone (northeast of Florida) did not have any seagrass. During my field work, I confirmed the association of the point with the anticipated state of the variables. Using SPSS 11.0 (MacOSX), I tested binary multiple logistic regression of all models with the *Caulerpa* data as the dependant variable and all combinations of the four independent variables: the GPS coordinate, presence of seagrass (1: present/0: absent), neighboring population density (1: high/0: low), and proximity to marina (1: with the 2 km buffer zone/0: outside the 2 km buffer zone). There was a significant correlation between temperature and latitude (-0.94, n = 207). I used the Akaike's Information Criterion (AIC) for selecting the "best" fitting model in multiple linear regression. It was: $-2(\log \text{likelihood}) + 2K$ (Burham & Anderson 2002). The parameters of this model were then used to

predict the probability of *Caulerpa* occurrence across the Florida shoreline based on a multi-layered grid. This grid was created (1000 m x 1000 m cells) from the initial data layer discussed above and the centroid of each cell was used to assign X and Y coordinates for that cell. Using Microsoft Excel and the best logistic regression model from SPSS, the X and Y coordinate data, along with the other factors (marina, seagrass, and city presence / absence) were used to assign a probability for *Caulerpa* presence to each cell. These probabilities were added to the attribute table of the grid data layer. The probability field was used to create a graduated color map for the entire state showing the probability of *Caulerpa* presence of the entire coast (Fig. 15). The probability ranges were chosen to reflect the maximum heterogeneity of the data.

CHAPTER THREE: RESULTS

I found *Caulerpa* in 26 of 132 surveyed zones sites, including *C. prolifera* (15 occurrences), *C. sertularioides* (10), *C. paspaloides* (9), *C. mexicana* (9), *C. cupressoides* (7), *C. ashmeadii* (5), *C. lanuginosa* (5), *C. verticillata* (3), *C. racemosa* (3) and *C. microphysa* (1) (Table 1; Fig. 16). Among the 26 sites where *Caulerpa* species were found, 24 were in seagrass beds. Eighteen of the 26 sites where *Caulerpa* species were found were in locations of low populations (< 25,000 inhabitants). Eighteen of the 26 sites where *Caulerpa* species were found were within 2 km of a marina (< 2km).

Local species richness of *Caulerpa* increased as the latitude decreased, with the presence of seagrass and in sites with low human density (Inverse function, $r^2=0.297$, $n=132$, $P < 0.0001$ and $y= -10.733 + 346.255/GPS + 0.647*\text{seagrass} - 0.604*\text{population density}$) (Fig. 17; Table 2). The probability of *Caulerpa* species occurrence increased as the latitude decreased (Fig. 18), with the presence of seagrass beds, in sites with low density of human populations (< 25,000 inhabitants) and when in close proximity to marinas. An assessment of the possible logistic regression models with these variables using Akaike's information criteria indicated that the full model for *Caulerpa* species including all these four parameters was the best (weight of 0.84) (Table 3). Percent correct of *Caulerpa* presence and absence for this model were 61.5% and 98.1%, respectively. We used the parameters of this model to predict the occurrence of *Caulerpa* species along Florida shoreline (Table 5).

I also did an assessment of the possible logistic regression models with the same variables using Akaike's information criteria for single species (Table 4, 5). Only *C. prolifera*, *C. paspaloides*, *C. mexicana* and *C. sertularioides* had significant correlation ($P < 0.05$) with one parameter, the latitude. Percent correct of *C. prolifera* presence and absence for this model were

13.3% and 97.4%, respectively. Percent correct of *C. paspaloides* presence and absence for this model were 55.6% and 99.2%, respectively. Percent correct of *C. mexicana* presence and absence for this model were 77.8% and 98.4%, respectively. Percent correct of *C. sertularioides* presence and absence for this model were 50% and 99.2%, respectively.

CHAPTER FOUR: DISCUSSION

Sampling strategy and prediction model

Mapping species distributions is a key issue in ecology and conservation (Brotons et al. 2004). To map species distributions at large spatial scales, Guisan and Zimmerman (2000) showed that habitat-suitability modeling techniques use information on species location records and environmental factors to generate statistical functions that allow predictions of potentially suitable habitat. We used presence/absence data that has been shown to be more accurate in prediction than presence only data (Guisan & Zimmerman 2000). This supports the idea that the *Caulerpa* species observed and analyzed settled preferably in specific habitats, making absence data reliable and useful to enhance the model calibration (Guisan & Zimmerman 2000). Gibson et al. (2004) used a similar approach modeling the habitat suitability of the swamp antechinus (*Antechinus minimus maritimus*) in the coastal heathlands of southern Victoria, Australia. Likewise, our prediction model provides information about the location of potentially suitable zones of settlement for *Caulerpa* species, making it an important conservation tool. The positive association between *Caulerpa* species presence with decrease in latitude, presence of seagrass bed, population under 25,000 inhabitants, and proximity to marinas strongly suggests that these species occurs preferentially in warmer waters, zones where seagrass occurs, zones of low human influence, and in close proximity to marinas where human access from the shore and from the sea combine to increase the probability of release, settlement and spread. These results are in accordance with previous studies that have shown these correlations (William 1984, 1990; Villele & Verlaque 1994; Komatsu et al. 1994; Boudouresque et al. 1995; Chisholm 1997; Relini et al. 1998a, b, c; Smith & Walters 1999; Ramey 2001; Silva 2002; Magalhaes et al. 2003; Loope 2004; Madl & Yip 2005).

In their study on the optimal strategy for sampling, Hirzel and Guisan (2002) suggest that the most critical parameter of a sampling design is the sample size. As sampling is a time-consuming task, prioritization of requirements is of great importance (Hirzel & Guisan 2002). The choice of using an “equal-stratification” sampling strategy for this research proved to be both efficient and cost-effective in determining the zones of survey.

Variable selection and model performance

One must remember that other potential environmental variables influencing the occurrence of *Caulerpa* species certainly play a role in habitat selection (*i.e.* water chemistry, bathymetry, substrate type, etc.). However, due to the size of the sampling area (state of Florida), the small number of sites surveyed ($n = 132$), and the small number of sites where the species was present (26), the number of variables that should be used in the modeling process was restricted (Harrell 2001). Harrell (2001) suggested that no more than $n/10$ variables should be included in the final model, where n is the total sample size, or in the case of binary response, the sample size of the least represented category. In our case, using binary responses, $n/10 = 6.6$. Thus, the choice of four predictor variables in the final model is appropriate and the analysis shows that they were meaningful.

Akaike’s information criteria selected the best model out of all possibilities (Tables 3, 4, 5). Because of the limitation of the sample size, the model would be poor (Burnham & Anderson 2002). To avoid this problem, the selection of the variables and consequent models, must be well founded and post hoc evaluation of the performance of the model is equally as important (Fielding & Bell 1997; Guisan & Zimmermann 2000; Pearce & Ferrier 2000). This could be done by performing a “ground truthing” or by using independent data (Fielding & Bell 1997; Manel et al. 1999; Pearce & Ferrier 2000; Scott et al. 2002). However, an independent data set for this

research does not exist at the state level for Florida. Only limited areas have been studied, and most classify *Caulerpa* only at the genus level. Thus, it is not usable for this research where species determination was essential. With the data collected in this study, the predictive success of the selected model for absence and presence of *Caulerpa* species was shown to be high (98.1% and 61.5%, respectively) indicating a good fit of the model to the original data. Adding new data to the current data to assess the full adequacy of this model to predict *Caulerpa* occurrence should be performed.

Prediction model application for all Caulerpa species together

My data analysis led to six unique prediction models. The first model uses the four chosen environmental variables to predict overall *Caulerpa* species occurrence (Table 3). The second one used 3 variables (*i.e.* latitude, seagrass, marina) that were found to be significantly associated with the occurrence of *C. prolifera* (Table 4). Three other models showed the negative correlation of *C. mexicana*, *C. paspaloides* and *C. sertularioides* with the GPS variable only. The other species, *C. verticillata*, *C. ashmeadii*, *C. lanuginosa*, *C. cupressoides*, *C. microphysa* and *C. racemosa*, did not reveal any significant correlation with any of the parameters. A sixth observation we can make from this research is the confirmation that *Caulerpa* species richness increased as latitude decreased (Table 2, Figure 17).

The analysis for all *Caulerpa* species present in Florida showed that the presence of seagrass bed is the best predictor of the four. Every zone where *Caulerpa* species were found was closely related to a seagrass bed regardless of the association of all other parameters. Seagrasses depend on sediment-based decomposition of organic matter and elemental recycling (McRoy & McMillan 1977; Klug 1980; McRoy & Lloyd 1981; Williams 1990) and are particularly prone to human disturbances (Thayer et al. 1975; Lewis 1987; Livingston 1987; Williams 1990).

Seagrasses obtain a large fraction of their nutrient demands from the sediment via roots while leaf uptake is considered of secondary importance (Pedersen & Borum 1993; Ceccherelli & Cinelli 1997). Marine algae, such as *Caulerpa* species, can utilize both sediment and water column nutrients (Williams 1984). This suggests that algae such as *Caulerpa* spp. would receive a selective advantage when competing with seagrasses. In areas where “near eutrophication” occurs, *Caulerpa* spp. would consequently more likely outgrow seagrass beds or profit of moderate human disturbance to replace a dying seagrass community as shown by Relini et al. (1998a, b, c). Ceccherelli and Sechi (2002) suggested that a seagrass such as *Cymodocea nodosa* and *Caulerpa* spp. are likely to coexist over the long term. The presence of *C. taxifolia* specifically did not significantly affect *C. nodosa* shoot density (Ceccherelli & Sechi 2002). This suggests that the presence/absence of seagrass beds is an appropriate and valuable parameter. However, because *Caulerpa* spp. are known to be first colonizers of areas later colonized by seagrass beds (Williams 1984) as well as opportunistic species that would eventually out-compete and replace seagrasses (Chisholm 1997; Relini et al. 1998a, b, c), tells us how important it is to consider the historical mapping as well as the development models of seagrass beds to consider all potential areas for eventual *Caulerpa* spp. settlement.

