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An algorithmic model for invasive species: Application to *Caulerpa taxifolia* (Vahl) C. Agardh development in the North-Western Mediterranean Sea

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Abstract

The purpose of the study is to evaluate the propagation of the green alga of tropical origin *Caulerpa taxifolia* (Vahl) C. Agardh in the north-western Mediterranean sea—introduced in 1984—by means of an algorithmic computer model. In order to take into account spatial interactions and anthropic dispersion or activities such as eradication and introduction of specific predators, the model is based on a coupling of a geographical information system (GIS) with a stochastic discrete event simulation. Even if the model has to cope with incomplete data and sampling difficulties encountered in the hostile environment of the sea, interesting calibration and validation procedures have been achieved, including spectral analysis of spatial simulation results. At this stage, the model seems capable of achieving a certain level of prediction: local pattern of expansion, increase of *C. taxifolia* biomass and covered surfaces, and invasive behaviour towards existing communities. © 1998 Elsevier Science B.V. All rights reserved.

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1. Introduction

In 1984, the French coast of the Mediterranean sea near Monaco was the initial site of the development of *Caulerpa taxifolia* (Fig. 1), a green alga of tropical origin introduced by accident (Meinesz and Hesse, 1991). Twelve years latter, this species

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had colonized several thousand hectares (Meinesz and Boudouresque, 1996) of the French and Italian coasts and was detected in numerous areas of the north-western Mediterranean coast, from Croatia (Adriatic sea) to the Balearic islands (Spain). This surprising development may locally induce an intense and irreversible alteration of the coastal ecosystems both on endogenous species distribution (alga, cnidaria, sponges, echinoderms, fishes, etc.) and on the ecosystem functioning (trophic levels relationships). Indeed, we can observe the progressive elimination of the benthic flora and fauna in stations heavily occupied by *C. taxifolia* (Villèle and Verlaque, 1995; Bellan-Santini et al., 1996; Boudouresque et al., 1996). On the other hand, the social and economic repercussions of such damage on the ecosystems would be important but cannot yet be estimated accurately (incidences on fisheries, tourism, etc.).

In order to predict the development of *C. taxifolia*, a simulation study was undertaken through an interdisciplinary joint venture between marine ecologists, biologists and computer scientists. This paper presents the different modelling constraints which were kept in mind while designing the model, as well as the technical choices and the first results.

The study of *C. taxifolia* settlement and development on precise locations has been realized to facilitate the validation of simulation results (Sargent, 1984; Hill, 1995; Youngblood and Pace, 1995).

Three settlement sites have been mapped yearly by marine ecologists since the beginning of the 1990s (Fig. 2). The first zone, in the bay of Villefranche-sur-Mer-sur-mer, was mapped at two different scales: at decametric scale in Passable, a 60-m wide depression made by a World War II bomb impact; and at hectometric scale in the La Darse harbour, ≈ 0.5 km long. The second zone of study is the oldest settlement site colonized by the alga in France, situated at the headland of Cap Martin (≈ 2.5 km wide). This zone has been studied since 1989 and the maps were established to gain some observations on the kilometric scale. The third zone is comprises the area between Menton and Villefranche-sur-Mer-sur-mer (≈ 30 km of coast). In spite of the absence of exhaustive mapping we considered that enough data were available in that area to attempt some simulations on a large scale.

