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ORIGINAL PAPER

Predicting risks of invasion of macroalgae in the genus *Caulerpa* in Florida

Christian G. Glardon · Linda J. Walters · Pedro F. Quintana-Ascencio · Lisa A. McCauley · Wytze T. Stam · Jeanine L. Olsen

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Abstract 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. Since that time, it has flourished and now covers thousands of hectares of near-shore waters. More recently, aquarium strains of *C. taxifolia* invaded southern California and Australian waters. Our goal was to evaluate potential invasion of *C. taxifolia* to Florida's coastal waters. We looked for evidence of *C. taxifolia*—aquarium strain, as well as the present distribution of all species of *Caulerpa*, in Florida's near-shore waters. We surveyed 24 areas in six zones along the Floridian coastline, and evaluated the association of potential indicators for the presence of *Caulerpa*. Latitude, presence of seagrass beds, human population density, and proximity to marinas were the four variables simultaneously considered. *Caulerpa taxifolia*—aquarium strain was not found at any of our survey locations. However, 14 species of *Caulerpa* were found at 31 of the 132 sites visited. Percent correct for our model was 61.5% for presence and 98.1% for absence. There was a positive correlation between *Caulerpa* spp. and seagrass beds and proximity to marinas. There was a negative correlation with latitude and human population density. The parameters in the logistic regression model assessing the association of *Caulerpa* occurrence with the measured variables were then used to predict current and future probabilities of *Caulerpa* spp. presence throughout the state. This prediction model will allow resource managers to focus their efforts in future surveys.

Keywords Algae · *Caulerpa taxifolia* · Chlorophyta · Coastal · Invasive species · Prediction models

C. G. Glardon · L. J. Walters · P. F. Quintana-Ascencio (✉) · L. A. McCauley
Department of Biology, University of Central Florida, 4000 Central Florida Blvd., Orlando, FL 32816, USA
e-mail: pquintan@mail.ucf.edu

W. T. Stam · J. L. Olsen
Department of Marine Benthic Ecology and Evolution, Biological Centre, University of Groningen, Kerklaan 30, P.O. Box 14, 9750 AA Haren, The Netherlands

Introduction

The introduction of non-indigenous species has been recognized as a major environmental problem for over 100 years (e.g., Bax et al. 2001; McNeely 2001; Loope and Howarth 2003; Barnard and Waage 2004; Perrings et al. 2005). In the marine environment, macroalgae in the genus *Caulerpa* are of particular concern because of their recent expansions, ability to propagate from asexual fragments, and negative impacts on the invaded communities. *Caulerpa taxifolia*—aquarium strain (Vahl) C. Agardh, known worldwide as the "killer alga," was first observed in

Mediterranean waters adjacent to the Monaco Oceanographic Museum in 1984 (Meinesz and Hesse 1991; IUCN 2003). It spread from an initial patch of $\sim 1^2$ m to cover hundreds of kilometers of Mediterranain coastline, where it has overgrown all native flora and fauna, impacting fisheries and tourism in coastal communities (e.g., Meinesz and Hesse 1991; Relini et al. 2000; Meinesz et al. 2001; Meinesz 2002). In 2000, *C. taxifolia*—aquarium strain was discovered in two lagoons in southern California (Jousson et al. 2000) and in New South Wales, Australia in the Port Hacking, Careel Bay and Lake Conjola regions (Grey 2001; Wiedenmann et al. 2001; Millar and Talbot 2002; Schaffelke et al. 2002). Eradication was successful in California (R. Woodfield, personal communication), while its spread continues in Australia (Millar 2004). It is suspected that human activities, either boating or aquarium releases, were responsible for all invasions (e.g., Meinesz 1999; Raloff 2000; Millar and Talbot 2002).