Latitude was the second most significant predictor for *Caulerpa* spp. occurrence. This is in accordance with the fact that *Caulerpa* species are endemic to tropical and subtropical regions around the world (Cresse et al. 2004). However, Silva (2003) mentioned that *Caulerpa* spp., usually located in warmer tropical waters, can also grow in location like the Onslow Bay, North Carolina, at latitude 34°N or in Moreton Bay, at latitude 27°S, in Australia. Florida state lies between latitude north 24° and 30° and thus, has the potential for recruitment along its entire coastline for *Caulerpa* spp. However, as shown in Figure 17, the species richness was highly correlated to latitude (0.94, n = 207). Possibly, the high tidal regime and wave exposures on the

northern Atlantic seaboard of Florida that prevent seagrass establishment also prevent *Caulerpa* spp. recruitment (L. Morris pers. com.). During my surveys, I never encountered *Caulerpa* species on beaches of bare sand that fronted the Atlantic Ocean, or the Gulf of Mexico in the Panhandle. This is supported by de Vaugelas (1999), who showed that unstable substrates such as ripple-marked sediments and shallow rocky shores exposed to strong wave action are some of the rare locations where *C. taxifolia* cannot become established. This suggests that protected areas, such as lagoon or exposed areas bounded by hard substrates or coral reefs offer better potential for *Caulerpa* spp. settlement. Along the Panhandle region of Florida, some of the visited areas were on beaches having also high tidal and strong wave action influence. These areas were systematically devoid of seagrasses. Most were long expanses of sandy bottom. However, for the Panhandle, many of my survey locations were in or close to estuaries and bays, such as Pensacola Bay and Choctawhatchee Bay near Fort Walton Beach, West and East Bays near Panama City and Apalachicola Bay near Apalachicola. High fresh water runoff, as well as higher population densities characterized all these locations. The salinity in these areas was often lower than 10 ppt, lethal salinity for *Caulerpa* (Madl & Yip 2005). This is likely to be the main reason why I did not find *Caulerpa* in these locations. When found south of 29°N, *Caulerpa* was found in more protected environment such as lagoons, in seagrass beds as in the Florida Keys, or attached to highly structured surfaces, such as jetties or hard corals.

Proximity to marinas was third in significant correlation to *Caulerpa* spp. occurrence. This correlation confirmed the hypothesis that areas with easy access to coastal waterways for humans are likely to be areas where species that are the object of trade for home aquarium industry have a significant probability to be found in the wild (Loope 2004; Padilla & Williams 2004; Walters et al. 2006). Marinas are also areas where boat traffic favors the spread of species through ballast water or through fragments attached to anchors (Loope 2004; Padilla & Williams

2004; Madl & Yip 2005). Florida is a state known for its recreational activities related to the sea and its fishing industry. This shows how prone these areas are to marine invasions and how careful we must be to prevent these areas to become invaded by *Caulerpa* spp.

Population density was also correlated to *Caulerpa* spp., but in a negative way. Heavy populated areas (> 25,000) might be areas of too many disturbances for *Caulerpa* spp. recruitment. During the surveys, I often observed these areas to have anoxic substrates and high turbidity. These conditions do not favor angiosperms or macroalgae species (Plus et al. 2003). However, Chisholm et al. (1997) showed that *C. taxifolia* – aquarium strain, proliferated in areas of urban wastewater pollution even if turbidity stays as a factor that affect *C. taxifolia* growth (Creese et al. 2004). This might be a unique feature of this new invasive strain of *Caulerpa*.

Combined, these four predictors offer a robust prediction model (Table 3). The prediction model using the four variables was the strongest one with a weight of 0.84, which demonstrated that the use of these four parameters is an appropriate choice of predictors. This is supported by the percent correct of *Caulerpa* presence and absence for this model that was 61.5% and 98.1%, respectively. Nevertheless, sample size was very small and further data collection will be indispensable in order to increase the level of confidence we might give to this prediction model (Hirzel & Guisan 2002). Applying a predictive distribution model within a spatial context relies on the existence of landscape scale variables that define suitable habitat for these species and one might think about adding more precise and finer variables to ameliorate the prediction (Gibson et al. 2004). Nonetheless, finer-scaled habitat variables, such as nutrient availability, are unlikely to be captured or available at a landscape level (Austin 2002). Consequently I believe that this approach helps to refine the selection of zones of survey at a large scale.

Application of the model for single species

Caulerpa cupressoides, *C. ashmeadii*, *C. lanuginosa*, *C. verticillata*, *C. racemosa* and *C. microphysa* were found less frequently and, beside *C. racemosa*, were all only observed in the Florida Keys. They showed no significant correlation with any of the parameters. The sample size is likely to be the major reason why no inference can be made at that point (Hirzel & Guisan 2002). *Caulerpa prolifera*, *C. mexicana*, *C. paspaloides* and *C. sertularioides* seems more likely to settle further north than other species. These four species showed a negative correlation with latitude and *C. prolifera* also showed positive correlation to seagrass bed presence and marina proximity (Table 4, 5). Thus, prediction models were also calculated individually for these species (Table 4, 5).

Caulerpa prolifera has been observed growing in coastal lagoons, in the southeast Iberian Peninsula, in salinities that ranged from 42 to 47 ppt (Terrados & Ros 1991). Fertilization experiments indicate that growth of *C. prolifera* was primarily limited by nitrogen (Terrados 1991). Also, *C. prolifera* was adapted to photosynthesize in low light environments (Terrados & Ros 1992). The Indian River Lagoon (26°4N to 27°0N), offered these conditions for *C. prolifera*, giving us a bigger sample size for this species. *Caulerpa prolifera* was most abundant in the Indian River Lagoon, in highly human impacted areas, and was usually associated with seagrass beds (mainly *Halodule wrightii* and *Syringodium filiforme*). This observation was supported by the observation that *C. prolifera* grows best in soft sediments, although it will also grow on sand, clay or rock (Terrados & Ros 1991). Presence of marinas was also a positively correlated to *C. prolifera* occurrence. In the Indian River Lagoon, a recreational area for fishing and boating, many fragments of *C. prolifera* can be created. These fragments have the capacity to vegetatively form a new thallus from small fragments that drift in water, allowing it to rapidly colonize new

areas (Terrados & Ros 1991; Smith & Walters 1999). This confirms the importance of marinas as a variable for at least some species of *Caulerpa*.

Caulerpa mexicana, *C. paspaloides* and *C. sertularioides* were found to be negatively correlated with latitude (Table 5). We created a prediction model for these species based on this one parameter. This observation showed that the latitude was an important factor to consider for *Caulerpa* species recruitment more than giving us a tool to select zones for specifically targeting them. *Caulerpa paspaloides* was the species I found furthest north (28°35N). However, in my opinion latitude should not be used as single parameter to estimate the suitability of habitat for *Caulerpa* spp. For a large scale study, one predictor only makes the model too weak. Moreover, latitude being directly linked to the water temperature range, is likely to change seasonally and during episodes of global warming. Again, only increasing the sample size would allow more precise and robust predictions.

In the event of Caulerpa taxifolia invasion

Caulerpa taxifolia – aquarium strain has lower lethal temperature limit than the native strain, 7°C and 14°C respectively (Komatsu et al. 1994; Ramey 2001). Thus, the distribution of the aquarium strain would be expected to extend further north along the Atlantic seaboard compared to the native species of *Caulerpa* observed during my project. However, it appeared that the absence of *Caulerpa* spp. occurrence in the northeastern part of Florida was also influenced by substrate profiles and exposure to tides and waves action. This is confirmed by the fact that *Caulerpa* species are present further north and can grow in location like the Onslow Bay, North Carolina, at latitude 34°N (Silva 2003). Although our model is being based on native species, and since latitude was chosen to predict *Caulerpa* spp. occurrence, our predictions may

still be useful to predict invasion by *Caulerpa* exotic species such as *C. taxifolia* – aquarium strain.

CHAPTER FIVE: CONCLUSION

The choice of these four parameters, latitude, seagrass beds presence / absence, human population density and proximity to marinas, to prepare the “equal-stratified” sampling strategy for this research allowed us to select and target specific zones, a process that revealed itself to be highly valuable and successful. I believe that these four parameters are the best among different possibilities of “smaller subset” of predictors that provide good fit to the observed data. All parameters were represented around the whole state and available on GIS mapping gave a very realistic prediction model. They showed a correlation to *Caulerpa* spp. occurrence and the model can be a useful tool in the future to select zones of survey that would be likely to have *Caulerpa* species.

This research had the purpose to “predict the risks of invasion of *Caulerpa* species in Florida”. We succeeded in this goal because it is possible to use our prediction model to select sites that would more likely be invaded. Nevertheless, we know that *C. taxifolia* – aquarium strain has particular characteristics that make it a tremendous invader. This suggests that areas that are too cold for native species of *Caulerpa* around Florida would be suitable for *C. taxifolia* – aquarium strain. This might also signify that the results of Chisholm’s research (1997) that showed how *C. taxifolia* – aquarium strain was successful around wastewater discharge in the Mediterranean Sea, would be reproducible here in Florida and would result not in a negative but in a positive correlation to population density. Also we have to consider that climate change is likely to shift the distribution of suitable areas for many species (Williams et al. 2004) making this model, as any other model, a temporary tool in need of constant adaptation to new environmental and human factors.