2. Modelling goals

The model we designed had to (i) integrate the physical and biological parameters which were identified as sensitive and (ii) evaluate and predict in an acceptable manner *C. taxifolia* propagation on previous sites at different map scales. The main goals assigned to our approach can be synthesized in four points:

1. Simulate *C. taxifolia* expansion on precise sites with a knowledge model based on ecological data obtained in situ or available through the bibliography.
2. Predict the expansion according to the environmental parameters (bathymetry, substrates, biocenosis) of the studied sites. This imposes the subsequent obligation that the model has to take into account the spatial effects (heterogeneity of the sites, long and short distances interactions between organisms).
3. In addition to statistical results, the software has to produce new maps following the Geographic Information System format used at the Laboratoire Environnement Marin Littoral (abbreviated as LEML hereafter), so that they can be compared with real maps in order to validate the model. Quantitative results such as biomass, production, contaminated surfaces and residual biomass of competing

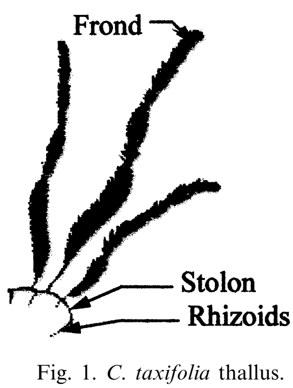

Fig. 1. *C. taxifolia* thallus.

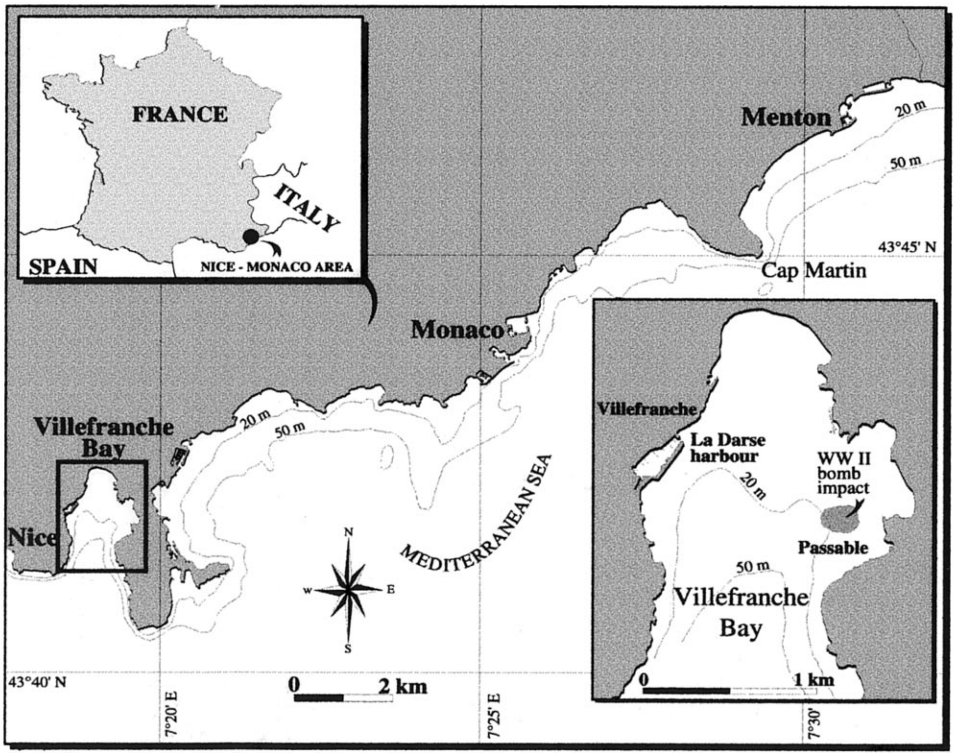

Fig. 2. Studied sites.

species (especially the protected seagrass *Posidonia oceanica* (L.) Delile) are also computed.

4. Exploration of the numerous possible trajectories of the system depending on input parameters organized in experimental scenarios (pattern of currents, anthropic dispersion…).

3. Data sampling

The thallus of *C. taxifolia* is composed of stolons which support numerous fronds (up to 60 cm long and 2 cm wide). Rhizoids allow *C. taxifolia* to anchor on most substrates, mineral or those covered with encrusting organisms (Fig. 1).

