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A century of warfare shoots holes in anti-*Caulerpa* campaign

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Effort to have all varieties of the marine alga *Caulerpa taxifolia* listed as noxious weeds hinges on the argument that the alga's proliferation in the Mediterranean Sea is a cause and not a consequence of environmental degradation. Until now, the occurrence of two populations in a pristine part of the northern Mediterranean near the island of Porquerolles has upheld this claim. Here we show that the alga's development at Porquerolles is indeed a consequence of environmental degradation caused by military weapons' impacts on seagrass beds during the last century. The available data show that substratum enrichment plays a key role in fostering development of *Caulerpa*, irrespective of whether this results directly from pollution or from the impacts of pollution and other anthropogenic factors on benthic vegetation cover.

A campaign has been waged to have all species of the marine algal genus *Caulerpa* listed as noxious weeds or, at a minimum, all varieties of the species *Caulerpa taxifolia* (Vahl) C. Agardh (1). This effort derives from claims that a strain of *Caulerpa taxifolia* has spread indiscriminately throughout the western Mediterranean and Adriatic seas to blanket more than 30,000 acres of the seabed with devastating effects on the native biota (2-8). The alga's acclaimed ability to expand exponentially on any type of substratum and thereby displace keystone species such as the seagrass *Posidonia oceanica* L. Delile has been ascribed to exceptional, morphological and physiological traits (gigantic size, amplified growth rate, exceptional cold resistance, enhanced chemical toxicity, reproduction from small fragments), which it supposedly acquired through prolonged aquarium culture (2, 7, 9, 10). Contradictory data indicate that the alga does not possess abnormal traits (11-13), nor covers 30,000 acres of the Mediterranean seabed (14,15), nor develops on any type of substratum but preferentially exploits nutrient resources in polluted or organically enriched substrata (16-18). The latter argument is supported by a correlation between the extent of

Caulerpa taxifolia development in the coastal waters of the Riviera, where more than 90% of the alga's biomass in the Mediterranean is found (19), and the quantity and treatment level of wastewater discharged from adjacent human settlements (14-16; Figs S1 and S2).

A notable exception to this rule occurs off the Island of Porquerolles in southern France, where two, dense, strongly delimited populations of *Caulerpa taxifolia* exist in the absence of human habitation or wastewater discharge. The two populations are situated exclusively on dead parts of an otherwise vigorous *Posidonia oceanica* bed.

Militarily, the Island of Porquerolles has had a long and eventful history. For most of the last century, its northeast corner served as a weapons' test site for the French Armed Forces. The island also held strategic significance during the Second World War, due largely to its proximity to the naval port of Toulon. The resulting scars of warfare are imprinted upon a series of high-resolution, aerial photographs taken by the French Institut Géographique National (IGN).

Beginning in 1909, the former flagship of the French navy, the battleship *Iéna*, which had been irreparably damaged by fire while at dock five years earlier, was towed to the northeast corner of Porquerolles and used as a target to test the efficacy of projectiles based on the then top secret explosive, melinite (Fig. 1, A and B) (20). The impacts of these projectiles caused damage to the *Posidonia* bed surrounding the *Iéna* (20), from which the seagrass has not recovered (Fig. 1, C-E).

In 1950, four, larger, partially superimposed, circular impact zones were evident approximately 350 m from the sunken wreck of the *Iéna* (Fig. 1C). Bombs dropped prior to the allied invasion of southern France in August 1944 were likely responsible.

Finally, in 1993, an excellent colour photograph reveals two, very large, circular dead areas in the *Posidonia* bed immediately north of the *Iéna* (Fig. 1D), where none was apparent eleven years earlier (Fig. 1E). All records of the weapons' tests that were carried out at Porquerolles after 1970 have been classified for 60 years, which forced us to turn to the sediment record for clues as to what had happened.