New species introductions – the pace of which is accelerating fast – can be prevented in some cases or newly introduced species can be eradicated before reproductive populations become established (Barnard & Waage 2004). Without more effective prevention and control programs, the number of invasions and their subsequent effects will only increase (Bax et al. 2001). In order to prevent further dramatic establishment, effective collaborative efforts of many individuals, nationally and internationally needs to be done. One of the problems has always been the fact that those whose actions result in invasions seldom bear legal responsibility for those actions (Perrings et al. 2005). This is a call not only for action in terms of management of the environment, outreach and education, but also for action at the government level in legislation and law enforcement. Because we can never be certain about the behavior of a non-native species imported into a new environment, we should do everything possible to prevent all invasions, carry out careful assessments before intentionally introducing an species into a new environment, build a stronger awareness among the general public about the problems of invasive alien species, mobilize conservation organizations to address the problems, and build an ethic of responsibility among all citizens (Mac Neely 2001). The several spectacular large-scale eradication successes, such as the eradication program of the fire ant species *Wasmannia auropunctata* on the island of Marchena, are encouraging for all of us who work in outreach, education and prevention. We must avoid repeating such mistakes by learning from history. Any organizations that deal with aquatic species should focus on the prevention of introduction and the early detection of introduced species (IUCN 2003).

This project allowed us to build a model that gives very good predictability for *Caulerpa* occurrence. In other words, this model can be used as a start to select locations of possible invasions for management and prevention purposes. However, it is not a fully representative data set, because some areas or habitats are probably under-represented or missing (Knollová et al.

2005). Collecting more data combined with a gap analysis should be done in order to improve the reliability of the model. Extending this model to other areas of the world for comparison with our research in Florida would also give precious indication of the adequacy of our research.

APPENDIX A – FIGURES

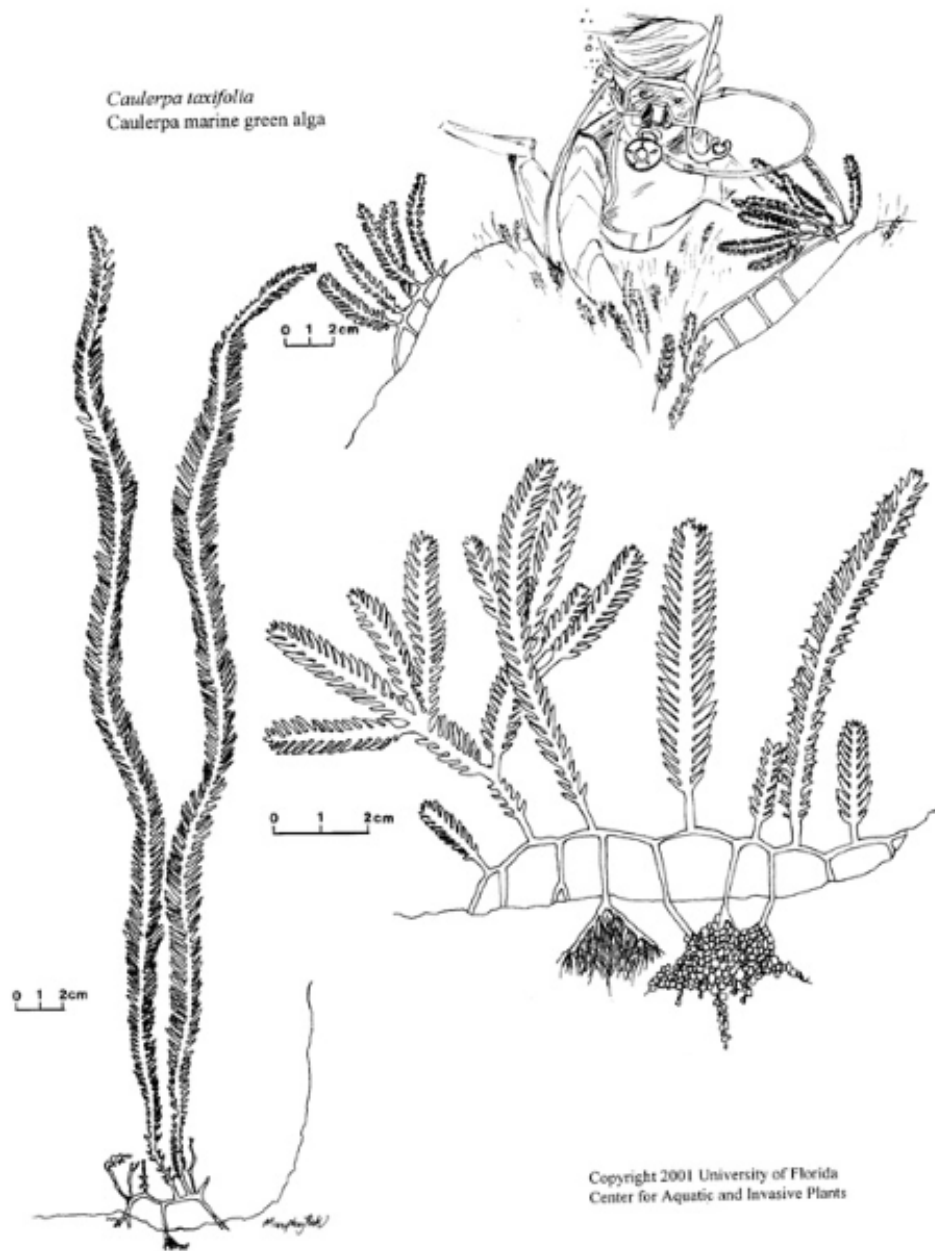


Figure 1. *Caulerpa taxifolia* - aquarium strain (Vahl) C. Agardh.

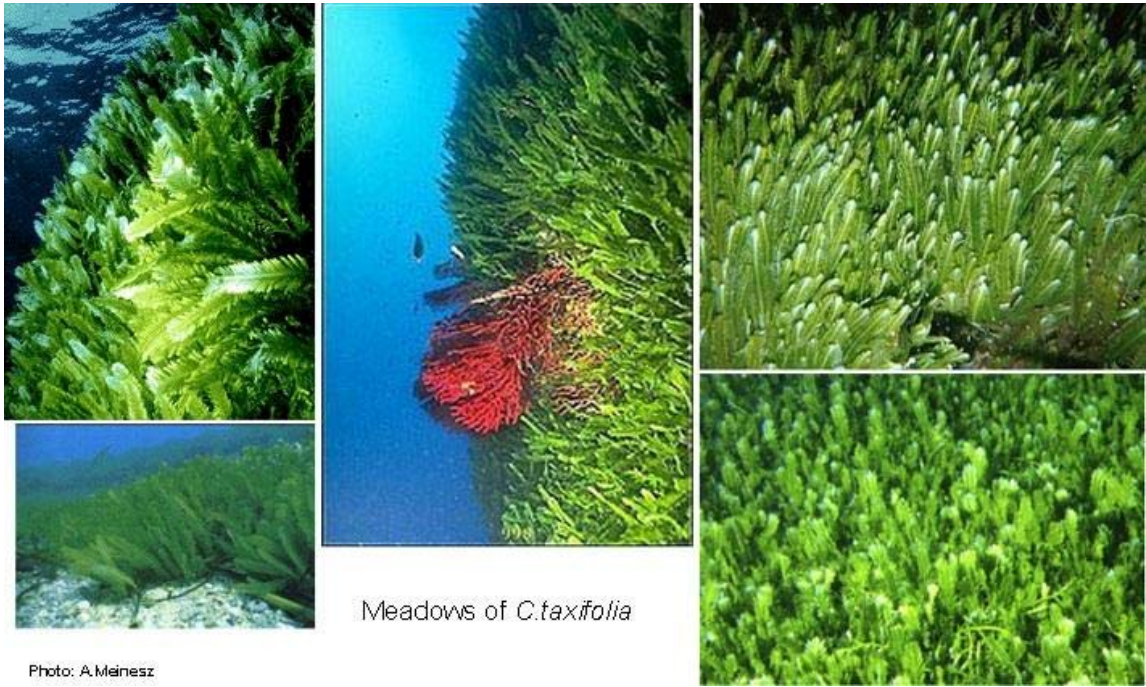


Figure 2. *Caulerpa taxifolia* - aquarium strain in the Mediterranean Sea



Figure 3. *Caulerpa racemosa* (Forsskål) J. Agardh.



Figure 4. *Caulerpa brachypus* Harvey.



Figure 5. *Caulerpa scalpelliformis* (Turner) C. Agardh.