Several other *Caulerpa* species may be able to outcompete native macrophytes and create monospecific beds (Verlaque and Fritayre 1994; Piazzi et al. 2001; Piazzi and Ceccherelli 2002, 2006). Since 1990, *C. racemosa* var. *cylindracea* has been rapidly spreading and dramatically expanding throughout the Mediterranean Sea and Canary Islands (Verlaque et al. 2000, 2003; Ruitton et al. 2005). Similarly, in 2001, non-native *C. brachypus* created concern along the east coast of south Florida, where it was locally abundant, displacing native flora and fauna (Schrope 2003; Jacoby et al. 2004; SFER 2005). *Caulerpa brachypus* spread north into the Indian River Lagoon system, which was consistent with prevailing coastal currents, but it has not been reported in west Florida (Schrope 2003). Most *C. brachypus* did not survive Hurricanes Frances and Jeanne that battered Florida in the late summer of 2004 (B. LaPointe, personal communication).

Florida's coastline closely matches environmental conditions of other areas invaded by *C. taxifolia*—aquarium strain and the risk is significant that this state will be invaded in the near future. Non-invasive *C. taxifolia* has a lower lethal temperature of 14°C, while mortality of the aquarium strain of *C. taxifolia* from Mediterranean waters is 7°C (Komatsu et al. 1994; Ramey 2001). Seagrasses are frequently associated with various *Caulerpa* species. In some cases, the presence of one can facilitate the other through stabilization of the substrate (Williams 1984, 1990; Smith and Walters 1999; Magalhaes et al. 2003). In disturbed areas, however, the situation is different (e.g., Stafford and Bell 2006). In a number of areas along the Mediterranean coastline, *C. taxifolia* was able to outcompete *Posidonia oceanica* (Chisholm and Jaubert 1997; Villele and Verlaque 1994) and *Cymodocea nodosa* (Relini et al. 1998a, b, c).

High human population density may increase or decrease the probability of a marine macrophyte invasion. Boaters increase the potential and frequency of transport via fragments and propagules in ballast tanks, live wells, or attached to propellers and hulls. Along the French Mediterranean coast, all areas colonized by invasive *C. racemosa* var. *cylindracea* (Sonder) Verlaque, Huisman et Boudouresque were associated with human activities and over 40% were in fishing areas (Ruitton et al. 2005). Releases of aquarium organisms into storm drains or local waterways by well-meaning hobbyists will also increase as the population density and number of aquaria increases. Although the aquarium strain of *C. taxifolia* is banned from importation and interstate transport in the USA, other species of *Caulerpa* remain very popular with hobbyists. For example, non-invasive strains of *C. taxifolia* and 12 additional species of *Caulerpa* are readily available via local and Internet retailers as well as Internet auction sites (Walters et al. 2006; Zaleski and Murray 2006). Coastal population pressure also holds a higher potential for greater pollutant loads, freshwater and nutrient run-offs; these may prevent or increase algal growth (Morand and Merceron 2005). In the Mediterranean, *C. taxifolia*—aquarium strain was concentrated in zones with extensive development (Madl and Yip 2005).

Considering the length of Florida's shoreline and the economic and environmental importance of these waters, it is urgent to be prepared for a human-mediated introduction of *Caulerpa*. Our goal was to determine locations that are most susceptible to *Caulerpa* invasion by aquarium releases or boating activities, and that would be most suitable for recruitment of species of the genus *Caulerpa*. Being able to concentrate on areas that are more at risk would greatly help prevention and eradication efforts. Two questions are fundamental to this goal: (1) What habitat(s) are most suitable for *Caulerpa*?, (2) What areas are most likely to be invaded, especially if home aquarium releases or recreational boating are involved?

Methods

We used a stratified sampling design to assess the current distribution of *Caulerpa* spp. along the Florida shoreline and then to test the association of *Caulerpa* spp. occurrence with variables allowing us to evaluate its risks of invasion (see below). We chose to stratify the Florida shoreline to reflect the latitudinal and longitudinal variation in water temperature, seagrass presence/absence, local human population density, and the presence/absence of boat marinas. All GIS data were downloaded from the Florida Geographic Data Library (2006).