While diving on SCUBA, we extracted a target sediment core (100 mm diameter) from the region of overlap of the two dead areas (Station 1) and a background core from a control site 6 km away (Station BG; see Fig. 1D). We froze the cores and sliced them transversely into 10 mm thick sections. The sections were lyophilised, sieved through a 250 μm mesh, homogenised, and analysed for anthropogenic and natural radionuclides (^{137}Cs, ^{239,240}Pu, ^{210}Pb, ^{226}Ra, ^{234}U, ^{235}U and ^{238}U), organic carbon, and non-radioactive tracers (Fe, Pb, Si, Zn and others). We then derived ^{210}Pb$_{excess}$ from the measured ^{210}Pb and ^{226}Ra profiles in order to date the cores by reference to their sediment accumulation rates (21) and we cross checked the resulting chronologies by reference to the Chernobyl event horizon.

The target and background cores differed in several respects (see Fig. 2). First and most importantly, the target core possessed a region extending from approximately 11 to 18 cm in which the normally observed pattern of exponentially declining ^{210}Pb$_{excess}$ activity in undisturbed sediments (21) was obliterated (Fig. 2A). Afterward, sediment accumulated at a much faster rate (0.9 ± 0.1 cm y^{-1}, $r^2 = 0.87$, as compared with 0.26 ± 0.03 cm y^{-1}, $r^2 = 0.92$, beforehand). Second, the 18 cm threshold coincided with reversals in the profiles of ^{137}Cs, ^{239,240}Pu, ^{238}U, organic C, Pb and Fe (Fig. 2, C-H) and other trace elements for which the data are not shown. Third, the target core generally contained much larger quantities of organic matter and thus had significantly higher concentrations of radionuclides and trace elements that are naturally accumulated in living tissue (Fig. 2, C-H).

On the basis of these data, we argue that powerful military weapons destroyed the seagrass cover at Station 1 causing rapid formation of a new layer of organically rich sediment, approximately 8 cm deep. Thereafter, microbes decomposed the more labile organic fractions, releasing accumulated nuclides and trace elements down a diminishing oxygen gradient beneath the sediment horizon, leaving peaks in their activities and concentrations near the lower limit of the added sediment layer (see Fig. 2) (22, 23). By the time of core extraction in 2001, approximately 10 cm of new sediment had accumulated above the $^{210}Pb_{excess}$ anomaly at a rate of 0.9 ± 0.1 cm y^{-1}, thus indicating that the event responsible had occurred between 1987 and 1991, which correlates well with the photographic evidence (Fig. 1D).

This interpretation can further explain the downward displacement of several important tracer peaks in the target core profiles relative to those of the background core. According to the $^{210}Pb_{excess}$ data, sediment accumulated at an average rate of 0.6 ± 0.1 cm y^{-1} ($r^2 = 0.78$) at Station BG, thus the ^{137}Cs peak observed in the background core near 10 cm was produced by fallout from the Chernobyl reactor meltdown in 1986 (Fig. 2C). The equivalent maximum in the target core occurred approximately 8 cm deeper (i.e., near 18 cm), which is consistent with the rapid deposition of a new layer of sediment close to the time or shortly after the Chernobyl accident (Fig. 2C). This argument is further supported by similar offsets in the positions of $^{239,240}Pu$, organic C, Pb and Fe maxima (see Fig. 2, D and F-H).

We conclude that the two, large, dead areas in the *Posidonia oceanica* bed at Porquerolles (Fig. 1D) were produced by the series of weapons' impacts described above. The cover of *Caulerpa taxifolia* that has since developed is perfectly superimposed upon them (Fig. 1F), providing further demonstration of the alga's unique ability to proliferate upon highly refractory organic substrata (18). Moreover, following development of the alga, there is now evidence of re-colonisation by *Posidonia oceanica*, in accordance with observations made elsewhere that species of *Caulerpa* aid in the establishment of *Posidonia* beds by trapping the drifting, vegetative, shoot bundles of the seagrass while they take root in the substratum (24).