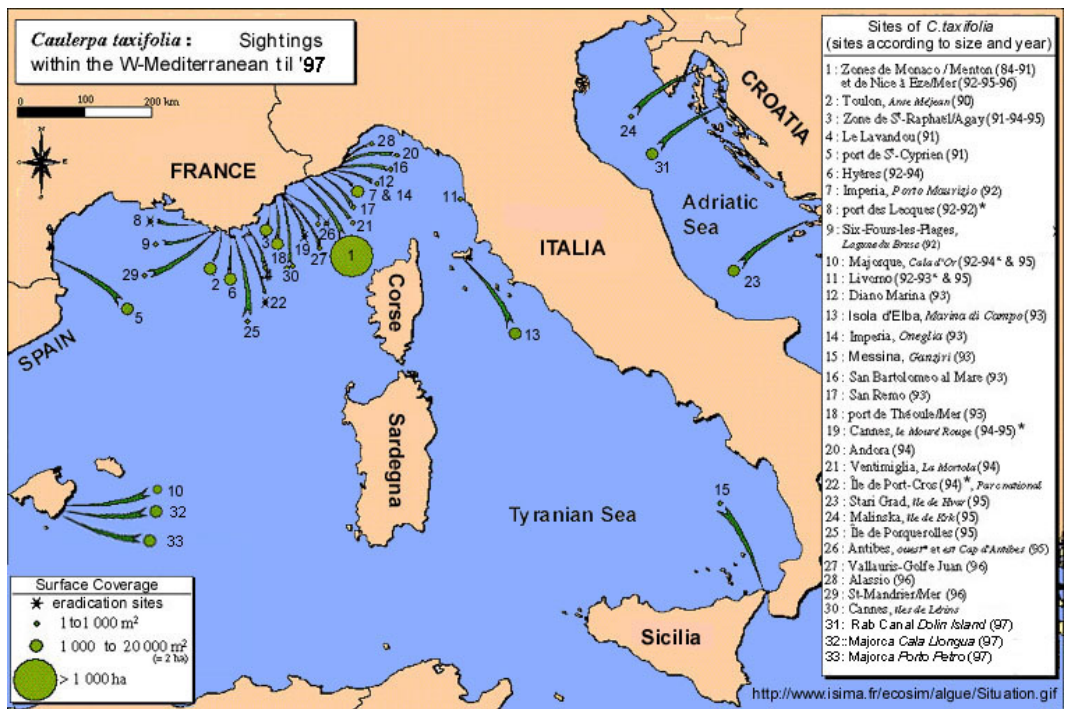


Figure 6. *Caulerpa taxifolia* – aquarium strain: sightings in the western-Mediterranean Sea until 1997.

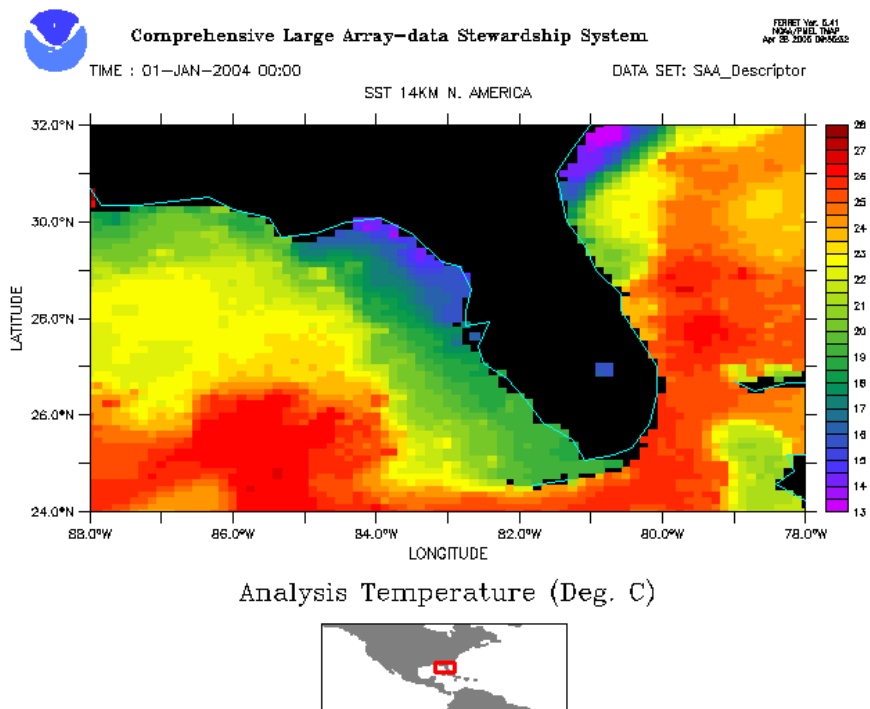


Figure 7. Satellite imagery showing the sea surface temperature around Florida using a grid of 14 km by 14 km. (CLASS-NOAA).



Figure 8. GIS map of seagrass zones around Florida (from www.fgdl.org) .

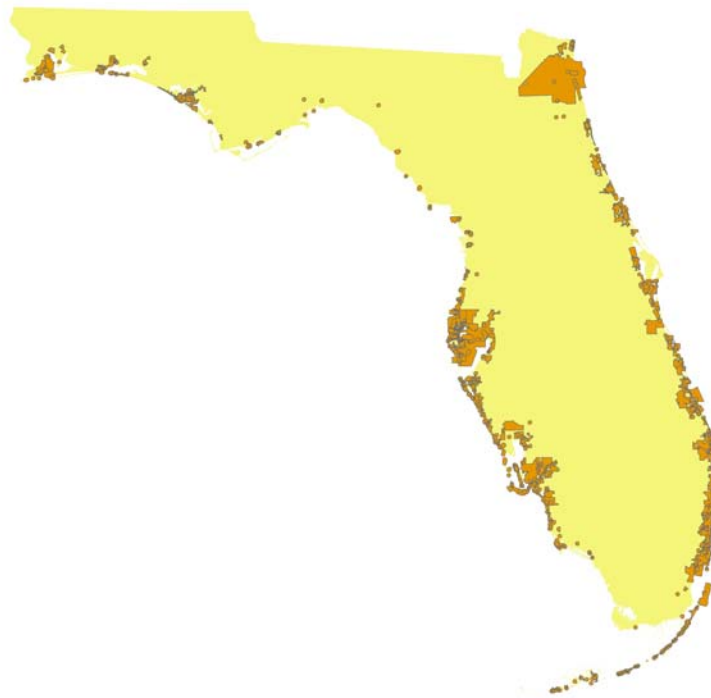


Figure 9. Limit of cities along the Floridian coastline (from www.fgdl.org).

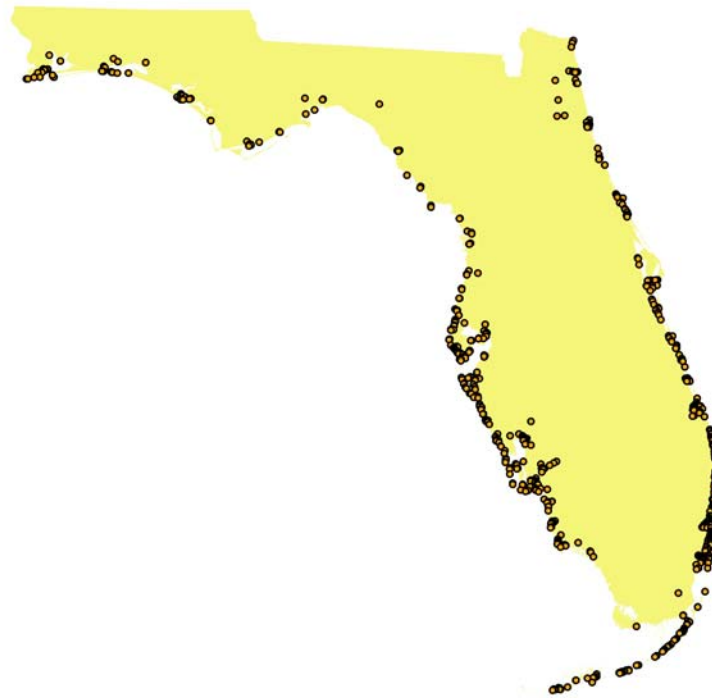


Figure 10. Locations of marinas along the Floridian coastline (from www.fgdl.org).

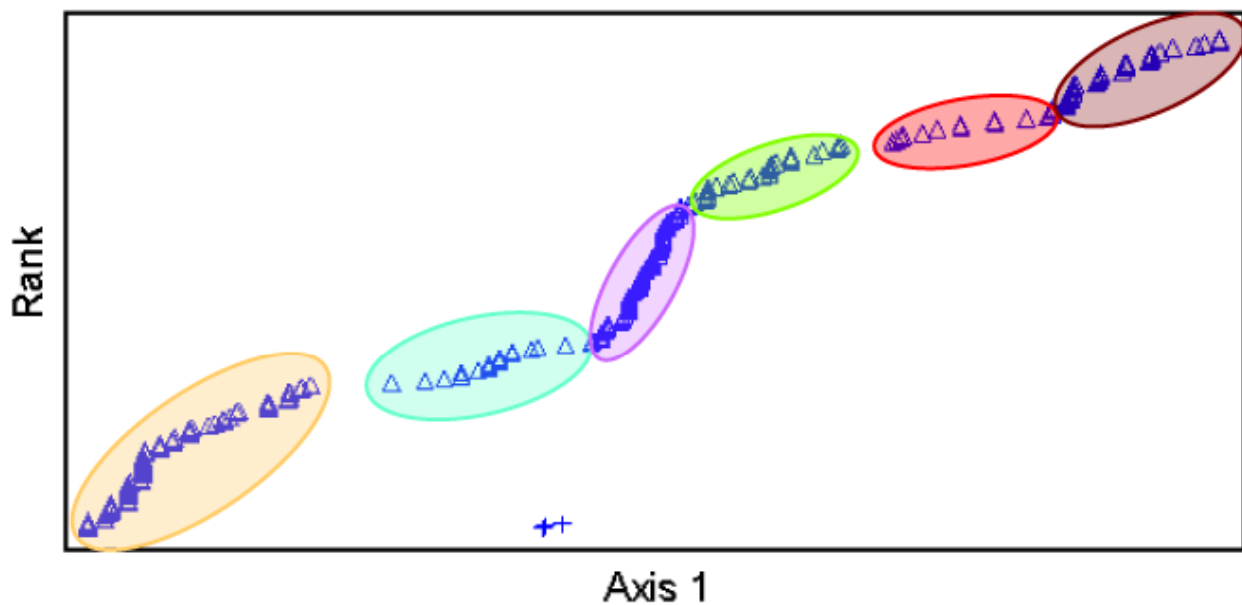


Figure 11. Ordination for each temperature data around the coastline of Florida using PC-ord (MjM Software Design). The six groups show the six different zones of different temperature range used as the base for the stratification of the state.

