Vol. 263: 75–82, 2003 | MARINE ECOLOGY PROGRESS SERIES Mar Ecol Prog Ser | Published November 28

Re-evaluation of the extent of *Caulerpa taxifolia* development in the northern Mediterranean using airborne spectrographic sensing

Jean M. Jaubert[1,2,6,*], John R. M. Chisholm[1], Audrey Minghelli-Roman[1,3], Manuel Marchioretti[1], John H. Morrow[4], Herb T. Ripley[5]

[1]Observatoire Océanologique Européen, Avenue Saint-Martin, 98000 Monaco
[2]The Cousteau Society, 710 Settlers Landing Road, Hampton, Virginia 23669-4035, USA
[3]IRD, École des Mines de Paris, CENERG Rue Claude Daunesse, 06904 Sophia Antipolis, France
[4]Biospherical Instruments, 5340 Riley Street, San Diego, California 92110-2621, USA
[5]Hyperspectral Data International, Suite 119, 7071 Bayers Road, Halifax, Nova Scotia B3L 2C2, Canada

[6]*Present address:* University of Nice, Parc Coromandel (Emeraude B), 18 Avenue Gravier, 06100 Nice, France

ABSTRACT: There has been significant concern over development of the tropical green alga *Caulerpa taxifolia* in the Mediterranean Sea. Reports dating back to 1991 predicted that the species would expand exponentially on all types of substrata and displace major components of the coastal benthic flora, in particular the dominant native seagrass *Posidonia oceanica*. A pilot study of the Bay of Menton, SE France, where *C. taxifolia* has been established since at least 1989, indicated that these predictions might not be correct and that more sophisticated methods might be needed to gain a better estimate of the alga's abundance. We thus surveyed 44 % of the total area reportedly colonized by *C. taxifolia* to a depth of 20 m on the south coast of France by compact airborne multispectral imaging and validated our maps by an extensive underwater survey. Our data indicate that the cover of *C. taxifolia* has been overestimated by at least 1 order of magnitude and that *C. taxifolia* has not substantially impacted the cover of *P. oceanica*. They also indicate that exponential expansion of the alga is only likely to have occurred on substrata situated in the vicinity of sewage outfalls and storm water drains, suggesting that it principally occupies partially vacant niches in stressed environments. In the light of these results, we consider that the risk to most endemic species should be considerably lower than formerly predicted.

KEY WORDS: *Caulerpa taxifolia* · *Posidonia oceanica* · Airborne sensing · Spectra · Surface cover · Underwater survey

INTRODUCTION

Species invasions pose a significant threat to the biodiversity of natural ecosystems, and the increasing frequency of their occurrence is associated with worldwide growth in commerce and tourism (Boudouresque et al. 1994, Farnham 1997, Carlton 1999). On any given day, between 3000 and 6000 species are estimated to be in transit in the ballast tanks of ships (Carlton 1999, S. Gollasch, Chairman of the ICES Working Group on Introductions and Transfers of Marine Organisms, pers. comm.). Marine species introductions also occur via detachment from the fouled hulls or anchor chains of boats, via migration through manmade waterways (e.g. the Suez Canal) and by deliberate or accidental release from aquaria or mariculture facilities (Por 1978, Boudouresque et al. 1994, Farnham 1997).

Proliferation of introduced species such as the European zebra mussel, European shore crab, North American comb jellyfish, green alga *Codium fragile*, brown alga *Sargassum muticum* and toxic dinoflagellates has stimulated international action plans to combat the

*Email: jean.jaubert@unice.fr

threat posed by biological invasions. In many instances, however, the introduction of a foreign species has little measurable impact upon native communities (Nolan 1994, Reise et al. 1999). Responsibility thus rests with the scientific community to provide decision-makers with accurate data that allow for appropriate allocation of human effort and public funds.

One of the best known species invasions in recent times has been that of the green alga *Caulerpa taxifolia* Vahl C. Agardh in the Mediterranean Sea. It is presumed that *C. taxifolia* was introduced in 1984 (Meinesz & Hesse 1991). Reports dating back to 1991 claim exponential expansion of the alga (Meinesz et al. 1991, Belsher et al. 1993, Meinesz et al. 1997), culminating in an estimated surface cover of more than 6000 ha by 2000 (Jousson et al. 2000) and 30 000 ha by 2002 (Withgott 2002). Proliferation on substrata adjacent to beds of the seagrass *Posidonia oceanica* L. Delile gave rise to predictions that the alga would displace this keystone species of the Mediterranean coastal flora (Meinesz & Hesse 1991, de Villèle & Verlaque 1995) that stabilizes fine sediments, limits beach erosion, and underpins the trophic web (Pérès & Picard 1975, Pergent et al. 1995).

Study of the Bay of Menton, where *Caulerpa taxifolia* has existed since at least 1989 (Jaubert et al. 1999), showed that the alga had not spread as much as previously reported (Meinesz et al. 1997) and had not caused deleterious alterations in *Posidonia oceanica* beds (Jaubert et al. 1999). We thus decided to map the cover of *C. taxifolia* in the (reportedly) most heavily colonized areas of southern France to gain a better understanding of the alga's overall abundance. As in the Bay of Menton study (Jaubert et al. 1999), we used state-of-the-art airborne remote sensing technologies and conducted extensive underwater surveys to validate the results. Airborne remote sensing technologies are able to survey large areas of the shallow seabed at high resolution in real time, thereby eliminating the need to extrapolate from small scale data sets obtained underwater (Mumby et al. 2001).