3.1. *C. taxifolia* growth and dispersal

Up to now there is no scientific evidence of a sexual reproduction for the Mediterranean strain of *C. taxifolia* (Meinesz, 1992; Meinesz et al., 1993; Meinesz and Boudouresque, 1996). The reproduction is only vegetative (elongation and ramification followed by fragmentation and dispersion of the fragments). The individual growth is measured as the annual extension of the stolon (up to 1.860 m year^{-1}), including the length of the ramifications occurring during the same period (Komatsu et al., 1994).

The dispersion of the alga is linked to the production of numerous fragments due to the thallus fragmentation during winter. A long-term study began at Passable with a very detailed map (1:1000) and enabled us to obtain the distribution parameters of fragments, i.e. distribution range and number of fragments per square meter (Fig. 3). We immediately saw that the collected data did not fit with any usual statistical distribution that we expected and which was first tried, such as a Gaussian distribution. A classical circular uniform distribution seemed to better represent the cuttings' dispersion with an approximate radius of 20 m in sites under weak hydrological conditions.

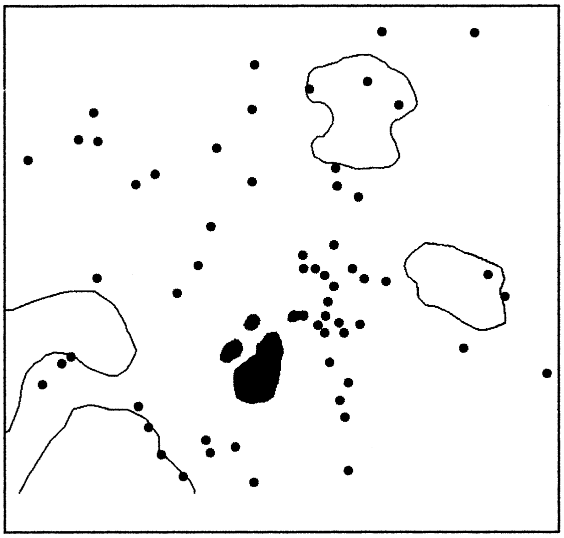

Fig. 3. Spreading of 59 fragments which have successfully settled in 5 months (June–November 1994), within a maximum radius of 20 m, ≈ 1 m^2 densely covered by *C. taxifolia*. In the same time, the initial colony (in gray) has grown up to 3.5 m^2 and some cuttings have developed three additional colonies. The envelopes are outlining the *P. oceanica* beds.

The lack of data concerning local currents as well as in situ sampling difficulties reduced the quality of acquired data and predictions. However this limitation may be partially overpassed through modelling choice of a uniform law, justified in case of lack of precise collected data due to the hostile environment affecting the usual statistical study of simulation input data (Box and Muller, 1958; Banks and Carson, 1984; Law and Kelton, 1991). Indeed, the choice of a uniform distribution was unexpected and it reflects that the algae seem to be spreading by jumps. The spread (not a distribution) of fragments is considerably affected by tidal influence summed to local currents, the main strength and direction of which are specified when they are known for a simulated site. The main current tendency is thus modelled with a spatial shift of the probability distribution. A flat Gaussian distribution would have been more 'natural', and of course it could have been retained and 'forced' to fit with our small data samples, but the uniform law reflects the fact that, within a monthly time step, the cuttings seem to be jumping from one place to another, mainly due to the fast daily growth of stolons (up to 3 cm per day) and the daily change of local currents which appear to spread cuttings uniformly on favourable substrates.

Conditions in the littoral environment and simulations on several sites showed that this simple uniform model was only able to reproduce the very local dispersion of fragments, but it was unable to reproduce the long distance spreading which characterizes the unsheltered sites such as Cap Martin. We then introduced a two level dispersion model : some of the fragments are spread out at short distances according to the kind of substrate on which *C. taxifolia* grows (see Section 5.1), others are spread at long distances (i.e. several hundreds meters).

In addition, anthropic action (fishing nets, anchors of yachts) is probably the main factor for long distance dispersion of fragments (Sant et al., 1994). No accurate statistics are actually available for these events.