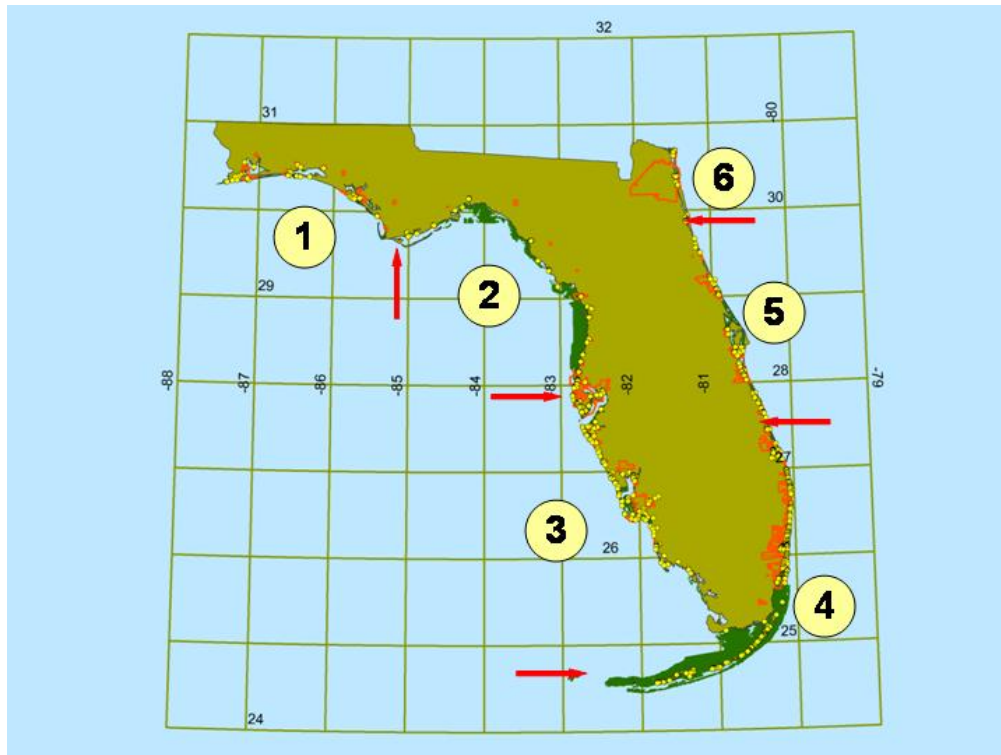


Figure 12. Stratification of the state of Florida into six zones of different temperature ranges. 1 = 16°C – 31.5°C, 2 = 12.5°C – 31.5°C, 3 = 17°C – 31.5°C, 4 = 23°C – 31°C, 5 = 20°C – 30°C, 6 = 12.5°C – 31.5°C.



Figure 13A-D. A. Selection of the zone 5 using ArcMap 9.1.

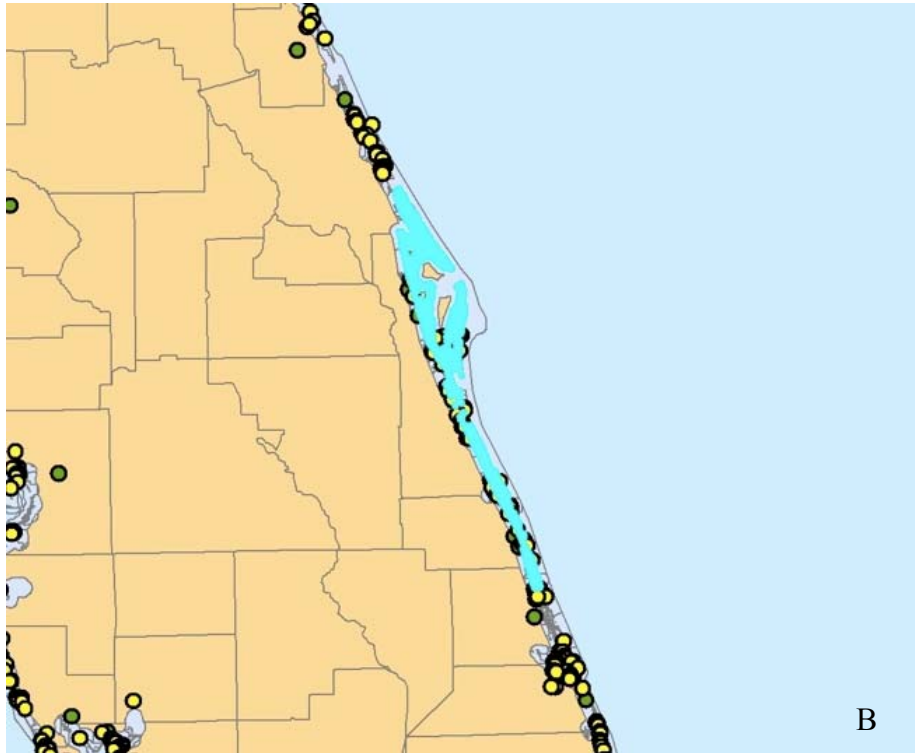


Figure 13. Continued. B. Selection of the zones with seagrass in the zone 5 using ArcMap 9.1

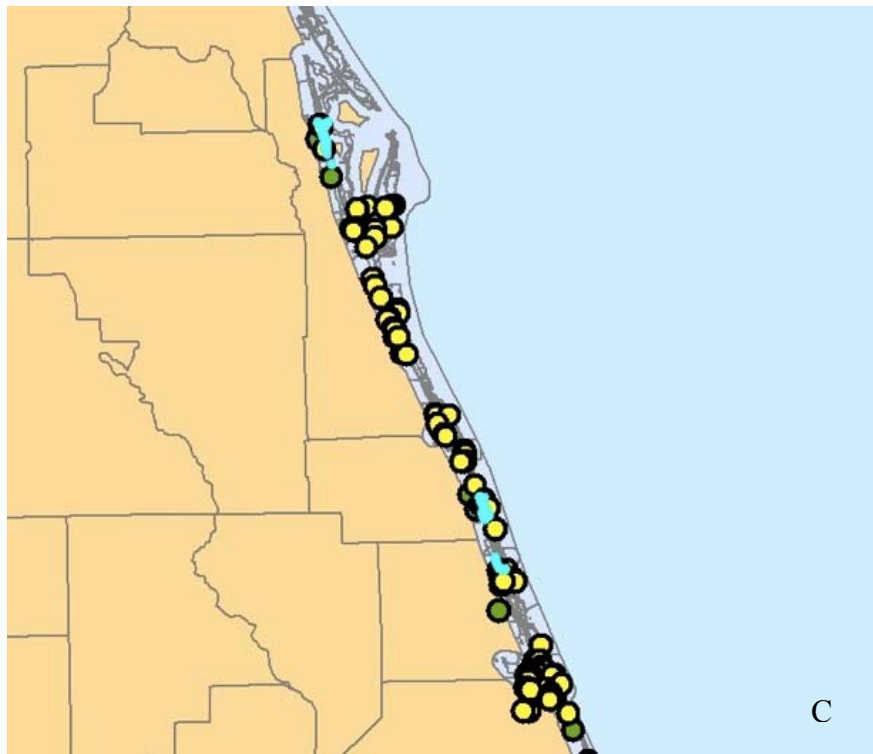


Figure 13. Continued. C. Selection of zones of high population density within the zones with seagrass within the zone 5.



Figure 13. Continued. D. Selection of zones with marinas more than 2 km away within zones with high population density within zones with seagrass within zone 5.

Temperature Zone 1	Seagrass	High Population	MARINA
		Low Population	NO MARINA
	No Seagrass	High Population	MARINA
		Low Population	NO MARINA
Temperature Zone 2	Seagrass	High Population	MARINA
		Low Population	NO MARINA
	No Seagrass	High Population	MARINA
		Low Population	NO MARINA
Temperature Zone 3	Seagrass	High Population	MARINA
		Low Population	NO MARINA
	No Seagrass	High Population	MARINA
		Low Population	NO MARINA
Temperature Zone 4	Seagrass	High Population	MARINA
		Low Population	NO MARINA
	No Seagrass	High Population	MARINA
		Low Population	NO MARINA
Temperature Zone 5	Seagrass	High Population	NO MARINA
		Low Population	MARINA
	No Seagrass	High Population	NO MARINA
		Low Population	MARINA
Temperature Zone 6	Seagrass	High Population	NO MARINA
		Low Population	MARINA
	No Seagrass	High Population	NO MARINA
		Low Population	MARINA

Figure 14. 48 different associations of parameters with the example of figures 13 highlighted in red.