In the context of understanding the factors that drive *Caulerpa taxifolia* proliferation, Porquerolles represents a crucial singularity, as the area is considered to be pristine by coastal northwest Mediterranean standards, due to its relative isolation from human population centres. For this reason, advocates of the genetic alteration theory have alluded to Porquerolles as proof that the alga's rapid development is independent of environmental degradation, which is not the case. The available data demonstrate that substratum enrichment plays a key role in fostering development of *Caulerpa* (16, 25), irrespective of whether this results directly from pollution (26, 27), from the impact of pollution on sensitive species such as *Posidonia oceanica* (16, 18), or from other impacts that cause a similar collapse in benthic cover, as reported here.

The veracity of this conclusion can be evaluated by considering the conditions under which the alga first developed below the Oceanographic Museum of Monaco in 1984 (2). Much earlier in the century, *Posidonia oceanica* covered the seabed at this location (28) but discharge of untreated sewage and offal from the old town of Monaco caused its demise at least 30 years before the alga appeared (P. Rolland, diver, Oceanographic Museum of

Monaco, personal communication). The surface area occupied by *Caulerpa taxifolia* reportedly increased from 1 m^2 in 1984 to 30000 m^2 in 1990 at dry tissue densities of up to 0.613 kg m^{-2} (= approximately 6.13 kg fresh tissue m^{-2}) (2, 29). During this period, Monaco continued to discharge untreated waste into the near shore environment. In 1990, Monaco opened an advanced treatment facility to process human waste and land run-off to secondary level and discharge it further offshore (16). A few years later, the cover of *Caulerpa taxifolia* started to decline, in harmony with the pattern that *Caulerpa* outbreaks have taken in other parts of the world (15), such that little of the formerly luxuriant meadow exists today (Fig. 3).

These cycles of boom and bust are not unusual for *Caulerpa* species (15). They reflect the alga's unique ability to exploit subterranean nutrient resources by penetrating soft sediments or porous hard substrata with its rhizoids (17, 18), excreting labile photosynthetic product into the rhizosphere, thereby enhancing microbial turnover of organic matter (18), and by taking up and assimilating nutrients from the substratum (17, 30). In the absence of further pollution or physical impact, these processes serve to reduce substratum nutrient loads to levels that favour the re-emergence of formerly dominant native species (18), such as *Posidonia oceanica*, as can now be observed in various parts of the western Mediterranean (14).

We argue that proliferation of *Caulerpa taxifolia* is primarily a consequence of environmental degradation and we suspect that other aquatic invasions may be propelled by the same phenomenon. Development of the zebra mussel *Dreissena polymorpha* in the Great Lakes, the comb jellyfish *Mnemiopsis ledyjii* in the Azor, Black, Caspian and Marmora seas, and the water hyacinth *Eichornia crassipes* in Lake Victoria all occurred in the wake of deteriorating water quality (31-35). Other species that have been transported on the hulls of ships for centuries have only recently become successful invaders. When the potential compounding effects of climate change are taken into consideration (36) it is clear that existing effort to prevent the spread of invasive species must be complemented by much better information on the role that environmental factors play in their development.