We obtained bi-monthly sea surface temperature for the Floridian coastline (2001–2004). Data were available as a grid of 14 km per side (Comprehensive Large Array-Data Stewardship System: http://www.class.noaa.gov). We transferred the temperature data along the coastline to an Excel spreadsheet (207 pixels) and performed a non-metric, multi-dimensional scaling ordination for each summary temperature (monthly, seasonal, and annual) using PC-Ord (McCune and Grace 2002). The mean temperature for January each year had the largest range of temperatures and sorted into six distinct groups (Fig. 1). We used gaps or switches in the values of the final single ordination axes to define the groups. From the western extreme of the Floridian coastline, the first zone ended at 85°W longitude; the second zone ended near Tampa at 28°N; the third zone went down to Key West, FL Keys; the fourth went from Key West up the east coast to longitude 27°N; the fifth up to the longitude 29°N; and the sixth up to the Georgia border (Fig. 2). In our analysis we used latitude instead of temperature because there was a significant correlation between temperature and latitude (-0.94, $n = 207$); this allowed us to directly map the model results.

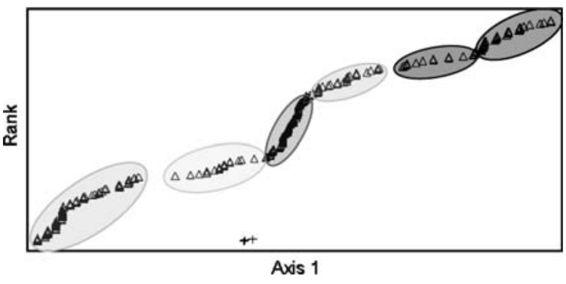

Fig. 1 Single axes of a non-metric, multi-dimensional scaling ordination for temperature data around the coastline of Florida (MPC-Ord MjM Software Design). The six groups show the six different zones of different temperature range used as the basis for the stratification of the state

We considered all seagrasses occurring in Florida, including *Halodule wrightii*, *Syringodium filiforme*, *Thalassia testudinum*, *Halophila johnsonii*, *Halophila decipiens*, *Halophila engelmanii*, and *Ruppia maritime* (Virnstein and Morris 1996). GIS coverages of their distribution around the coastline of Florida were available from a number of sources: Florida Fish and Wildlife Conservation Commission, Florida Marine Research Institute and Coastal and Marine Resource Assessment (Fig. 2). We arbitrarily chose 25,000 inhabitants within the city limits to be the cut-off between low human-impacted and high human-impacted areas. Boat traffic transporting species from one area to another makes marinas prone to becoming primary invasion sites (Boudouresque et al. 1995; Loope 2004). Docks are also frequently areas where people have easy access to marine environment, making them logical locations for disposing of unwanted aquarium plants and animals. Marinas are well represented around the state of Florida (FGDL 2006) (Fig. 2).

Bathymetry was not chosen as a variable because our sampling was restricted to depths of <10 m. This should, however, not pose a problem since most native *Caulerpa* spp. occur above 20 m (Littler et al. 1989). Thibaut et al. (2004) also reported higher biomasses of *C. taxifolia*—aquarium strain between 6 and 10 m. However, invasive *C. racemosa* var. *cylindracea* along the French Mediterranean coast was found primarily between 10 and 35 m (Ruitton et al. 2005). Substrate type (e.g., grain size) and shoreline vegetation were not chosen because of the lack of support from the literature that would give an eventual correlation with marine species occurrence. Water chemistry was not used because data was limited to certain stations and did not cover the entire coastline.

Using ArcMap 9.1, we combined data layers of five variables: latitude and longitude (as continuous variables), and seagrass presence/absence, local low/high human population density, and presence/absence