MATERIALS AND METHODS

Compact airborne spectral imaging. We mounted a CASI (Compact Airborne Spectrographic Imager, ITRES Research) aboard a Cessna Caravan seaplane equipped with advanced autopilot capabilities and obtained multispectral imagery over 44% of the total area reportedly affected by *Caulerpa taxifolia* between the depths of 0 and 20 m on the south coast of France (Meinesz et al. 2001; Fig. 1). Our methodology was similar to that implemented and described in Jaubert et al. (1999), Minghelli et al. (2002) and Mumby et al. (2001, in press). We acquired data with a ground spatial resolution of 1.0 to 2.5 m over 12 to 18 spectral bands that were effective in resolving the major classes of vegetation (*Caulerpa taxifolia*, *C. prolifera*, *Posidonia oceanica*, *Cymodocea nodosa* and mixed photophilic algae dominated by *Dictyota*, *Padina* and *Acetabularia*) and substratum (sand, mud, rock). The 2.5 m data were acquired at an altitude of 1875 m at the following spectral bands (nm): 409 ± 5, 425 ± 8, 439 ± 7, 454 ± 6, 470 ± 7, 485 ± 8, 499 ± 6, 536 ± 20, 582 ± 13, 614 ± 13, 644 ± 12, 675 ± 13, 705 ± 11, 734 ± 11, 763 ± 11, 792 ± 11, 821 ± 12, 849 ± 12; 1 m data were acquired at an altitude of 750 m at: 467 ± 8, 508 ± 8, 523 ± 8, 535 ± 5, 544 ± 5, 554 ± 6, 565 ± 5, 574 ± 5, 585 ± 6, 595 ± 5, 644 ± 5, 845 ± 5. Spectral data were acquired in September 1999 and October 2000, when the bio-

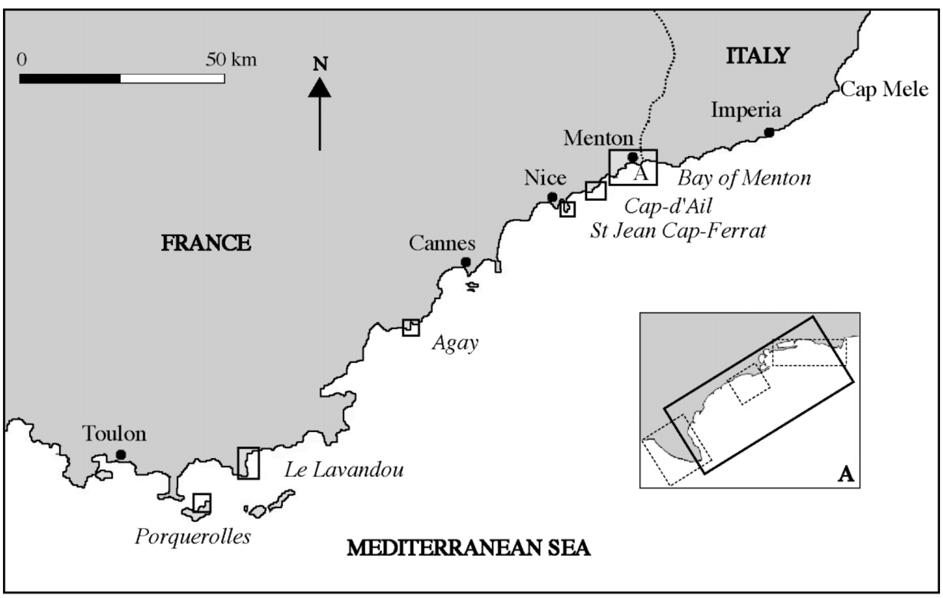

Fig. 1. Zones mapped by multispectral airborne sensing; insert A shows 3 areas mapped at 1.0 m ground spatial resolution in the Bay of Menton (dashed line boxes) and 1 area mapped at 2.5 m resolution (thick line box), all other zones were mapped at 1.0 m resolution

mass of *C. taxifolia* was close to its annual maximum, and at the beginning of June 2001, when the alga's biomass was close to minimum (Verlaque & Fritayre 1994). Imagery was acquired on cloudless days at sun angles below 45° to minimize sun glint.

We placed white, blue and green spectral reference sheets (≥16 m^2 surface area) on beachheads in the flight path of the aircraft to determine atmospheric light attenuation. To determine water column light attenuation [k (m^{-1})] from the CASI imagery, we secured white spectral reference sheets to the seabed at depths of 5, 10 and 15 m. Also, simultaneously with the flights, we recorded vertical profiles of spectral downwelling irradiance in multiple locations with a rapid data-acquisition (200 ms) Profiling Reflectance Radiometer (PRR-800, Biospherical Instruments) and calculated the average diffuse spectral attenuation coefficient for downwelling irradiance for the water column in each of the imaged areas. We further used the PRR-800 to obtain multiple *in situ* spectral reflectance profiles for each dominant class of benthic vegetation and substratum (≥50 per class) at 3 or more depths while diving with SCUBA. Recurring differences in the spectral reflectance profiles were subsequently used to discriminate between the major classes of vegetation and substratum (see below).