The average biomass of *C. taxifolia* is 0.5 kg fresh weight (F.W.) m^{-2} according to data sampled at various depths and substrates (Meinesz et al., 1995).

3.2. Bathymetry influence

C. taxifolia is able to densely colonise various substrates at various depths ranging from 1 to 100 m. However, the settlement in places deeper than 50 m (some individuals have been observed at 90 m (Belsher and Meinesz, 1995)) is much slower, due to a low level of light and cold temperature. For modelling purposes the probability of settlement success has been established as a function of depth according to numerous in situ observations during the past 6 years (Table 1).

Table 1
Probabilities of *C. taxifolia* settlement as a function of depth

Depths (m)	0–3	3–5	5–10	10–20	20–50	>50
P (settlement)	0.01–0.1	0.1–1	1	0.5–1	0.01–0.1	0–0.01

In situ observations indicated that these probabilities had to be adjusted for each site as a function of hydrodynamic pattern for the superficial depths (effect of waves and turbulence).

3.3. Substrates

We distinguished six main substrates which were colonized by *C. taxifolia* and mapped on the different studied sites: unstable sand with ripple-marks, dead seagrass beds, *P. oceanica* seagrass beds, rocky substrate (with photophilous algal cover), sediment (from muddy sand to coarse gravel) and harbour mud. Table 2 summarizes the probabilities of fragment settlement on these substrates. These probabilities have been established from numerous observations since 1990 on several sites (Ribera et al., 1994).

3.4. Seasonal variation

The growth of *C. taxifolia* starts in May–June, ending in December. In Winter and Spring the cold temperatures ($\approx 13°C$) induce a degeneration of the alga biomass as shown in Table 3. The table has been set both by observations and measurements (Gayol et al., 1994; Garcia et al. 1996; Meinesz et al. 1995).

3.5. Currents

No statistics are available for current intensity at high resolution spatial scales. In the sheltered site of Villefranche bay (La Darse harbour and Passable) the distribution of new fragments surrounding a place of first settlement did not show any obvious trend in the action of currents (Fig. 3). However in high hydrodynamic situations such as Cap Martin, the retained model consisted of modifying the scattering of fragments in an ellipse, the diameters of which were determined as a function of the direction and intensity of the current. Obviously this approximation cannot reflect the whole complexity of this factor but at this time it seems impossible to meaningfully improve this algorithm due to the absence of current measurements.

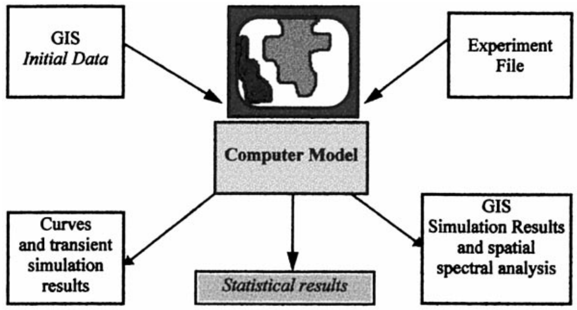

Fig. 4. Input–ouput data and coupling GIS data-DES model (explanations in the text).

4. Modelling and implementation choices

4.1. Simulation technique

As described in Section 3, the simulation technique had to take into account the fact that the development of *C. taxifolia* imposed some considerations of spatial effects, those effects (currents, spatial heterogeneity, fragments spreading, etc.) being considered as major parameters influencing the colonization process and finally the whole system functioning.

The retained modelling technique was discrete event simulation (DES) (Zeigler, 1976; Ripley, 1987; Kleijnen and Groenendaal, 1992; Fishwick, 1995; Hill, 1996), recently used in the last decade for ecological modelling purposes (Turner et al., 1982; Huston et al., 1988; Pukkala, 1988; Auger and Faivre, 1993; Baveco and Smeulders, 1994; Breckling and Müller, 1994; Hill et al., 1994; Jorgensen, 1994; Maxwell and Costanza, 1994; Coquillard, 1995; Breckling, 1996). The model is no longer specified with only a mathematical formalism but with an algorithm which describes the system functioning (Appendix A).