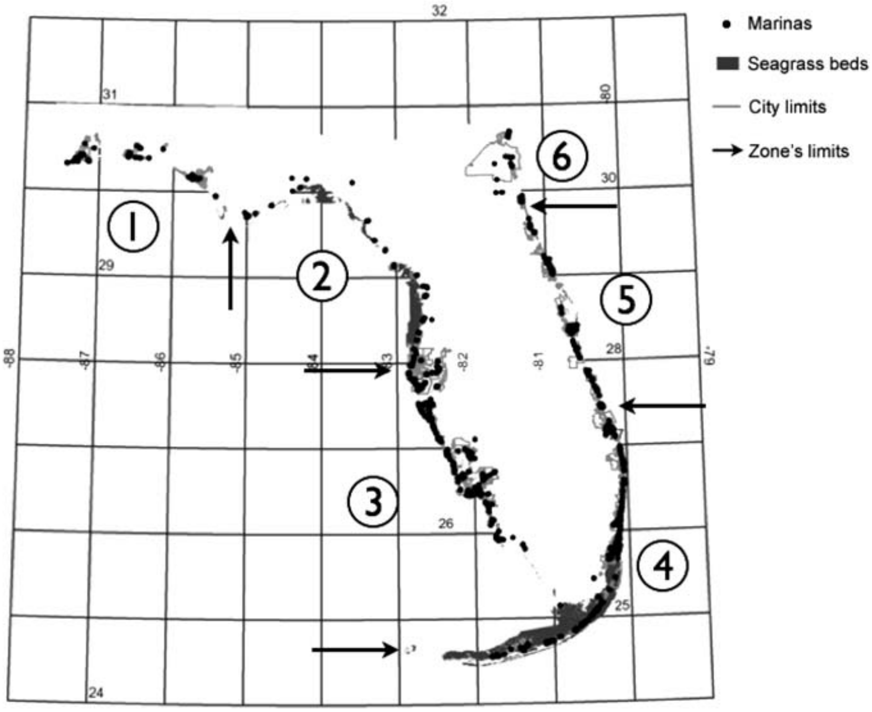

Fig. 2 Stratification of the state of Florida into six zones of different temperature ranges (1 = 16–31.5°C, 2 = 12.5–31.5°C, 3 = 17–31.5°C, 4 = 23–31 C, 5 = 20–30°C, and 6 = 12.5–31.5°C), and locations of seagrass beds, marinas, and areas with >25,000 people per square mile

of boat marinas (as categorical variables). A line data layer of the Florida coastline was buffered by 3 km in order to integrate lagoons and estuaries. We concentrated only on recruitment that might have resulted from a release from a marina. Hence, the data layer for marinas had a buffer of 2 km around each marina. The spreading of *Caulerpa* fragments showed that there is a gradient of natural fragment dispersal over short distances (several hundred meters, Hill et al. 1998). City/town (with city limits) and seagrass presence/absence data layers were merged with the buffered marinas data layer. The marina/seagrass/city data layer was merged with the buffered temperature zones data layer and the merged data layer was clipped to the extent of the zones layer (3 km around the entire coastline).

We used this map to delimit the areas that corresponded to all the possible combinations of parameters and for choosing our survey locations (Fig. 2). Within each delimited area for the 48 different associations of variables (six zones × three replicates × 2^3 = 144 locations), we randomly choose three sample points after eliminating areas that were inaccessible (i.e., US Air Force Bases). Exact GPS coordinates were used to access each location using a handheld Garmin e-Trex GPS receiver (accuracy < 14 m). Once on site, we snorkeled over a rectangular area that extended 20 m perpendicular from the shoreline and 100 m parallel the shoreline (centered on the GPS point), and recorded the presence of each species of *Caulerpa*.

We located and surveyed 132 points of the 144 points anticipated, and entered the data in an Excel spreadsheet. Twelve points were not considered because the sixth temperature zone (northeast Florida) did not have any seagrass. During the fieldwork, we confirmed the association of the point with the anticipated state of the variables in each location.

We used multiple logistic regression models (all possible nested models; SPSS 11.0, MacOSX) to test the association of *Caulerpa* with the four independent variables: GPS latitude coordinate, presence of seagrass (present/absent), population density (high/low), and proximity to marina (with the 2 km buffer zone/outside the 2 km buffer zone). We next used the Akaike's Information Criterion (AIC) to select the "best" multiple linear regression model (Burnham and 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. We created a 1,000 × 1,000 m^2 cell grid from the initial data layer described above