CASI image analysis. We corrected the CASI data for electronic offset, dark current, scattered light and frame-shift smear using the manufacturer's software (ITRES Research) and geo-referenced the imagery to the Universal Transverse Mercator using synchronously acquired Global Positioning System (GPS) data and PCI Easi/Pace software. We adjusted the spectral data for variation in downwelling irradiance (radiometric correction) by reference to measurements made with an Incident Light Sensor (ILS) mounted on the wing of the aircraft, coupled by fibre-optic cable to the CASI. We corrected for image distortion caused by angular deviation of the CASI sensor by reference to measurements made with a gyroscope (Fig. 2A).

Sun glint was reduced from the imagery by determining the linear relationship between near infrared and visible radiance over an area of water that was too deep for the seabed to have influenced the spectral radiance signature. Data were adjusted for atmospheric light attenuation by relating the CASI-determined radiances of the beachhead spectral reference sheets (R_s) in each of the measured spectral bands (λ) to their absolute reflectance ($\rho_{s\lambda}$):

$$\rho_{s\lambda} = a_\lambda R_{s\lambda} + b_\lambda \quad (1)$$

where a and b are constants.

Pixel bathymetry was interpolated from a natural log-linear plot of green to red light reflectance from a reference surface (sand or a seafloor target sheet) over a series of depth intervals (Philpot 1989). Reflectance of the seafloor (ρ_f) was then calculated for every pixel in the imagery using:

$$\rho_{f\lambda} = [(\rho_{s\lambda} - \rho_{w\lambda})/e^{-2k_\lambda z}] + \rho_{w\lambda} \quad (2)$$

where ρ_w is the reflectance of the water in an area too deep for the seabed to be of influence (Maritorena et al. 1994, Fig. 2B) and z is the depth.

Finally, using the maximum likelihood approach, data were classified according to the shortest Mahalanobis distances between the measured *in situ* spectra of the vegetation and substratum classes and the spectra of the image pixels using the software package ENVI v. 3.4 (Research Systems) according to the methods given in Jaubert et al. (1999, Fig. 2C; see e.g. Mumby et al. 1998, Hochberg & Atkinson 2000, Mumby et al. 2001, in press).

Field survey. The thematic maps were validated by making a large number of underwater observations in different field locations, particularly when we had identified in our imagery areas where the spectral reflectance from the seabed was altered due to sun glint at the sea surface or was too weak. This was mostly where water depths approached 20 m. Within these areas, we extracted the position, in real world coordinates, of groups of pixels that were assigned to different benthic classes according to our classifications. We then positioned ourselves at those locations in a small boat with the aid of a portable differential GPS (Trimble NT200D; accuracy ±3 m) and dived with SCUBA to determine whether the subject classes had been correctly identified. We also used an underwater positioning system (acoustic interferometer PLSM Instrumentation AQUA-METRE D100) to determine (accuracy ±3 m) the locations of multiple patches of *Caulerpa taxifolia*, *Posidonia oceanica*, *C. taxifolia* mixed with *P. oceanica* and sand at depths of 2 to 20 m. To do this, we referenced our acoustic positioning system to the real world by measuring fixed positions on either side of the emitting antenna with the same differential GPS. We then compared the locations and identities of these benthic features with those represented on our thematic maps. In total, we verified 305 benthic subjects.

RESULTS

Comparison of our classified imagery with published data on the cover of *Caulerpa taxifolia* in the same localities revealed major quantitative discrepancies (Fig. 3). We estimated the total cover of the alga in the areas mapped to be 65 ha, compared with the most conservative published estimate of 751 ha (Table 1). *Posidonia oceanica* covered an area 11.6× larger