Probability of *Caulerpa* presence in Florida, USA

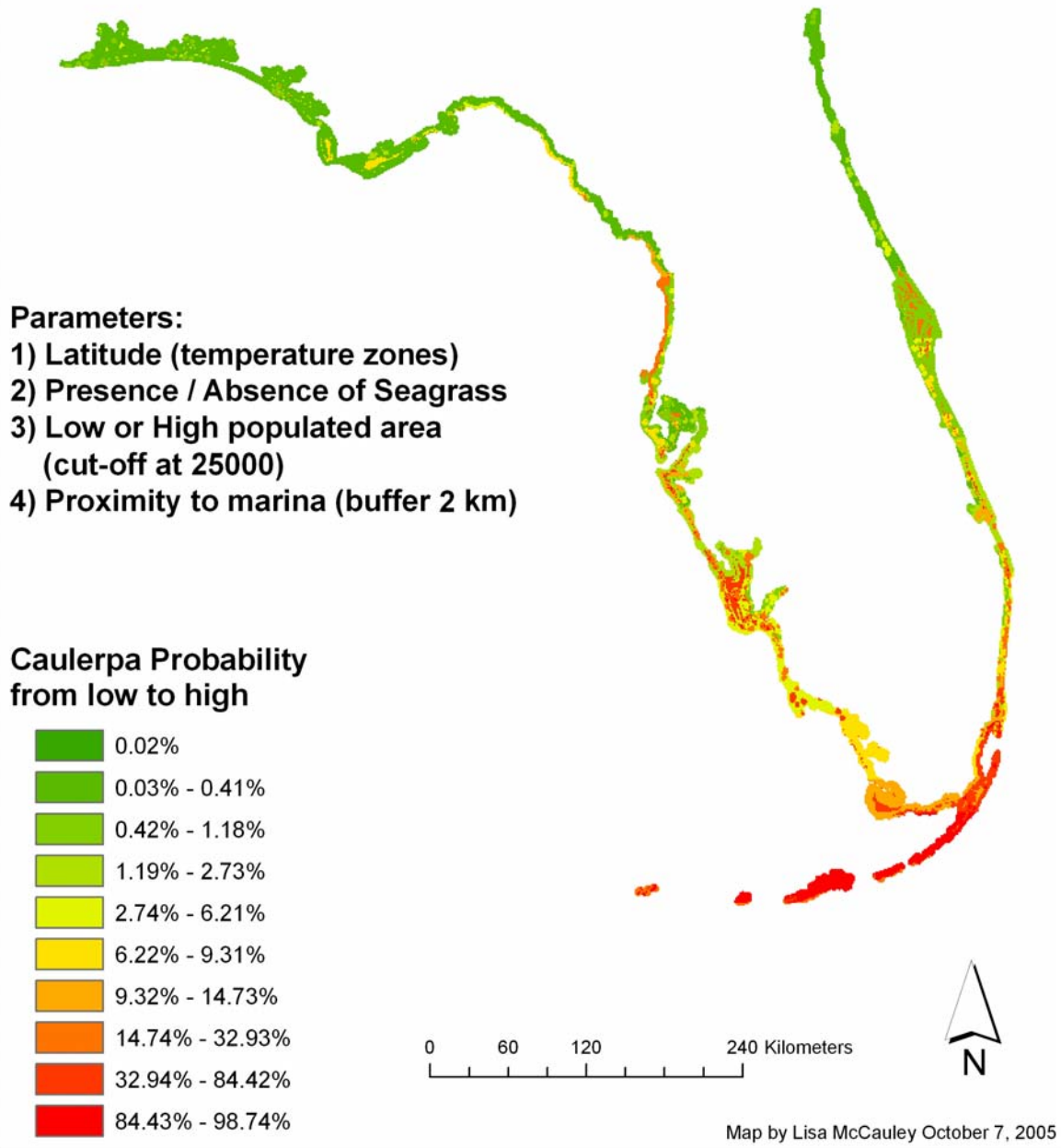


Figure 15. Map showing the probability of *Caulerpa* spp. presence along the Floridian coastline.

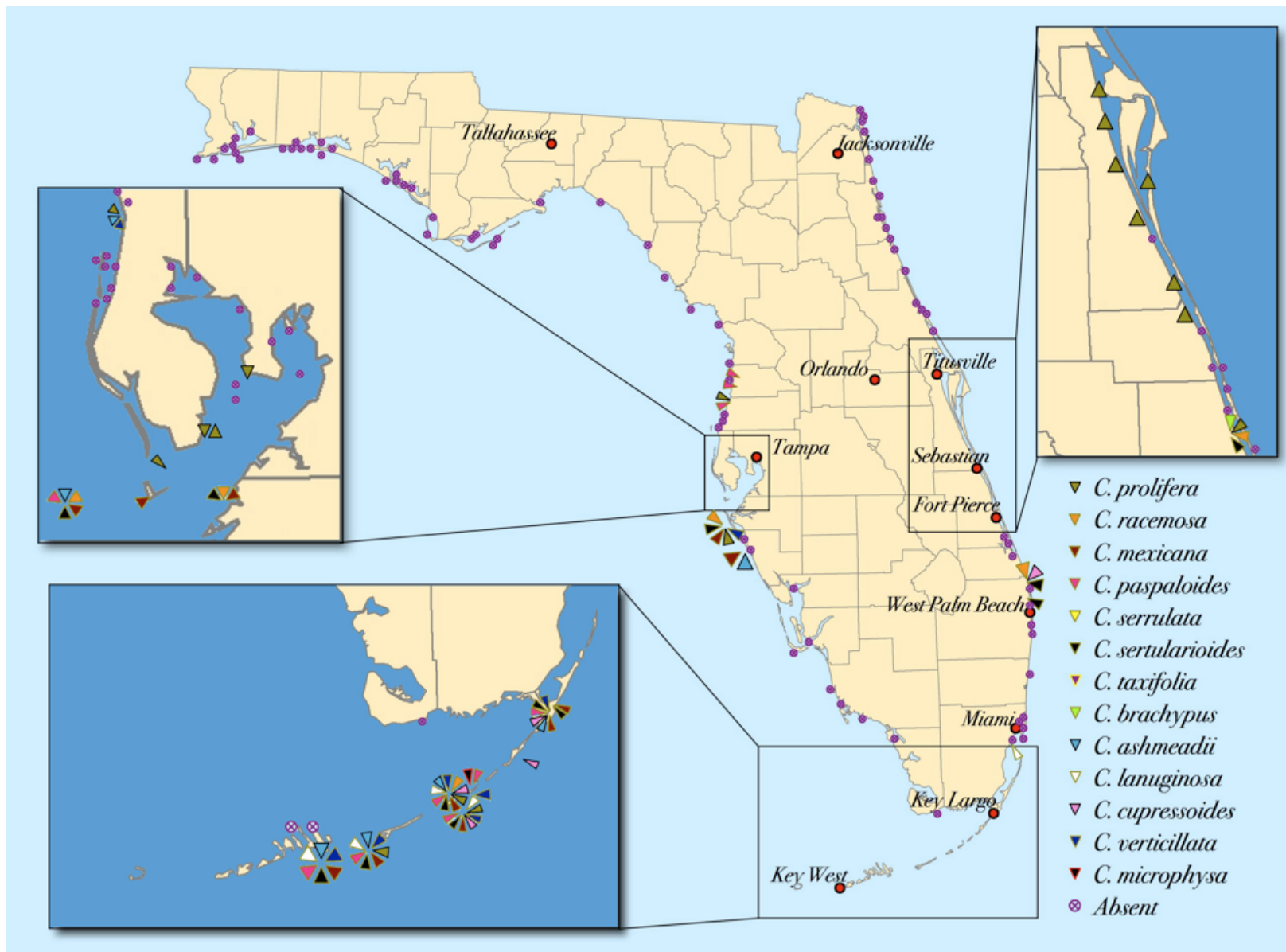


Figure 16. 132 sites surveyed with indication of *Caulerpa* spp. occurrence.

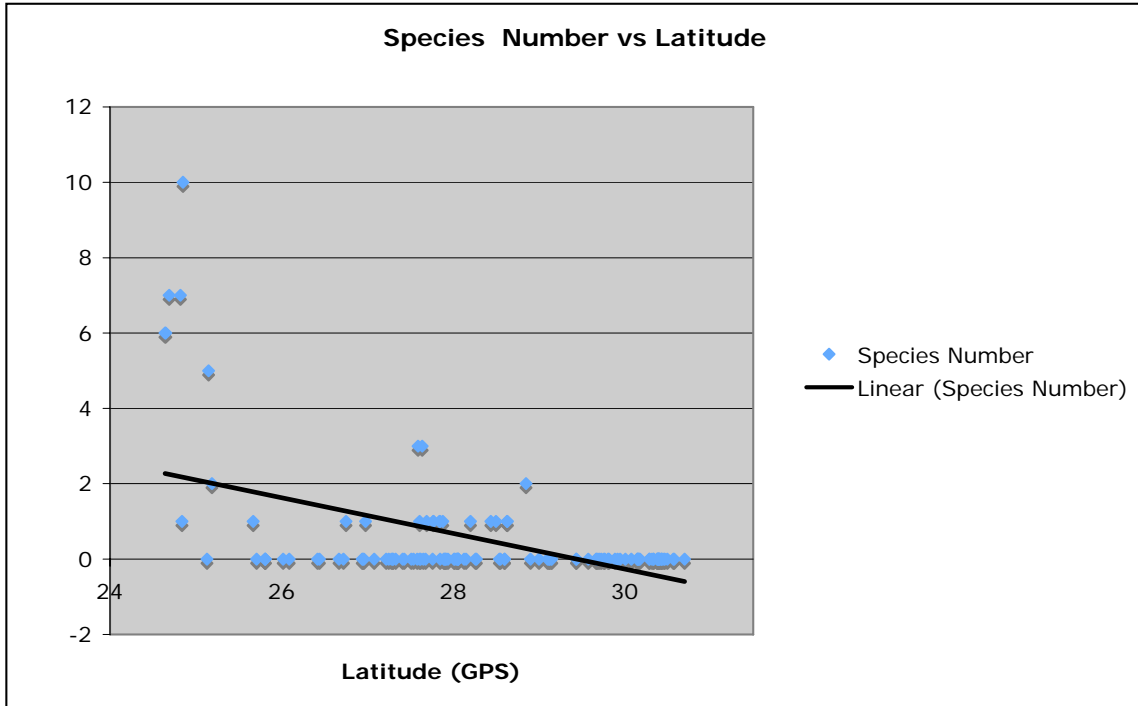


Figure 17. *Caulerpa* species richness plotted against the latitude with associated linear regression.