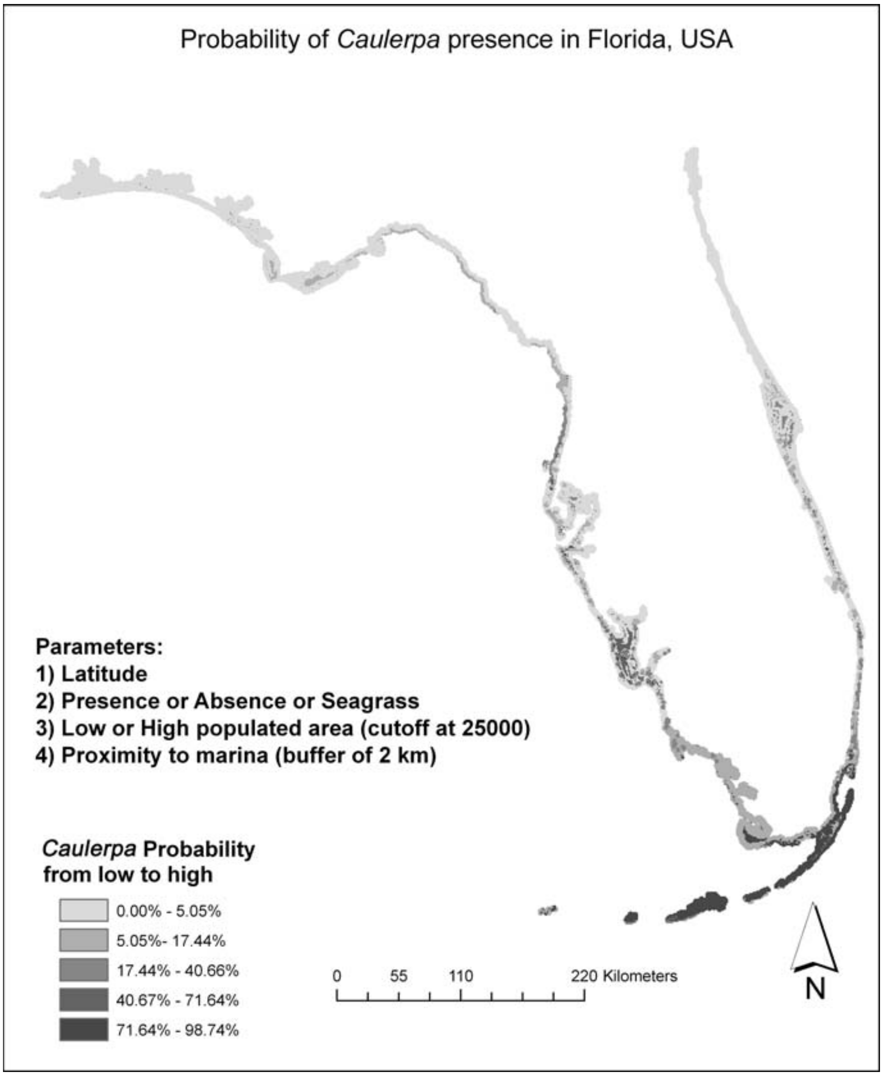

Fig. 3 Probability of *Caulerpa* spp. presence along the coastline of Florida based on logistic regression using latitude, seagrass presence/absence, population density, and marina proximity. The best model was selected using Akaike's Information Criterion

and the centroid of each cell was used to assign the environmental variables for that cell. We predicted the probability of *Caulerpa* presence in each cell using the parameters of the best logistic regression model and created a graduated color map for the entire state showing these probabilities for the entire coast of Florida (Fig. 3). The probability ranges were chosen to reflect the maximum heterogeneity of the data.

Results

We found *Caulerpa* in 31 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) (Fig. 4). No *C. taxifolia* was observed in our surveys. Among the 31 sites where *Caulerpa* species were found, 24 were in seagrass beds. Eighteen of the 31 sites where *Caulerpa* species were found were in locations with low populations (<25,000 inhabitants). Eighteen of the 31 sites with *Caulerpa* spp. were within 2 km of a marina (<2 km). Local species richness of *Caulerpa* increased as latitude decreased (an inverse relationship), and with the presence of seagrass, and decreased with human density ($r^2 = 0.378$, $n = 132$, $P < 0.0001$, and $y = -11.733 + 346.255/\text{GPS} + 0.647 \times \text{seagrass}—0.604 \times \text{population density}$).