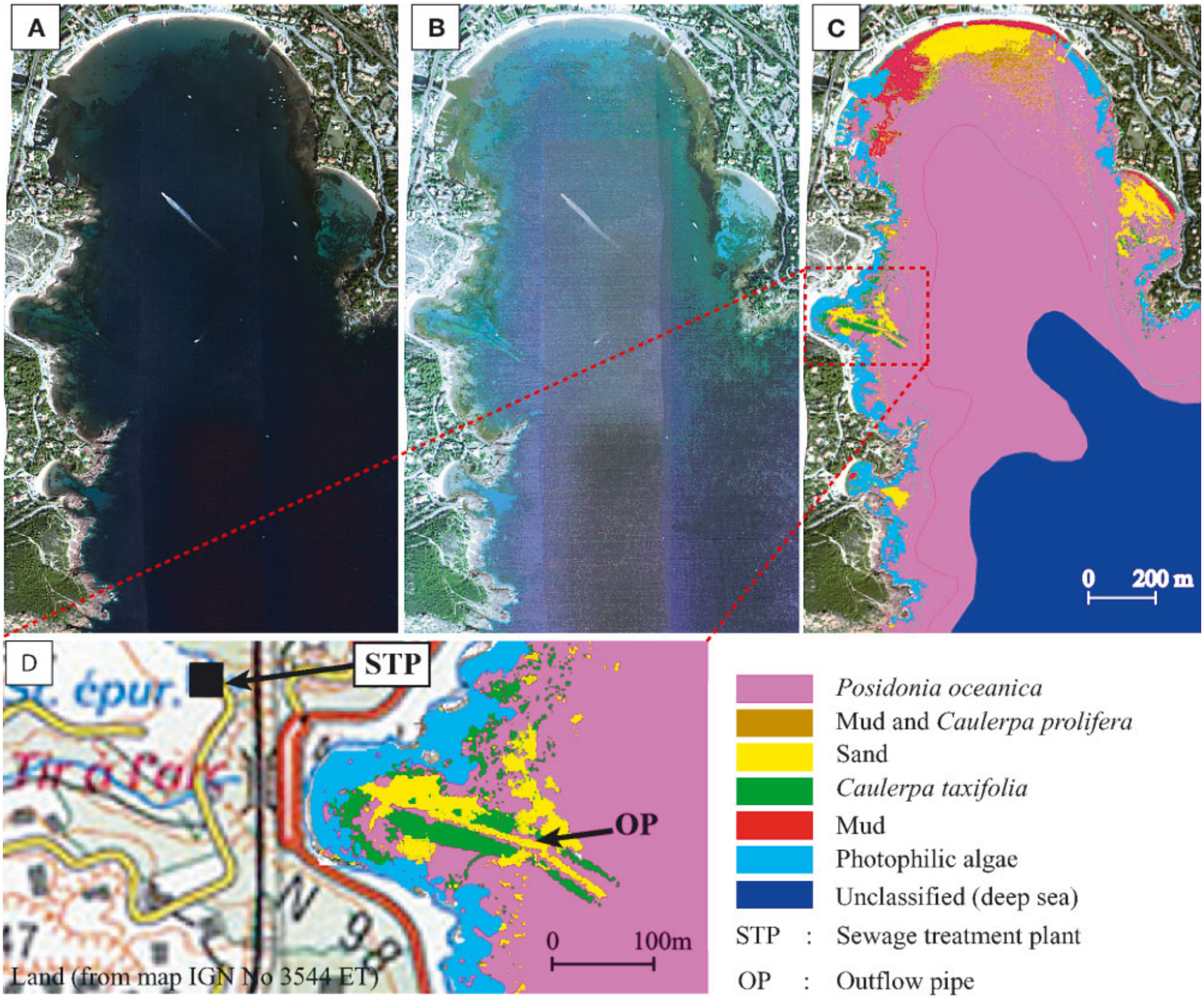

Fig. 2. Sequence of analytical steps performed on compact airborne spectrographic imagery (CASI) obtained for the Bay of Agay, culminating in production of a thematic map of vegetation and substrata. (A) Mosaic of raw images; (B) imagery corrected for atmospheric and water column light attenuation after determination of pixel bathymetry; (C) thematic map; (D) expanded section (red box), juxtapositioned with IGN map No 3544 ET, showing that *Caulerpa taxifolia* is principally localized close to the outfall of a sewage treatment plant

Table 1. *Posidonia oceanica* and *Caulerpa taxifolia*. Seabed cover (ha) obtained over the depth interval 0 to 20 m in this study, compared with the surface cover of *C. taxifolia* over the same depth interval by transect survey (Meinesz et al. 2001). Difference calculated as ([B–A]/A) × 100

	Bay of Menton	Cap d'Ail	St Jean Cap-Ferrat	Agay	Lavandou	Porquerolles	Total
This study							
Area mapped	219.8	100.6	99.7	144	418.5	240	1222.6
Posidonia oceanica	88.8	82.2	91	114.4	212.1	167.3	754
Caulerpa taxifolia (A)	47.7	5.3	2	1.8	2.1	6	65
Meinesz et al. (2001)							
Caulerpa taxifolia (B)	310.7	136.8	38.3	52	2.2	211	751
Difference (%)	**551**	**2461**	**1838**	**2738**	**4**	**3396**	**1055**