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Figure Legends

Fig. 1. Military activities and their impact on seabed vegetation cover off the northeast corner of the Island of Porquerolles, southern France (area concerned: 6º13'35" – 6º14'30"E; 41º1' – 41º1'30" N). **A,** The battleship *Iéna* before catching fire, which led to her decommissioning and subsequent use as a target for weapons' tests; the greater than normal thickness of her hull provided for superior tests of the efficacy of shells based on the newly developed explosive, melinite. **B,** The *Iéna* on her side prior to sinking after shelling in 1909; inset map indicates the locations of the core sampling stations (St 1, close to the *Iéna*, and St BG, the control site). **C,** An aerial photograph taken in 1950 by the IGN with relevant areas contrast enhanced, exposing damage to the *Posidonia* beds surrounding the wreck of the *Iéna* (red arrow) and four, partially superimposed, circular dead zones in the seagrass bed approximately 350 m to her southwest (white arrows). **D,** A contrast enhanced aerial photograph taken in 1993 by the IGN showing two, very large, circular dead areas in the seagrass beds (white arrows) to the north of the *Iéna* (red arrow), together with the formerly impacted areas immediately landwards of her hull and 350 m to her southwest (white arrows). **E,** An aerial photograph taken in 1982 by the IGN with relevant areas contrast enhanced exposing the long term impacts of tests carried out in 1909 on the *Iéna* (red arrow) without sign of the two, large, impact zones that appear in **D** to her north. **F,** A thematic map of benthic vegetation cover off the northeast corner of Porquerolles, produced from multispectral airborne imagery obtained in 2000-2001 (15), showing growth of *Caulerpa taxifolia* (green) confined to the areas destroyed by the above-indicated suite of weapons' impacts; violet indicates living *Posidonia oceanica*; orange indicates dead *Posidonia oceanica*; turquoise indicates photophilic algae; yellow indicates sand.

Fig. 2. Comparative distributions of anthropogenic and natural radionuclides and non-radioactive tracers in sediment cores taken from Station 1 in December 2001 and from Station BG in September 2002. **A,** $^{210}Pb_{excess}$ activity in the target core decreased log-linearly from 0-10 cm, remained constant from approximately 11-18 cm (right hand bracket), and then again declined log-linearly to the limit of the measurable activity in the core. **B,** $^{210}Pb_{excess}$ activity in the background core declined log-linearly from the surface to the limit of measurable activity in the core. **C,** The background core contained a peak in ^{137}Cs activity near 10 cm, consistent with fallout from the Chernobyl accident, whereas the equivalent peak in the target core occurred near 18 cm. **D-G,** Peaks in the vertical distributions of $^{239,240}Pu$, ^{238}U, organic carbon, Pb, and to a lesser degree Fe also occurred near 18 cm in the target core, consistent with the microbial release of isotopes and elements in buried organic fractions. Bars represent standard uncertainties at the 1 σ level.

Fig. 3. Three-month, running mean biomass of *Caulerpa taxifolia* over the depth interval 15-25 m between 1996 and 2001 below the Oceanographic Museum of Monaco, obtained by blotting and weighing fresh tissues removed from six randomly selected square metre quadrats on a monthly basis; bars are standard deviations.