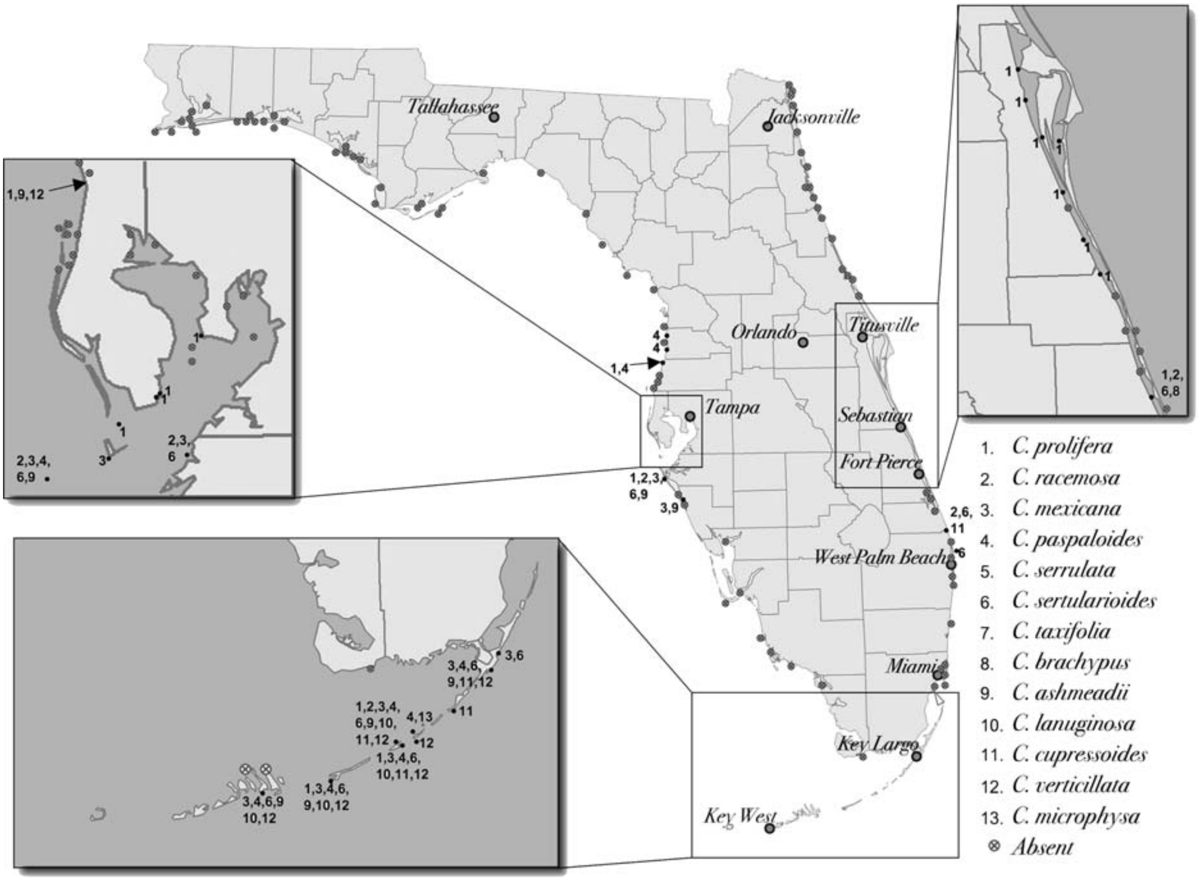

Fig. 4 Current distribution of *Caulerpa* by species around the coast of Florida. Numbers at each location list all species of *Caulerpa* found at that site and match the list on the lower right of the figure

Combined, the probability of *Caulerpa* occurrence increased as the latitude decreased, with the presence of seagrass beds, in sites with low density of human populations, and in close proximity to marinas (Table 1). An assessment of the possible logistic regression models with these variables using Akaike's information criteria indicated that the full model including all four parameters was the best (weight of 0.83; Table 1). Percent correct for *Caulerpa* presence and absence for this model were 61.5 and 98.1%, respectively (Table 2). We used the parameters of this model to predict the occurrence of *Caulerpa* along Florida shoreline (Fig. 3).