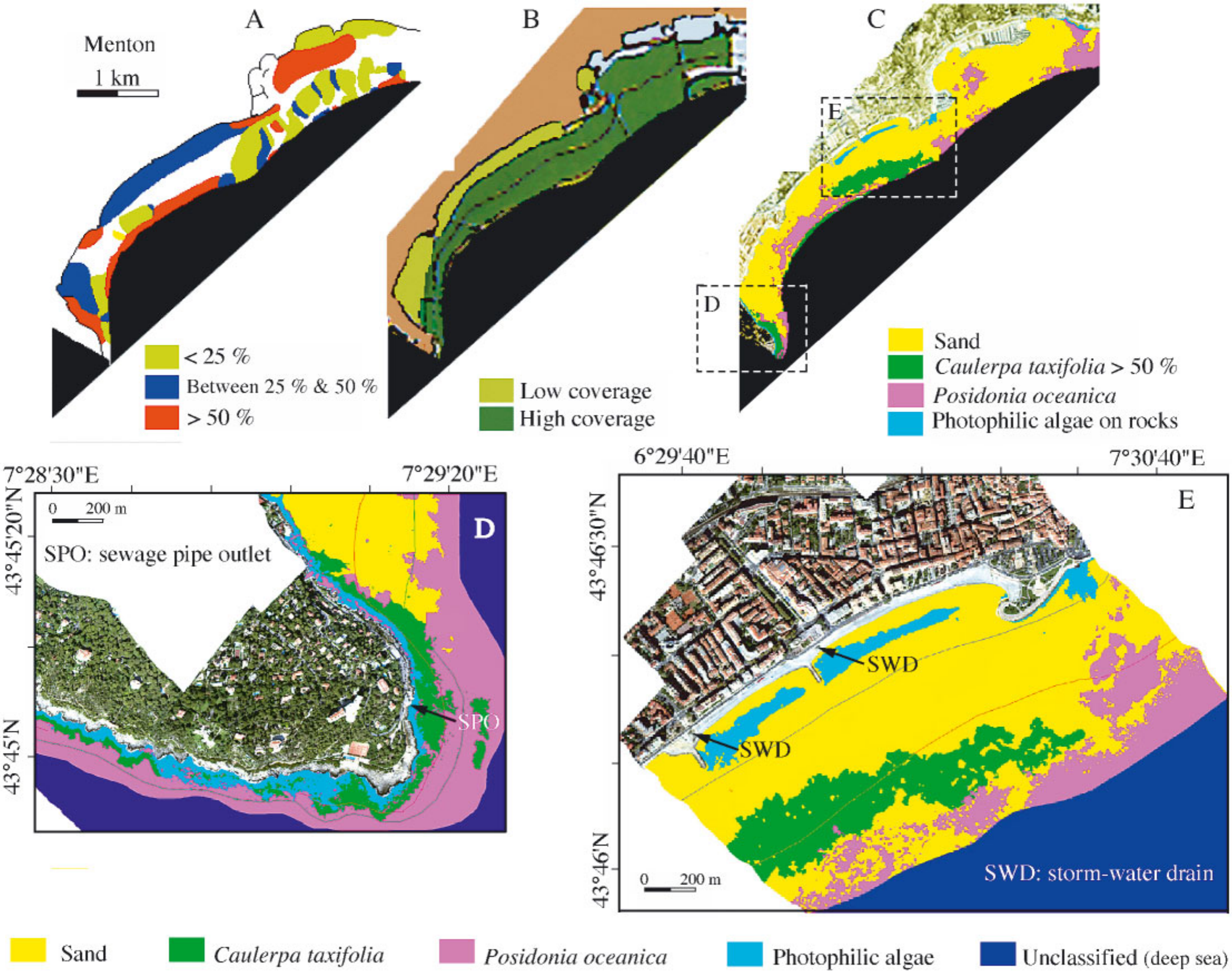

Fig. 3. Comparative thematic maps of the distribution of *Caulerpa taxifolia* in the Bay of Menton, illustrating differences in cover. (A) Available on the internet site of IFREMER (www.ifremer.fr); (B) a pamphlet made by A. Meinesz and collaborators (LEML-UNSA 2000), commissioned by the Agence de l'Eau Rhône Méditerranée Corse, the Conseil Régional Provence-Alpes-Côte d'Azur and the Ministère de l'Aménagement du Territoire et de l'Environnement, for distribution to the public as part of an interdepartmental action plan to combat the spread of *C. taxifolia*; (C) this study, from multispectral airborne imagery acquired in September 1999 at a ground spatial resolution of 2.5 m; (D,E) expanded sections showing that *C. taxifolia* is principally localized near the 2 major storm-water catchments that drain the city of Menton and near the outlet of the overflow pipe of the buffer tank of a domestic sewage plant that opens at the tip of Cap-Martin

(Table 1). In the study area, all of the large dense populations of *C. taxifolia* are situated in the vicinity of domestic sewages and/or storm-water drains, and/or in some cases they are associated with substrata affected by mechanical perturbations. In the Bay of Menton these populations are respectively situated (1) in front of the major storm-water collectors that drain the city and the surrounding hills (Fig. 3E), (2) along the shore of Cap-Martin, at the tip of which the outlet of the overflow pipe of a domestic wastewater tank opens (Fig. 3D), and (3) at greater depth on a seabed situated below the outlet of the city's sewage (Jaubert et al. 1999). The eastern half of the bay, situated upstream of these sources of pollution with regard to the dominant current, harbors only a few scattered small spots of *C. taxifolia* (Jaubert et al. 1999). Similar circumstances characterize all of the areas where the alga has proliferated and, in this regard, the situation that prevails around the Island of Porquerolles is particularly demonstrative. This pristine area harbors only 1 large and well-delimited *C. taxifolia* population that covers a dead mat situated where the wreckage of a large French warship and explosions have killed a large portion of a dense *Posidonia* bed. According to Meinesz et al. (1997), the *Posidonia* mat around the wreck was dead when the alga started to colonize it in 1995.

According to a field-verification survey, we obtained the following errors: 1.7% false positive results, where *Caulerpa taxifolia* was identified on the imagery but none was present on the seabed, and 14.5% false negative results, where the alga was present on the seabed but not on the imagery. The numbers and locations of samples giving rise to these results are given in Table 2. The false negative results were distributed as follows: 4% where dense cover of *C. taxifolia* (≥50%) was present on the seabed, but none was apparent on the imagery; 8.1% where sparse to moderate cover of *C. taxifolia* (<50%) was present on the seabed, usually mixed with other types of vegetation, but none was apparent on the imagery; and 2.4% where a mixture of *C. taxifolia* and *Posidonia oceanica* was present on the seabed, but not on the imagery.