Fig. 1

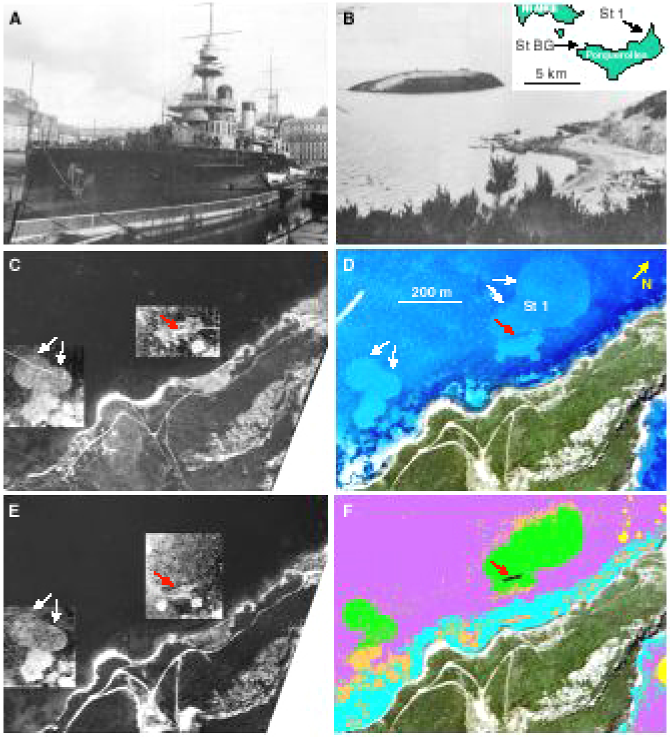


Fig. 2

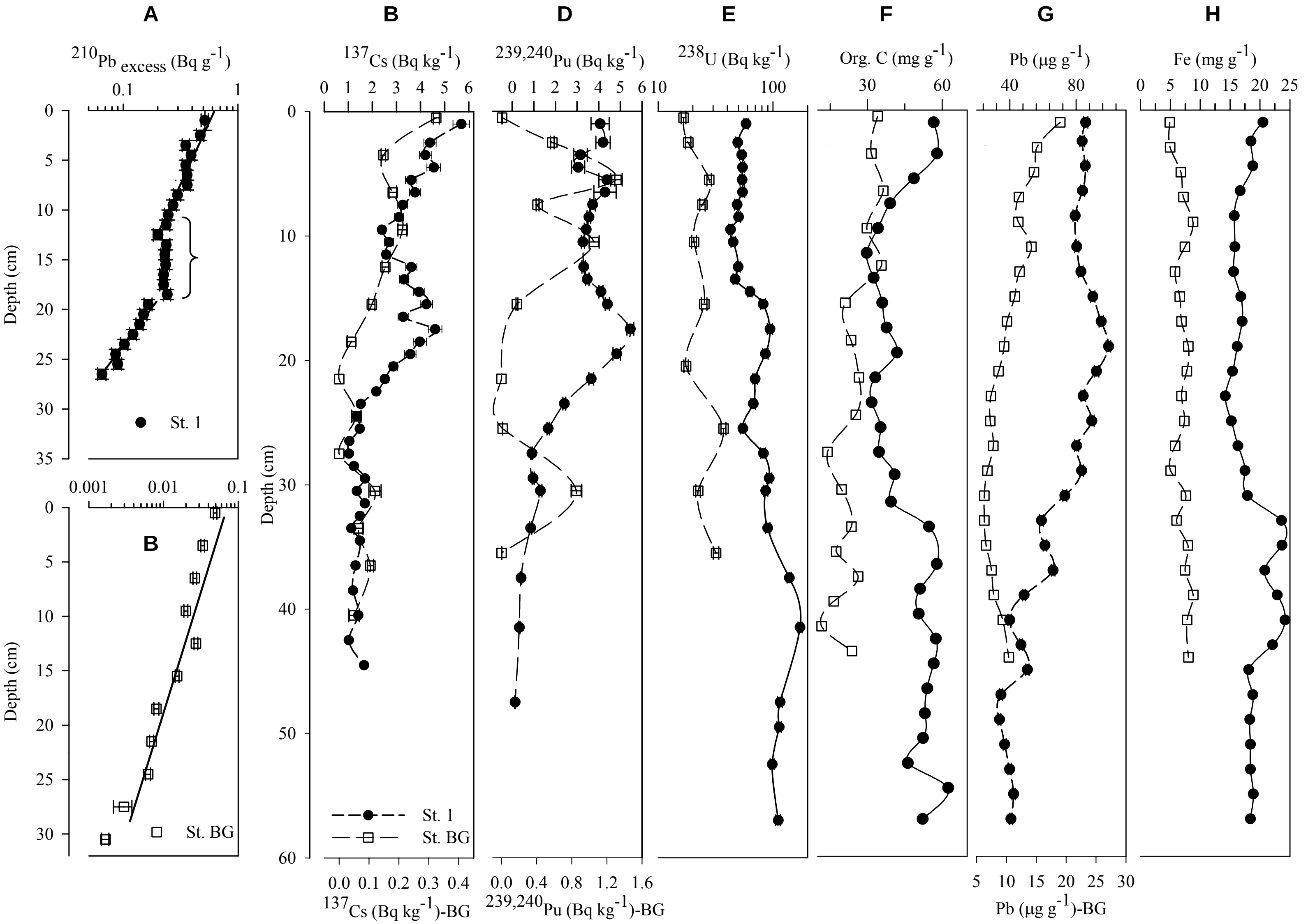
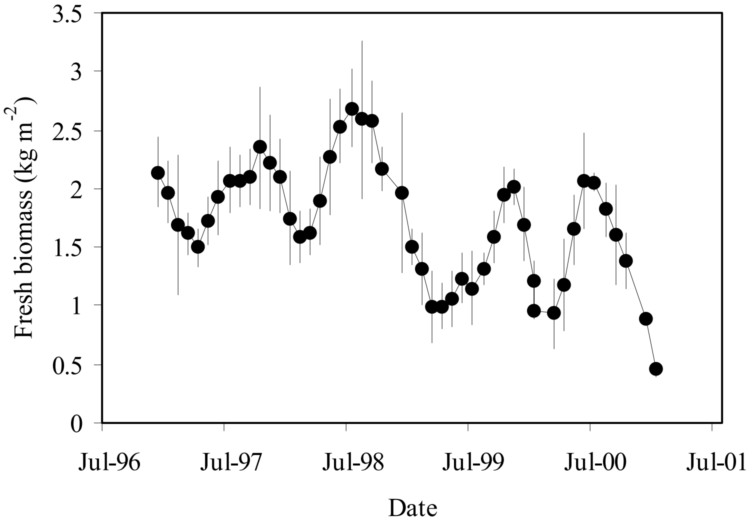