We also assessed the logistic regression models for single species. Separately, *Caulerpa prolifera*, *C. paspaloides*, *C. mexicana*, and *C. sertularioides* had significant correlations ($P < 0.05$) with latitude (*C. prolifera*: Table 3). Percent correct presence and absence for the model with latitude were 13.3 and 97.4%, respectively, for *C. prolifera*; 55.6 and 99.2%, respectively, for *C. paspaloides*; 77.8 and 98.4%, respectively, for *C. mexicana*; and 50 and 99.2%, respectively, for *C. sertularioides.*

Discussion

Our model provides information about current locations of *Caulerpa* species and of potential suitable zones for recruitment, making it an important conservation tool. In agreement with prior information, our model indicates that *Caulerpa* occurs preferentially in warmer waters and in habitats with seagrass. We differed from findings by Madl and Yip (2005) and Ruitton et al. (2005) that *Caulerpa* was associated with extensive human activities, as we found *Caulerpa* most frequently in areas of low human density areas. These differences may be

Table 1 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	76.1	0	0.83
GPS, seagrass, marina	69.49	5	79.5	3.4	0.15
GPS, seagrass, population	74.53	5	84.5	8.4	0.01
GPS, seagrass	79.74	4	87.7	11.6	0.002
Marina, seagrass, population	85.91	5	95.9	19.8	<0.001
Marina, seagrass	92.78	4	100.8	24.7	<0.001
Seagrass, population	92.78	4	100.8	24.7	<0.001
GPS, marina, population	92.85	5	102.8	26.7	<0.001
GPS, marina	96.20	4	104.2	28.2	<0.001
Seagrass	99.04	3	105.0	28.9	<0.001
GPS, population	100.81	4	108.8	32.7	<0.001
GPS	104.26	3	110.3	34.1	<0.001
Marina, population	121.02	4	129.0	52.9	<0.001
Marina	126.10	3	132.1	56.0	<0.001
Population	126.10	3	132.1	56.0	<0.001

Table 2 Summary statistics for the best models for all species of *Caulerpa* and single species occurrences

Model	Model parameters					
	Percent correct	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 (*prolifera*)	87.9	7.603	−0.427	2.081		1.428
GPS (*paspaloides*)	94.7	24.85	−1.008			
GPS (*mexicana*)	97	41.026	−1.628			
GPS (*sertularioides*)	95.5	32.203	−1.282			

Table 3 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	81.1	0	0.682
GPS, seagrass	76.21	4	84.2	3.065	0.147
Marina, seagrass	76.82	4	84.8	3.671	0.109
GPS, marina	80.18	4	88.2	7.031	0.020
Seagrass	81.00	3	87.0	5.849	0.037
GPS	85.01	3	91.0	9.86	0.005
Marina	89.65	3	95.6	14.505	0.0005

species-specific as we considered only native species and they focused on highly invasive strains. Unsurprisingly, close proximity to marinas was positively correlated with *Caulerpa* presence.

Our analysis showed that the presence of seagrass was the best predictor of the presence of *Caulerpa* among the four variables. About 24 of 31 sites with *Caulerpa* had seagrass, regardless of the association with all other parameters. Seagrasses depend on sediment-based decomposition of organic matter and elemental recycling and are prone to human disturbances (McRoy and McMillan 1977; Klug 1980; McRoy and Lloyd 1981; Thayer et al. 1975; Lewis 1987; Livingston 1987; Williams 1990). Seagrasses obtain a large fraction of their nutrients from the sediment via roots, while leaf uptake is considered of secondary importance (Pedersen and Borum 1993; Ceccherelli and Cinelli 1997). *Caulerpa* can utilize both sediment and water column nutrients (Williams 1984), which may account for the strong correlation. *Caulerpa* is endemic in tropical and subtropical regions around the world and latitude was a significant predictor of its native occurrence (Creese et al. 2004; Zaleski and Murray 2006; Stam et al. 2006). However, Silva (2002) mentioned that this genus can also grow in locations as high as 34°N. Although Florida lies between latitude north 24 and 30°N and thus, has the potential for *Caulerpa* recruitment along its entire coastline, we found that *Caulerpa* species richness and occurrence was negatively correlated to latitude. Other physical factors may explain this pattern. The large tidal regime, large expanses of bare sand and wave energy on the northern Atlantic seaboard of Florida and the Panhandle region of Florida (Gulf of Mexico) that prevent seagrasses from establishing may also prevent *Caulerpa* spp. recruitment (L. Morris personal communication). 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*—aquarium strain can not become established, while protected areas, such as lagoons or coral reefs, offer better potential for recruitment (de Vaugelas et al. 1999). In the Panhandle, many other 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. These sites were characterized by high fresh water runoff, as well as higher population densities. The low salinity in these areas, often <10 ppt, is lethal for *Caulerpa* (Madl and Yip 2005), and could also account for the lack of *Caulerpa* at these sites. South of 29°N, *Caulerpa* was found in protected environments such as lagoons, seagrass beds, or attached to highly structured surfaces, such as jetties or hard corals.