DISCUSSION

There has been considerable concern about the rapid spread of *Caulerpa taxifolia* in the western Mediterranean and Adriatic seas over the last 2 decades, and about the impact that extensive growth of this alga is having on native biota. However, this is not an isolated phenomenon. Episodes of *Caulerpa* sp. proliferation have occurred in many parts of the world over the last century, e.g. *C. prolifera* in the western Mediterranean during the 1920s (Ollivier 1929) and within the Levant Basin during much of the first half of the 20th century (Rayss 1941, Doumenge 1995); *C. filiformis* and *C. scalpelliformis* in SE Australia in the mid 1970s (May 1976) and 1990s (Davis et al. 1997), respectively; *C. racemosa* in Greece (Panayotidis & Montesanto 1994) and Florida during the 1990s (Lapointe et al. 1994); *C. verticillata* and *C. brachypus* in Florida at present (Lapointe & Barile 2003). In several instances, the *Caulerpa* species involved proliferated rapidly then, after varying periods of time and for reasons that are not well understood, disappeared or declined appreciably in abundance. A similar process of regression is likely occurring in the first reported site of *C. taxifolia* outbreak in the Mediterranean, below the Oceanographic Museum of Monaco (authors' unpubl. data).

Our data show that the alga appears to be 1 to 2 orders of magnitude less abundant than is commonly believed from the sea surface to a depth 20 m, which is the depth interval over which the most extensive populations are generally found (Meinesz et al. 2001).

Table 2. Ground verification of thematic maps performed at the indicated locations by comparing the true identities of 305 subjects observed on the seafloor (field) with those of different classes identified by classification of imagery (imagery). False negative results (in dark grey cells) are counted where classes of *Caulerpa taxifolia* found on the seabed have not been identified on the imagery and false positive (in light grey cells) where classes of *C. taxifolia* identified on the imagery have not been found on the seabed

Italian border		Field: *C. taxifolia*	Field: Other
Imagery	*C. taxifolia*	1	0
	Other	0	7

Bay of Menton		Field: *C. taxifolia*	Field: Other
Imagery	*C. taxifolia*	40	0
	Other	3	58

Cap-Martin		Field: *C. taxifolia*	Field: Other
Imagery	*C. taxifolia*	10	0
	Other	4	6

Cap-Ferrat		Field: *C. taxifolia*	Field: Other
Imagery	*C. taxifolia*	31	0
	Other	2	46

Bay of Agay		Field: *C. taxifolia*	Field: Other
Imagery	*C. taxifolia*	17	3
	Other	7	50

Lavandou		Field: *C. taxifolia*	Field: Other
Imagery	*C. taxifolia*	7	0
	Other	2	11

Total		Field: *C. taxifolia*	Field: Other
Imagery	*C. taxifolia*	106	3
	Other	18	178

Total in %		Field: *C. taxifolia*	Field: Other
Imagery	*C. taxifolia*	85%	1.7%
	Other	14.5%	98%

Based on the *Caulerpa taxifolia* cover we have measured and the reported time of the alga's first arrival (see Meinesz et al. 1998), we suggest that exponential expansion could only have taken place in localized zones adjacent to human population centers, generally on substrata exposed to wastewater pollution in the vicinity of sewage or storm-water outlets (Chisholm et al. 1997). Very often, this occurred where beds of *Posidonia oceanica* had died prior to the alga's arrival (Jaubert et al. 1999).

The existence of a correlation between domestic pollution and the proliferation of algae belonging to the genus *Caulerpa* is well documented. Towards the beginning of the last century, Ollivier (1929) suspected that increasing domestic pollution had triggered the proliferation of *Caulerpa prolifera* in the French Riviera. Similar observations were made by May (1975) about the spread of *C. filiformis* in Botany Bay near Sydney, Australia. Meinesz (1976, 1977) noticed that *C. prolifera* could quickly cover substrata heavily polluted by decomposing organic matter, and was planting this species in the French Riviera to restore habitats damaged by organic pollution (Meinesz 1976, 1977). In Florida, recent blooms of *C. verticillata* and *C. brachypus* in coastal ecosystems are supported by domestic pollution (Lapointe & Barile 2003).

These facts support the hypothesis that *Caulerpa taxifolia* proliferation is limited to substrata containing substances from which the alga derives nutrients (Chisholm et al. 1996). It is still unclear which substance(s) is or are responsible for this proliferation, and more research is needed to determine the respective roles of high nutrient loads (Ceccherelli & Cinelli 1997) partly composed of domestic pollutants (Chisholm et al. 1997, Fernex et al. 2001) and also perhaps to identify other substances, which may play an important role.