This implied the development of a simulation software capable of handling any littoral site by interfacing it with a geographical information system (GIS) (Parker, 1996). Part of the simulation model input was initialised with digitized maps created in the GIS software MapGrafix™ (Fig. 4). For each site studied, two maps were used: one for substrates and one for bathymetry. In the same way, the spatial simulation results are provided in GIS format in addition to traditional curves and statistics (see also Section 3.3).

Table 2
Probabilities of C. taxifolia settlement as a function of substrate

Substrates	Unstable sand with ripplemarks	Dead seagrass beds	*Posidonia* beds	Harbour mud	Rocks with photophilous algal cover	Sediments
P (settlement)	0.01	0.80	0.20	0.90	0.90	0.10

Table 3
Monthly percentage of C. taxifolia biomass increase and degeneration

	January	February	March	April	May	June	July	August	September	October	November	December
Increase (%)	0	0	0	0	3	7	20	30	20	10	7	3
Degeneration (%)	0	3	5	7	7	3	0	0	0	0	0	0

The data sampling showed above led us to build a stochastic model. The results were computed as means with confidence intervals i.e. they were obtained by means of the replication technique (Shannon, 1975; Kleijnen, 1987). Independence, common mean, variance and normal distribution of the responses were attested by a Kolmogorov's test applied on results obtained from both 1000 and 10 000 replications (Hill et al., 1996).

4.2. Modelling elements

The simulation model relies on a set of holistic variables which are estimated and changed with the occurrence of discrete events. The sites under study are divided into cells and the grid size is an important model parameter. The cell size varies from 16 cm^2 to 370 m^2 depending on the scale of the studied site. Each cell possesses substrate and depth attributes (provided precisely by the GIS). The probability that *C. taxifolia* will grow in each cell is linked to a set of evolution rules depending on (i) the depth, (ii) the kind of substrate and (iii) the number of fragments arriving in the cell. The growth during a simulation session is based on a list of active cells (i.e. those containing *C. taxifolia* individuals) the evolution of which is calculated with linear coefficients fixed in the parameter initialization. An exploratory approach allowed us to determine the best parameters for each site. Simulations are initialized from experiment files (with 98 parameters). Experiment files contain:

1. simulation control parameters (duration, number of replications, GIS map specification, etc.),
2. model initial values (distribution rate of the fragments, current direction and strength, etc.),
3. settlement probabilities as a function of bathymetry, substrate, season, etc.,
4. monthly parameters for stolon growth, spread of fragments, biomass, degeneration.

The algorithm (Appendix A) integrates the different processes involved in the alga expansion, the two main processes being the stolon growth and the spread of fragments (the latter being detailed in Appendix A). For each active cell, the stolon growth can occur randomly in eight directions, depending on the monthly parameters and proportions. One to four directions are selected uniformly. Stolon growth occurs at both ends, the colonization of neighbouring cells depending on the monthly growth and on the site scale. The simulation time step retained is the month, so that the seasonal growth and degeneracy can be taken into account (Komatsu et al., 1994). To sum up, the main parameters considered in the model are:

1. bathymetry,
2. current direction and strength,
3. monthly temperature,
4. biocenosis and inventory list of substrates,
5. *C. taxifolia* growth and settlement parameters described above.

4.3. Implementation

The computer program implementing the model is written with GNU C++ (2.6.3) and is available on PC (running Linux) and Unix workstations under X-Windows (X11R5 or R6). We use an object-oriented approach which is now well recognised as best suited to deal with simulation, particularly in the field of ecological modelling (Lhotka, 1991) and the software tools developed follow the design of the Ecosystem Modelling Environment template we previously defined (Hill et al., 1994). The pseudo-random number generator is based on a generalized Lewis–Payne shift register technique, shuffled with a congruential one, resulting in a 2^{128} period generator (Leroudier, 1980; L'Ecuyer, 1990).