Proximity to marinas was the next most important variable correlated to *Caulerpa* spp. occurrence. The incidence of native *Caulerpa* around marinas suggests a higher risk of recruitment of native or non-native *Caulerpa* if disposed of at marina locations. Because of the favorable habitat and its easy access to humans, these coastal waterways can be areas where species that are the object of trade for home aquarium industry have a significant probability of successful release in the wild (Loope 2004; Padilla and Williams 2004; Walters et al. 2006; Stam et al. 2006). Marinas are also areas where boat traffic favors the spread of species through ballast water, live wells for bait, or through fragments attached to hulls, anchors or traps (Loope 2004; Madl and Yip 2005). Approximately 1 year after our surveys were completed (August 2006), we received inquiry from a scientist working in Destin Harbor, FL (Panhandle region) (J. Fry, personal communication). Their group had discovered two dense beds of *C. sertularioides* in ~3 m of water near the local marina. They had not previously recorded this species in this location. We had searched nearby waters (<1 km away) in August 2005 and found no evidence of *Caulerpa*. So, we now have our first evidence to suggest that marinas are good locations for *Caulerpa* to enter Florida waters. *Caulerpa sertularioides* is native to Florida, so eradication is unlikely unless it proves to be a new strain.

Human population density was negatively correlated to overall *Caulerpa* presence. Heavily populated areas (>25,000) might be areas with too many disturbances for *Caulerpa* spp. recruitment. During our surveys, we often observed these areas to have anoxic substrates and have high turbidity. These conditions do not favor recruitment or survival of either angiosperms or macroalgae (Plus et al. 2003). However, Chisholm et al. (1997) showed that *C. taxifolia*—aquarium strain proliferated in areas of urban wastewater pollution. This might be a unique feature of the invasive, aquarium strain of *C. taxifolia*.

Caulerpa cupressoides, *C. ashmeadii*, *C. lanuginosa*, *C. verticillata*, and *C. microphysa* were only observed in the Florida Keys (Fig. 4). None of these species were significantly correlated with any of the tested variables. Small sample size is likely to be the major reason why no inference could be made (Hirzel and Guisan 2002). *Caulerpa prolifera, C. mexicana, C. paspaloides, C. racemosa*, and *C. sertularioides* were more likely to settle further north than other species. These species showed a negative correlation with latitude.

Caulerpa taxifolia—aquarium strain has a lower lethal temperature limit than the native strain, 7 and 14°C, respectively (Komatsu et al. 1994; Ramey 2001). Thus, the potential distribution of the aquarium strain based on temperature extends throughout the entire Florida coastline and should extend further north along the Atlantic seaboard than any native species of *Caulerpa*. Although absent in our zone 6, *Caulerpa* species are present further north and can grow in locations like the Onslow Bay, North Carolina, at latitude 34°N (Silva 2003). This suggests that areas north of North Carolina that are too cold for native *Caulerpa* may be suitable for establishment of *C. taxifolia*—aquarium strain and resource managers should be aware of this.

Our data indicate that latitude, presence of seagrass, human population density, and proximity to marinas successfully predict the occurrence of *Caulerpa* species along the Florida coastline and can be a useful tool to select zones for survey that would be more likely to be invaded by *Caulerpa*. It now needs to be combined with effective monitoring programs that can lead to rapid identification and eradication. Otherwise, the number of invasions and their subsequent effects will only increase (Bax et al. 2001). Also, we must consider that climate change is likely to shift the distribution of suitable areas for many species, including *Caulerpa* (Williams and Schroeder 2004). Thus, this model, as any other model, is a temporary tool in need of constant adaptation to new environmental and human factors.

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