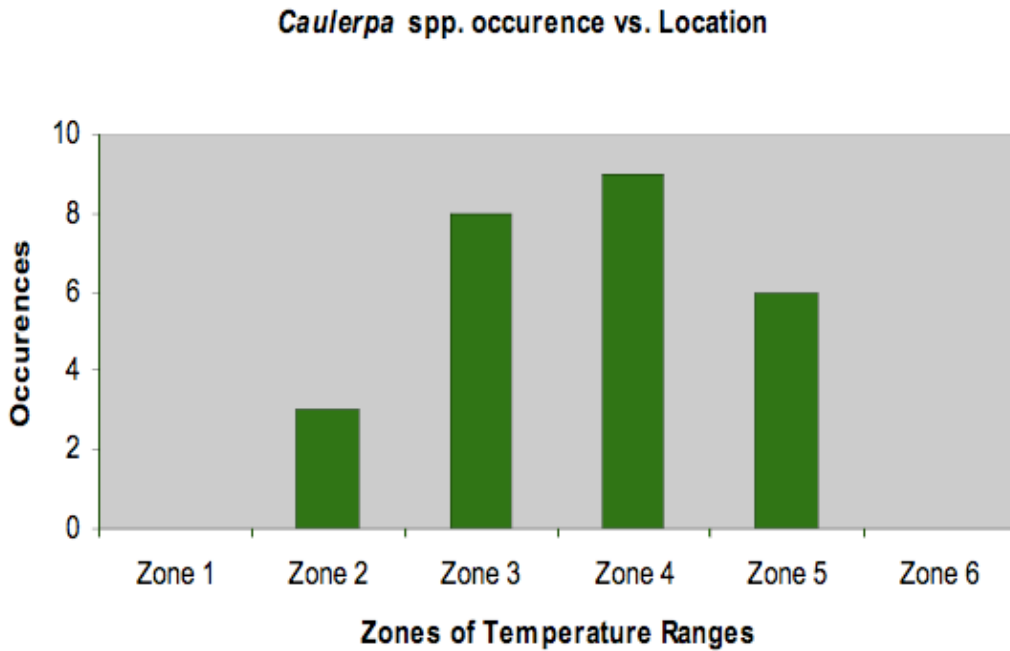


Figure 18. *Caulerpa* spp. occurrences versus latitude. Zone 1 = North West of Florida to longitude 85°W, Zone 2 = longitude 85°W to Tampa at 28°N, Zone 3 = 28°N to Key West (north portion of the Keys), Zone 4 = Key West (south portion of the Keys) to longitude 27°N on the east coast, Zone 5 = longitude 27°N to longitude 29°C, Zone 6 = longitude 29°N to the Georgian border.

APPENDIX B – TABLES

Table 1: Locations where *Caulerpa* spp. have been found with associated parameters. Temperature 1 to 6 and GPS Coordinate. Seagrass, Yes or No. Population Density, High (> 25,000) or Low (< 25,000). Marina, Yes (< 2km) or No (> 2km). Species : a = *C. prolifera*, b = *C. verticillata*, c = *C. ashmeadii*, d = *C. lanuginosa*, e = *C. sertularioides*, f = *C. paspaloides*, g = *C. cupressoides*, h = *C. mexicana*, i = *C. racemosa*, j = *C. microphysa*.

SITE	GPS	T° ZONE	SEAGRASS	POPULATION DENSITY	MARINA	CAULERPA SPP.	T°	SALINITY
STATE CREEK POINT	82°43.222'W 28°51.079'N	2	Y	H	Y	A, F	28	26
RICE CREEK BAY	82°39.600'W 28°30.202'N	2	Y	L	Y	F	29	10
GUN POINT	82°40.317'W 28°26.145'N	2	Y	L	N	F	30	10
THE PIER, TAMPA BAY DEVIL RAYS	82°37'26.78"W 27°46'1.80"N	3	Y	H	Y	A	-	-
MUD BAYOU (CABBAGE KEY), ST- PETERSBURG	82°43'22.96"W 27°41'40.54"N	3	Y	H	Y	A	26	33
PICNIC ISLAND BEACH, TAMPA BAY	82°33.199'W 27°50.860'N	3	Y	H	N	A	-	-
FORT DE SOTO	82°44'14.40"W 27°36'42.65"N	3	Y	L	Y	H	27	36
KEYS MARINE LAB	80°47'57.35"W 24°51'0.49"N	3	Y	L	Y	A, B, C, D, E, F, G, H, I, J	-	-
JOHN PENNEKAMP CORAL REEF STATE PARK	80°23'3.47"W 25°9'7.05"N	3	Y	L	Y	B, C, E, F, G, H	-	-
SKYWAY BRIDGE SOUTH END TAMPA BAY SIDE	82°36'45.33"W 27°35'12.76"N	3	Y	L	N	E, I, H	-	-
LONG KEY STATE PARK	80°49'18.96"W 24°49'24.76"N	3	Y	L	N	A, B, D, E, F, G, H	-	-
RIVIERA BEACH	80°03.161'W 26°45.146'N	4	Y	H	Y	E	29	18

TAHITI BEACH, MIAMI	80°15.670'W 25°40.327'N	4	Y	H	Y	D	34	20
KEY LARGO	80°21'045'W 25°11'494'N	4	Y	L	Y	E, H	32	37
TROPIC VISTA	80°5'24.95''W 26°59'0.51''N	4	Y	L	Y	E	29	33
MARATHON SOUTH	81°6'3823''W 24°41'19.16''N	4	Y	L	Y	A, C, D, E, F, G, H	-	-
BAHIA HONDA KEY	81°16'44.27''W 24°39'15.03''N	4	Y	L	N	A, C, D, E, F, G, H	-	-
CORAL GARDENS	80°42'20.67''W 24°50'19.01''N	4	Y	L	N	G	25	-
LONG PINE KEY SOUTH	81°20'24.25''W 24°38'12.39''N	4	Y	L	N	C, D, E, F, G, H	-	-
FORT PIERCE, SOUTH JETTY	80°17'28.50''W 27°38'15.68''N	4	N	H	Y	A, I, E	-	-
TITUSVILLE, ACROSS THE BRIDGE NORTH	80°48'58.29''W 28°37'40.41''N	5	Y	H	Y	A	28	30
MICCO	80°29'49.97''W 27°52'42.44''N	5	Y	L	Y	A	29	27
ROSELAND	80°28'36.33''W 27°50'18.76''N	5	Y	L	Y	A	29	27
LAGRANGE	80°49'03.39''W 28°37'4823''N	5	Y	L	Y	A	-	-
MERRITT ISLAND SOUTH	80°37'56.03''W 28°11'55.02''N	5	Y	L	N	A	-	-
ORCHID ISLAND	80°25'30.2''W 27°46'06.87''N	5	N	L	Y	A	-	-

Table 2: Summary statistics for the nested logistic regression for species richness.

Dependent	Mth	Rsq	d.f.	F	Sigf	b0	b1
TOTSP	Inv	0.297	130	54.9	0	-13.278	389.697

Table 3: Summary of Akaike's information criteria and associated statistics for the nested logistic regression models of *Caulerpa* occurrence data in the Florida Peninsula.

Model	-2 Log likelihood	par	AIC	AIC dif	weights	
gps, seagrass, marina, population	64.11	6	76.111	0	1	0.83192597
gps, seagrass, marina	69.49	5	79.495	3.384	0.184140179	0.153190997
gps, seagrass, population	74.53	5	84.53	8.419	0.014850633	0.012354627
gps, seagrass	79.74	4	87.744	11.634	0.002977128	0.00247675
marina, seagrass, population	85.91	5	95.906	19.795	5.02896E-05	4.18372E-05
marina, seagrass	92.78	4	100.778	24.667	4.40085E-06	3.66118E-06
seagrass, population	92.78	4	100.778	24.667	4.40085E-06	3.66118E-06
gps, marina, population	92.85	5	102.848	26.737	1.5633E-06	1.30055E-06
gps, marina	96.20	4	104.197	28.086	7.96361E-07	6.62514E-07
seagrass	99.04	3	105.039	28.929	5.2262E-07	4.34781E-07
gps, population	100.81	4	108.811	32.700	7.92853E-08	6.59595E-08
gps	104.26	3	110.255	34.144	3.85152E-08	3.20418E-08
marina, population	121.02	4	129.020	52.909	3.24254E-12	2.69756E-12
marina	126.10	3	132.098	55.987	6.95801E-13	5.78855E-13
population	126.10	3	132.098	55.987	6.95801E-13	5.78855E-13
			76.11057446		1.202030032	1

Table 4: Summary of Akaike’s information criteria and associated statistics for the nested logistic regression models of *Caulerpa prolifera* occurrence data in the Florida Peninsula.