5. Results

5.1. Calibration and sensitivity

At Villefranche-sur-Mer bay (Passable site) we started a calibration process with an initial zone of 3.5 m^2 of *C. taxifolia* at 80% of the maximum biomass density, which was mapped in 1994 (Fig. 5A). The simulation over 1 year showed that the colonization reached a surface of 58.4 m^2 (Fig. 5B), this value being comparable with the in situ measured surface: 59 m^2. The spectral analysis allowed us to identify some areas where the dispersion of cuttings is minimal. This is the case of *P. oceanica* beds, the long leaves of which trap the fragments and slow stolon growth.

Some variations of several parameters to extreme (and non-realistic) values did not induce any brutal bifurcation and abnormal behaviour of the model. Eventually the calibration and the sensitivity analysis demonstrated that the model can be considered as robust enough and the conceptual model consistent (Kleijnen and Groenendaal, 1992). Finally, numerous replications—up to 100 000—were carried out for verification purposes (the random number pseudo-period being long enough). They showed after the correction of inevitable programming bugs that the modifications of internal data flow never lead the model to exhibit abnormal behaviour or biased statistical results. In such conditions the model could be considered as 'reliable' according to the definition in use in the simulation community (SCS, 1979).

5.2. Model validation

We used four techniques for the validation phase (Balci and Sargent, 1989; Youngblood and Pace, 1995; Hill et al., 1996):

1. comparison validation: comparison of results from site to site,
2. confrontation validation: asking marine ecologists if the results and the behaviour of the model were consistent,
3. graphic validation: using visualization and animation to make use of the human ability to apprehend spatial relationships. For this type of simulation study, the spatial auto-correlation is strong because *C. taxifolia* contaminated zones tend to form aggregated spots. On the contrary, from one replicate to the other, peripheral spots distribution is totally different without apparent correlation. Thus, it can be interesting to sum up the results of a large