Our results suggest that *Caulerpa taxifolia* principally occupies partially vacant niches in stressed environments (Giaccone 1997, Occhipinti-Ambrogi et al. 2003), as do some other invasive species (Lüning 1990, Colinvaux 1993, Marino et al. 1999). This concurs with observations that the alga has not measurably impacted the pre-existing cover of *Posidonia oceanica* (Jaubert et al. 1999) and conflicts with the results of shorter-term experiments (de Villèle & Verlaque 1995, Ceccherelli & Cinelli 1997, 1998). Overall, our data provide a realistic perspective of the spread of *C. taxifolia*, indicating that the risk posed by the alga to major endemic species is much lower than was formerly predicted.

Acknowledgements. We are indebted to Prince Khaled bin Sultan bin Abdulaziz of Saudi Arabia and the Living Oceans Foundation for providing us with the services of the motor yacht 'Golden Shadow', her seaplane, and her captain, officers and crew. The Principality of Monaco and the Council of Europe additionally supported the work. We thank D. Cadot, L. Mangialajo, M. Monti, G. Passeron-Seitre, S. Pourlier, S. Purkis, S. Reynaud-Vaganay, F. Seguin, K. Woods and M. Zeichen for assistance in the field.

LITERATURE CITED

Belsher T, Youenou G, Dimeet J, Raillard JM, Bertrand S, Mereau N (1993) Evolution de *Caulerpa taxifolia* devant les côtes des Alpes Maritimes et de la Principauté de Monaco. Observations par vidéo-tractée (mars et octobre 1992). Rapport IFREMER/Centre de Brest/DEL. IFREMER, Toulon

Boudouresque CF, Briand F, Nolan C (eds) (1994) Introduced species in European coastal waters. Ecosystems Research Report 8, CIESM (Commission Internationale pour l'Exploration Scientifique de la Méditerranée), Monaco

Carlton JT (2000) *Quo vadimus exotica oceanica*? Marine bioinvasion ecology in the twenty-first century. In: Pederson J (ed) Marine bioinvasions: Proc 1st Nat Conf, Jan 24–27 1999. Institute of Technology, Cambridge, MA, p 6–23

Ceccherelli G, Cinelli F (1997) Short-term effects of nutrient enrichment of the sediment and interactions between the seagrass *Cymodocea nodosa* and the introduced green alga *Caulerpa taxifolia* in a Mediterranean bay. J Exp Mar Biol Ecol 217:165–177

Ceccherelli G, Cinelli F (1998) Habitat effect on spatio-temporal variability in size and density of the introduced alga *Caulerpa taxifolia*. Mar Ecol Prog Ser 163:289–294

Chisholm JRM, Fernex FE, Mathieu D, Jaubert JM (1997) Waste-water discharge, seagrass decline and algal proliferation on the Côte d'Azur. Mar Pollut Bull 34:78–84

Colinvaux J (ed) (1993) Ecology II. John Wiley & Sons, New York

Davis AR, Roberts DE, Cummins SP (1997) Rapid invasion of a sponge-dominated deep-reef by *Caulerpa scalpelliformis* (Chlorophyta) in Botany Bay, New South Wales. Aust J Ecol 22:146–150

Doumenge F (1995) Quelques réflexions sur les algues Caulerpes. Biol Mar Medit 2:613–633

Farnham WF (1997) Espèces invasives sur les côtes de la Manche et de l'Atlantique. In: Lavoisier (ed) Dynamique d'espèces marines invasives: application à l'expansion de *Caulerpa taxifolia* en Méditerranée. Académie des Sciences, Paris, p 15–26

Giaccone G (1997) Phytosociologie et écologie du genre *Caulerpa* en Méditerranée. In: Lavoisier (ed) Dynamique d'espèces marines invasives: application à l'expansion de *Caulerpa taxifolia* en Méditerranée. Académie des Sciences, Paris, p 131–144

Hochberg EJ, Atkinson MJ (2000) Spectral discrimination of coral reef benthic communities. Coral Reefs 19: 164–171

Jaubert JM, Chisholm JRM, Ducrot D, Ripley HT, Roy L, Passeron-Seitre G (1999) No deleterious alterations in *Posidonia oceanica* beds in the Bay of Menton (France) 8 years after *Caulerpa taxifolia* colonization. J Phycol 35:1113–1119

Jousson O, Pawlowski J, Zaninetti L, Zechman FW and 5 others (2000) Invasive alga reaches California. Nature 408:157–158

Lapointe BE, Barile PJ (2003) Invasive macroalgal blooms in coastal southeastern Florida supported by anthropogenic nitrogen. Estuarine Research Federation meeting, Seattle, Sep 14–18, 2003. Estuarine Research Federation, Port Republic, MD (Abstract)

Lapointe BE, Tomasko DA, Matzie WR (1994) Eutrophication and trophic state classification of seagrass communities in the Florida Keys. Bull Mar Sci 54:696–717

LEML-UNSA (2000) Observatoire sur l'expansion de *Caulerpa taxifolia* en Méditerranée. Laboratoire Environnement Marin Littoral, Université de Nice-Sophia Antipolis, Nice

Lüning K (ed) (1990) Seaweeds. John Wiley & Sons, New York

Marino G, Di Martino V, Giaccone G (1999) Diversità della flora della Penisola Maddalena (Siracusa, Sicilia SE): cambiamento ventennale ed evoluzione. Boll Accad Gioenia Sci Nat Catania 31:289–315