A
B
D
E
F
G
H
210Pb excess (Bq g-1)
0.1
1
0
5
10
15
20
25
30
35
Depth (cm)
St. 1
0.001
0.01
0.1
B
St. BG
137Cs (Bq kg-1)
0 1 2 3 4 5 6
0.0 0.1 0.2 0.3 0.4
137Cs (Bq kg-1)-BG
239,240Pu (Bq kg-1)
0 1 2 3 4 5 6
0.0 0.4 0.8 1.2 1.6
239,240Pu (Bq kg-1)-BG
238U (Bq kg-1)
10
100
Org. C (mg g-1)
30
60
Pb (µg g-1)
40
80
5 10 15 20 25 30
Pb (µg g-1)-BG
Fe (mg g-1)
0 5 10 15 20 25
40
50
60
St. 1
St. BG

Fig. 3



3.5
3
2.5
2
1.5
1
0.5
0
Fresh biomass (kg m^{-2})
Jul-96
Jul-97
Jul-98
Jul-99
Jul-00
Jul-01
Date

Supporting Information

Supplementary figure legends

Fig. S1. Comparative maps of the northeast coast of the western Mediterranean showing the distribution of *Caulerpa taxifolia* in relation to human population size and associated wastewater emissions on the land, close to the time of major *Caulerpa taxifolia* radiation in the western Mediterranean (1, 2). The upper map shows resident human population size from Toulon in France to the border between France and Italy in 1982 and from that border to Albenga in Italy in 1987, together with data on associated public wastewater outfalls (3). The lower map shows the estimated seafloor cover of *Caulerpa taxifolia* in the French section in 2000 (4) and in the Italian section in 1996 (2).

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Fig. S2. Scanned section of a map indicating the frequency of untreated private wastewater outlets and overflows that exist in addition to public wastewater outfalls (see Fig. S1) in high value, residential neighborhoods on the Côte d'Azur, in this case the periphery of St. Jean Cap-Ferrat, immediately east of the city of Nice (1).

1. Cellule d'Intervention contre la Pollution dans les Alpes-Maritimes, *Rapport d'Activities, Inventaires des Rejets en Mer*, 1984.