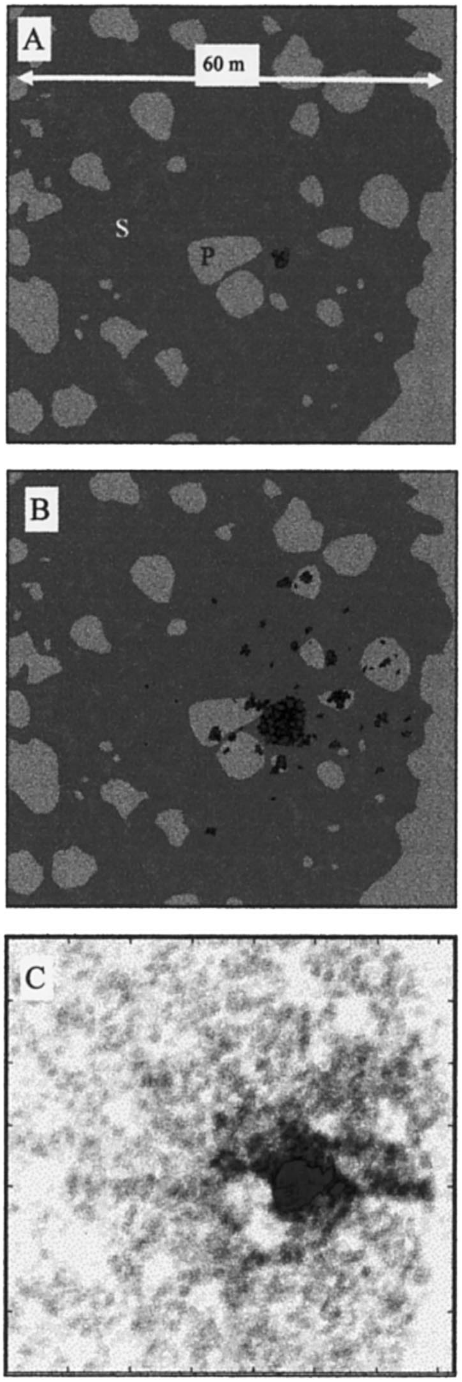

Fig. 5. One year simulation on Passable site (16 cm^2 resolution). P, *P. oceanica* beds; S, sediment (coarse gravel); approximate depth = 10 m. A. Initially sampled data (1994). In black the initial spot densely colonized by *C. taxifolia* (3.5 m^2). B. One possible (among an infinity) *C. taxifolia* extension obtained (58.4 m^2 covered). C. Spectral analysis (255 replications); the frequencies of settlement are as higher as the colors are dark. Clearest areas indicate that *Posidonia* beds slow the alga invasion.