Maritorena S, Morel A, Gentili B (1994) Diffuse reflectance of oceanic shallow waters: influence of water depth on bottom albedo. Limnol Oceanogr 37:1689–1703

May V (1976) Changing dominance of an algal species (*Caulerpa filiformis*) [Suhr] Hering). Telopea 1:136–138

Meinesz A (1976) Etude expérimentale de bouturage de certains végétaux sous-marins dans des ports et des plages artificielles. Rapport d'étude, Université de Nice, Nice

Meinesz A (1977) Note préliminaire concernant quelques expériences de repiquage de végétaux marins, en particulier de l'algue *Caulerpa prolifera* (Forskal) Lamouroux. Rapp Comm Int Mer Médit 24/4:169–170

Meinesz A, Hesse B (1991) Introduction et invasion de l'algue tropicale *Caulerpa taxifolia* en Méditerranée nord-occidentale. Oceanol Acta 14:415–426

Meinesz A, Cottalorda JM, Chiaverini D, Braun M and 7 others (1997) Suivi de l'invasion de l'algue tropicale *Caulerpa taxifolia* devant les côtes françaises de la Méditerranée: situation au 31-12-1996. Laboratoire Environnement Marin Littoral, Université de Nice-Sophia Antipolis, Nice

Meinesz A, Cottalorda JM, Chiaverini D, Cassar N, de Vaugelas J (1998) Suivi de l'invasion de l'algue tropicale *Caulerpa taxifolia* en Méditerranée: situation au 31 Décembre 1997. Laboratoire Environnement Marin Littoral, Université de Nice-Sophia Antipolis, Nice

Meinesz A, Cottalorda JM, Chiaverini D, Garcia D, Thibaut T, de Vaugelas J (2001) Suivi de l'invasion de l'algue tropicale *Caulerpa taxifolia* en Méditerranée: situation en France au 31 décembre 2000. Laboratoire Environnement Marin Littoral, Université de Nice-Sophia Antipolis, Nice

Minghelli-Roman A, Chisholm J R M, Marchioretti M, Jaubert JM (2002) Discrimination of coral reflectance spectra in the Red Sea. Coral Reefs 30:307–314

Mumby PJ, Green EP, Clark CD, Edwards AJ (1998) Digital analysis of multispectral airborne imagery of coral reefs. Coral Reefs 17:59–69

Mumby PJ, Chisholm JRM, Clark CD, Hedley JD, Jaubert J (2001) A bird's eye view of coral reef health. Nature 413:36

Mumby PJ, Hedley JD, Chisholm JRM, Clark CD, Ripley H, Jaubert J (in press) The cover of living and dead corals from airborne remote sensing. Coral Reefs

Nolan C (1994) Introduced species in European coastal waters. In: Boudouresque CF, Briand F, Nolan C (eds) Introduced species in European coastal waters. Ecosystems Research Report 8, CIESM (Commission Internationale pour l'Exploration Scientifique de la Méditerranée), Monaco, p 1–3

Occhipinti-Ambrogi A, Savini D (2003) Biological invasions as a component of global change in stressed marine ecosystems. Mar Pollut Bull 46:542–551

Ollivier G (1929) Etude de la flore marine de la Côte d'Azur. Ann Inst Océanogr, Monaco, Tome VII, fasc. III, p 1–173

Panayotidis P, Montesanto B (1994) *Caulerpa racemosa* (Chlorophyta) on the Greek Coasts. Cryptogam Algol 15: 159–161

Pérès JM, Picard J (1975) Causes de la raréfaction et de la disparition des herbiers de *Posidonia oceanica* sur les côtes Françaises de la Méditerranée. Aquat Bot 1:133–139

Pergent G, Pergent-Martini C, Boudouresque CF (1995) Utilisation de l'herbier a *Posidonia oceanica* comme indicateur biologique de la qualité du milieu littoral en Méditerranée: état des connaissances. Mésogée 54:3–27

Philpot WD (1989) Bathymetry mapping with passive multispectral imagery. Appl Optics 28:1569–1578

Por FD (1978) Lessepsian migration. The influx of Red Sea biota into the Mediterranean by way of the Suez Canal. Ecological studies 23. Springer-Verlag, Berlin

Rayss T (1941) Sur les Caulerpes de la côte palestinienne. Palest J Bot Jerus Ser 2:103–124

Reise K, Gollasch S, Wolff WJ (1999) Introduced marine species of the North Sea coasts. Helgol Meeresunters 52:219–234

Verlaque M, Fritayre P (1994) Modifications des communautés algales méditerranéennes en présence de l'algue envahissante *Caulerpa taxifolia* (Vahl) C Agardh. Oceanol Acta 17:659–672

Villèle de X, Verlaque M (1995) Changes and degradation in a *Posidonia oceanica* bed invaded by the introduced tropical alga *Caulerpa taxifolia* in the north western Mediterranean. Bot Mar 38:79–87

Withgott J (2002) California tries to rub out the monster of the lagoon. Science 295:2201–2202

Editorial responsibility: Otto Kinne (Editor), Oldendorf/Luhe, Germany

Submitted: November 12, 2002; Accepted: October 30, 2003
Proofs received from author(s): November 19, 2003