Fig. S1

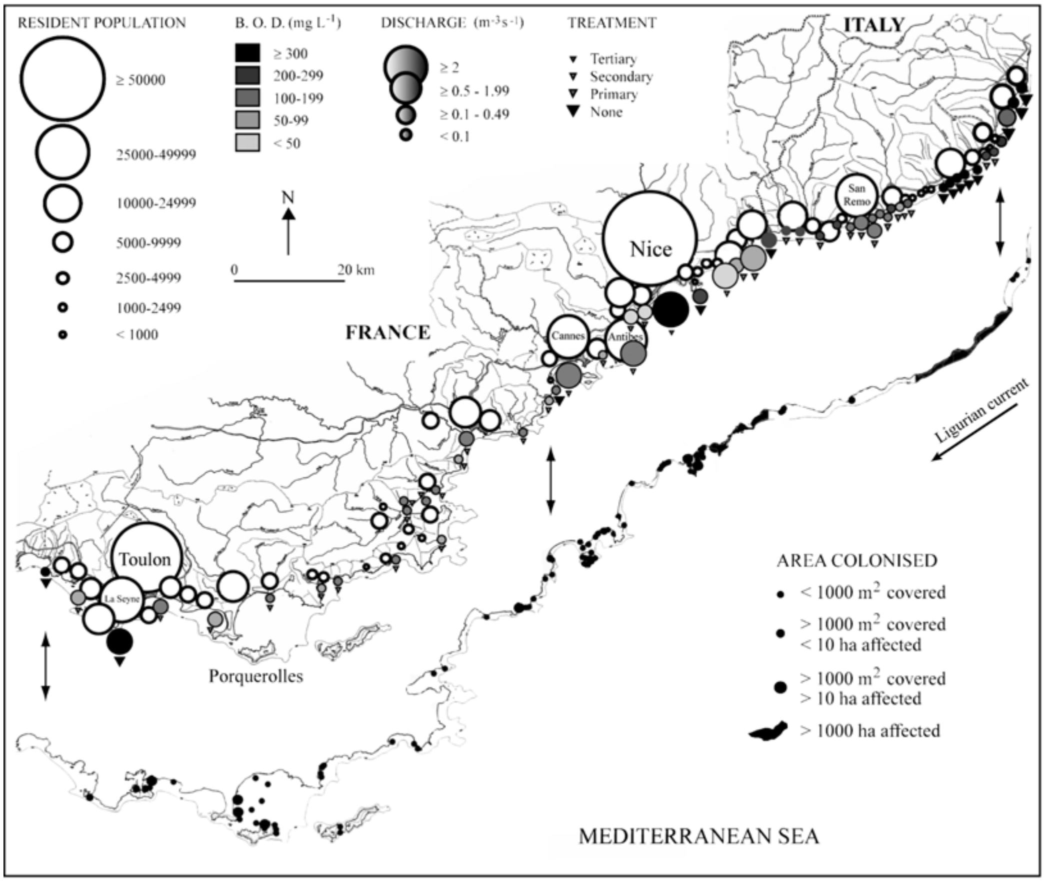
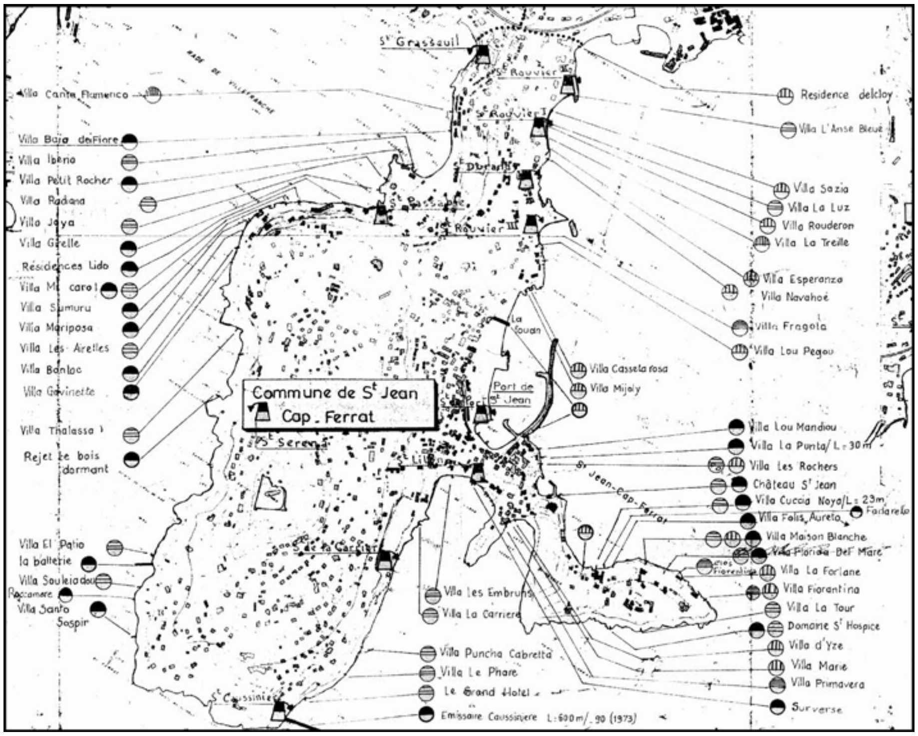