Model	-2 Log likelihood	par	AIC	AIC dif	weights	
gps, seagrass, marina	71.15	5	81.148	0	1	0.681715264
gps, seagrass	76.21	4	84.213	3.065	0.215995004	0.147247091
marina, seagrass	76.82	4	84.819	3.671	0.159533715	0.108756569
gps, marina	80.18	4	88.179	7.031	0.029732933	0.020269394
seagrass	81.00	3	86.997	5.849	0.053691531	0.036602336
gps	85.01	3	91.008	9.86	0.007226503	0.004926418
marina	89.65	3	95.653	14.505	0.000708401	0.000482928
			81.148	1.466888087		1

Table 5: Summary statistics for the best models for all species and single species occurrences.

Model	percent correct	model parameters				
		constant	gps	seagrass	popdens	marina
gps, seagrass, marina, population (all species)	90.9	21.029	-0.918	3.741	-1.491	2.127
gps, seagrass, marina (<i>prolifera</i>)	87.9	7.603	-0.427	2.081		1.428
gps (<i>paspalooides</i>)	94.7	24.85	-1.008			
gps (<i>mexicana</i>)	97	41.026	-1.628			
gps (<i>sertularioides</i>)	95.5	32.203	-1.282			

APPENDIX C – COPYRIGHTS

Christian Glardon
5461-H Lake Margaret Drive
Orlando, FL 32812

March 14, 2006

University of Florida, IFAS
Center for Aquatic and Invasive Plants
7922 NW 71st Street
Gainesville, FL 32653

Dear Ms. Brown,

This letter will confirm our recent email conversation. I am completing a master's degree at the University of Central Florida entitled "Predicting Risks of Invasion of *Caulerpa* Species in Florida." I would like your permission to reprint in my dissertation excerpts from the following:

<http://plants.ifas.ufl.edu/seagrant/cautax2.html#pauthor>

The excerpt to be reproduced is: the illustration of *Caulerpa taxifolia*.

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Sincerely,
Christian Glardon

PERMISSION GRANTED FOR THE USE REQUESTED ABOVE:



By: Ms. Karen Brown, University of Florida, IFAS, Center for Aquatic and Invasive
Plants 352-392-1799

Date: March 14, 2006

Fig 1

Copyright Figure 1. *Caulerpa taxifolia* - aquarium strain (Vahl) C. Agardh.
University of Florida.

Subject: Re: Photo use permission 2
Date: Tuesday, March 14, 2006 11:13 AM
From: Alexandre.MEINESZ@unice.fr
To: Christian Glardon <cglardon@mac.com>
Conversation: Photo use permission 2

Fig 2,6

Bonjour
Pas de problèmes ! Vous avez mon autorisation de publier mes photos !
Votre thèse est sur quel sujet ?

A. Meinesz

Christian Glardon a écrit :

> Cher monsieur Meinesz,
>
> J'ai aussi demandé à monsieur David Hill la permission d'utiliser une
> image. Il m'a répondu et m'a demandé de vous adresser la question. Je
> vous envoie donc une nouvelle lettre avec les 2 images concernées. Je
> répète ci-dessous la raison de cet échange.
>
> Je suis en train de terminer ma thèse de master en Biologie à
> l'université central de Floride. J'ai utilisé dans cette thèse l'image
> attachée. Les droits d'utilisation de cette image dans ma thèse
> m'oblige à vous demander l'autorisation pour sa publication dans ma
> thèse de Master seulement. Aussi, si autorisation il y a de votre
> part, je joins également la lettre (format imposé par l'université)
> qui devrait être signée par l'auteur de cette illustration et jointe
> ensuite à mon travail de thèse. Si vous acceptez, pourriez-vous
> s'il-vous-plaît compléter la lettre, donnant votre adresse là où j'ai
> mis un point d'interrogation?
>
> J'espère beaucoup en votre aide afin que ma thèse de Master puisse
> inclure cette image.
>
> En l'attente de votre réponse, je vous prie monsieur de recevoir
> l'expression de mes sentiments distingués,
>
>
> Christian Glardon
>
>
> /Christian Glardon
>
> Master of Science Candidate
> Department of Biology
> University of Central Florida
> Orlando, FL
> cglardon@mac.com
> /
> /
> /
>
> -----
>
> -----
>

Copyright Figure 2. *Caulerpa taxifolia* - aquarium strain in the Mediterranean Sea
Dr. Alexandre Meinesz, University of Nice, France.

Christian Glardon
5461-H Lake Margaret Drive
Orlando, FL 32812

March 25, 2006

Rachel Woodfield
5434 Ruffin Rd
San Diego, CA 92123

Dear Ms. Woodfield ,

This letter will confirm our recent phone/email conversation. I am completing a master's degree at the University of Central Florida entitled "Predicting Risks of Invasion of *Caulerpa* Species in Florida." I would like your permission to reprint in my dissertation excerpts from the following:

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Sincerely,
Christian Glardon

PERMISSION GRANTED FOR THE USE REQUESTED ABOVE:

By: Rachel Woodfield
Date: 14 Mar 06

Rachel Woodfield

Please credit photo - Rachel Woodfield

Fig 3

Copyright Figure 3. *Caulerpa racemosa* (Forsskål) J. Agardh. Rachel Woodfield, CA, USA.

Christian Glardon
5461-H Lake Margaret Drive
Orlando, FL 32812

March 25, 2006

Harbor Branch Oceanographic Institution
5600 US 1 North
Ft. Pierce, FL 34946

Dear Mr. Schrope ,

This letter will confirm our recent email conversation. I am completing a master's degree at the University of Central Florida entitled "Predicting Risks of Invasion of *Caulerpa* Species in Florida." I would like your permission to reprint in my dissertation excerpts from the following:

<http://www.hboi.edu/marinesci/dynamics.html>

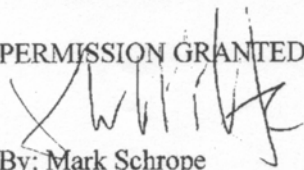
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Sincerely,
Christian Glardon

PERMISSION GRANTED FOR THE USE REQUESTED ABOVE:


By: Mark Schrope

Date: April 11, 2006

Copyright Figure 4. *Caulerpa brachypus* Harvey. Harbor Branch Oceanographic Institution, FL, USA.

Christian Glardon
5461-H Lake Margaret Drive
Orlando, FL 32812

Fig 5

April 9, 2006

Dr. John Huisman,
School of Biological Sciences and Biotechnology, Murdoch University, Murdoch, WA,
6150, Australia. Email: J.Huisman@murdoch.edu.au

This letter will confirm our recent email conversation. I am completing a master's degree at the University of Central Florida entitled "Predicting Risks of Invasion of *Caulerpa* Species in Florida." I would like your permission to reprint in my dissertation excerpts from the following:

http://www.algaebase.org/SpeciesDetail.lasso?species_id=1411&-session=abv3:D03CB10D0a02e01285Xjho2CF4A1#

The excerpts to be reproduced are: the photo of *Caulerpa scalpelliformis*.

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If these arrangements meet with your approval, please sign this letter where indicated below and return it to me in the enclosed return envelope. Thank you for your attention in this matter.

Sincerely,
Christian Glardon

PERMISSION GRANTED FOR THE USE REQUESTED ABOVE:

By: Dr. John Huisman



Date: April 10, 2006

Copyright Figure 5. *Caulerpa scalpelliformis* (Turner) C. Agardh. Dr. John Huisman, Australia.

Subject: Re: About one image in my thesis
Date: Sunday, April 9, 2006 7:06 PM
From: Jean de Vaugelas <vaugelas@hermes.unice.fr>
To: Christian Glardon <sonatedesheimes@hotmail.com>
Conversation: About one image in my thesis

Fig 6

>Cher Monsieur Vaugelas,
>
>Cet email vous avais été transféré il y a quelque temps. Malheureusement je
>n'ai toujours pas eu de réponse de votre part et le temps qu'il me reste
>pour donner ma thèse à l'éditeur est très court.
>
>J'espère avoir une réponse de votre part cette semaine.

Monsieur,

Je suis désolé de ce contretemps mais j'avais
prévenu David Hill déjà la semaine dernière qu'il
n'y avait pas de problèmes pour utiliser cette
carte dans votre thèse.

Je pensais qu'il vous avait communiqué notre autorisation.

Bien sincèrement,

Jean de Vaugelas

--
Dr. Jean de Vaugelas
LEML et AquaScience
Université de Nice-Sophia Antipolis
Parc Valrose
06108 Nice cedex 02
Tel. travail (33) 04 92 07 68 21
Tel. port (33) 06 11 34 81 24
Mail : vaugelas@unice.fr

Subject: Re: [Fwd: About one image in my thesis]
Date: Thursday, March 16, 2006 4:15 AM
From: David R.C. Hill <drch@isima.fr>
To: <Jean.VAUGELAS@unice.fr>
Cc: <cglardon@mac.com>
Conversation: [Fwd: About one image in my thesis]

Fig. 6

Salut Jean,
Merci pour ta réponse, et désolé pour
les codes cabalistiques ;)
Voilà l'image en JPEG dont parle Christian
ci-dessous (et en cc:)

Amités

david

Bonjour David,

Merci de votre prompte réponse. J'ai trouvé cette image sur
<http://www.sbg.ac.at/ipk/avstudio/pierofun/ct/caulerpa.htm>
de Pierre MADL et Maricela YIP.

Merci beaucoup,

Christian Glardon

Copyright Figure 6. *Caulerpa taxifolia* – aquarium strain: sightings in the western-Mediterranean Sea until 1997. Jean Vaugelas University of Nice, France.

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