RESIDENT POPULATION
≥ 50000
25000-49999
10000-24999
5000-9999
2500-4999
1000-2499
< 1000
B. O. D. (mg L⁻¹)
≥ 300
200-299
100-199
50-99
< 50
DISCHARGE (m⁻³s⁻¹)
≥ 2
≥ 0.5 - 1.99
≥ 0.1 - 0.49
< 0.1
TREATMENT
Tertiary
Secondary
Primary
None
ITALY
N
0
20 km
FRANCE
Nice
San Remo
Cannes
Antibes
Toulon
La Seyne
Porquerolles
Ligurian current
AREA COLONISED
< 1000 m² covered
> 1000 m² covered
< 10 ha affected
> 1000 m² covered
> 10 ha affected
> 1000 ha affected
MEDITERRANEAN SEA

Fig. S2


Commune de S^t Jean
Cap _ Ferrat
S^t Grassauil
Rouvier
S^t Rouvier I
Rouvier III
S^t Dubarry
S^t Passable
RADE DE VILLEFRANCHE
La Fouan
Port de S^t Jean
S^t Serena
S^t Lilian
S^t de la Carrière
S^t Caussinière
S^t Jean-Cap-Ferrat
Villa Canta Flamenco
Villa Baia deFiore
Villa Iberia
Villa Petit Rocher
Villa Radiana
Villa Joya
Villa Grelle
Résidences Lido
Villa Mi caro
Villa Sumuru
Villa Mariposa
Villa Les Airelles
Villa Banlac
Villa Gavinette
Villa Thalassa
Rejet le bois dormant
Villa El Patio
la batterie
Villa Souleiadou
Roccamare
Villa Santo Sospir
Residence delcloy
Villa L'Anse Bleue
Villa Sazia
Villa La Luz
Villa Rouderon
Villa La Treille
Villa Esperanza
Villa Navahoe
Villa Fragola
Villa Lou Pegou
Villa Casseta rosa
Villa Mijoly
Villa Lou Mandiou
Villa La Punta/ L = 30m
Villa Les Rochers
Château S^t Jean
Villa Cuccia Noya/L = 23m
Fadarello
Villa Folis Aureto
Villa Maison Blanche
Villa Florida Del Mare
Fiorentina
Villa La Forlane
Villa Fiorantina
Villa La Tour
Domaine S^t Hospice
Villa d'Yze
Villa Marie
Villa Primavera
Surverse
Villa les Embruns
Villa La Carriere
Villa Puncha Cabretta
Villa Le Phare
Le Grand Hotel
Emissaire Caussiniere L: 600m/- 90 (1973)