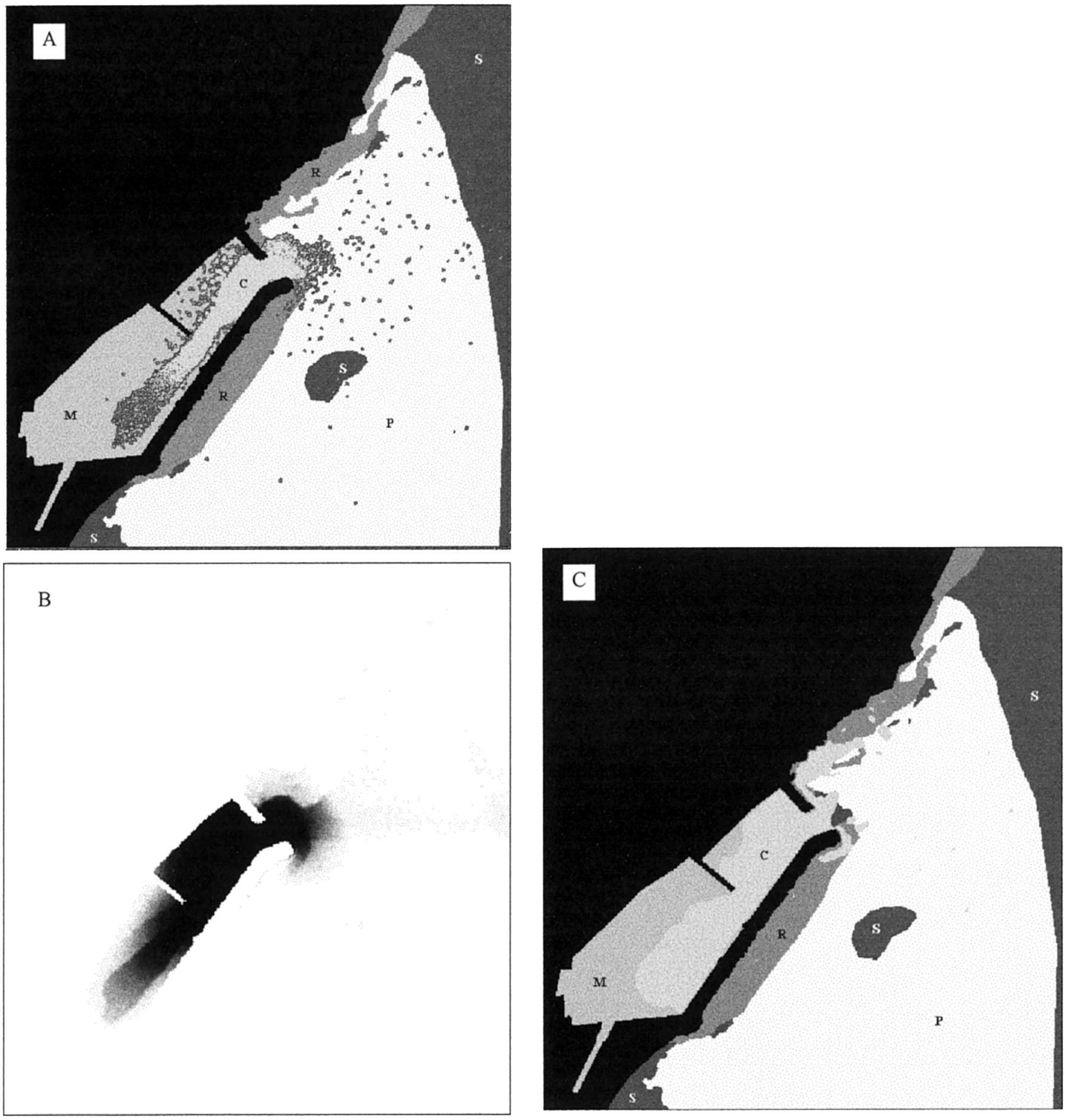

Fig. 6. Simulation over 5 years on Villefranche-sur-Mer harbour (La Darse) site. C, *C. taxifolia*; R, rocks; M, harbour mud; S, sediment; P, *P. oceanica* beds. A. Map provided by the model; *C. taxifolia* appears in a two gray scale: light gray corresponds to densities higher than 80%; the arrow points out the initial spot of *C. taxifolia* in 1991. B. Results of a spectral analysis (255 replicates†; same convention as for Fig. 5). C. Actual *C. taxifolia* settlement (November 1996).

number of replicates in a single representation of the frequencies, this constituting a discrete spectral analysis as previously defined (Coquillard and Hill, 1997). Spectral analysis helps to show areas which have a high probability of invasion by *C. taxifolia*. However, this leads to difficulties in result interpretation, because the visualized result is a sum in the space of possible solutions. Furthermore, the existence of a peak is not easy to analyse and would need a

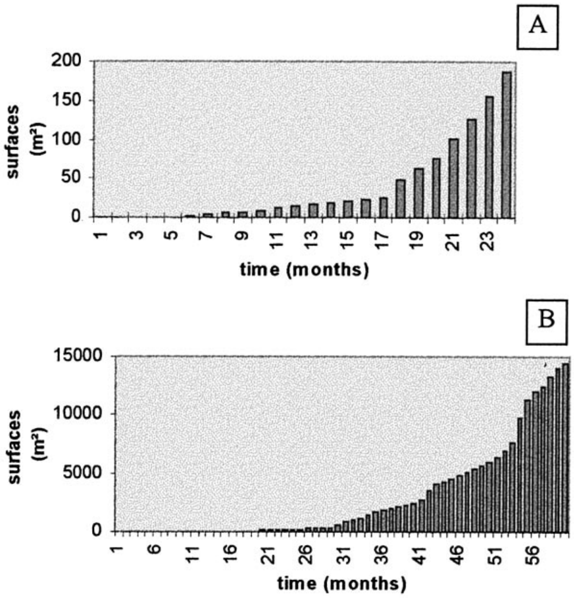

Fig. 7. Statistical results of the La Darse site simulation. A and B, Variation of the surfaces colonized by *C. taxifolia* as a function of time.

deeper study to discover possible spatial attractors (Kleijnen, 1987; Legendre and Fortin, 1989; Hill et al., 1996).

4. Statistical validation.

The model was run on three other sites:

1. The results for the Villefranche-sur-Mer harbour (La Darse, Fig. 6A) were considered to be consistent for a simulation of 5 years. For this 5-year simulation, a comparison with the real state of *C. taxifolia* colonization was achieved and no abnormal colonization (excess or default) was detected (points 1 and 2). The map resulting from the spectral analysis (Fig. 6B) is comparable with the map recorded by the divers (Fig. 6C). Furthermore, the simulations regularly predicted some fragment settlement in areas which were difficult to explore (long leaves of seagrass beds or

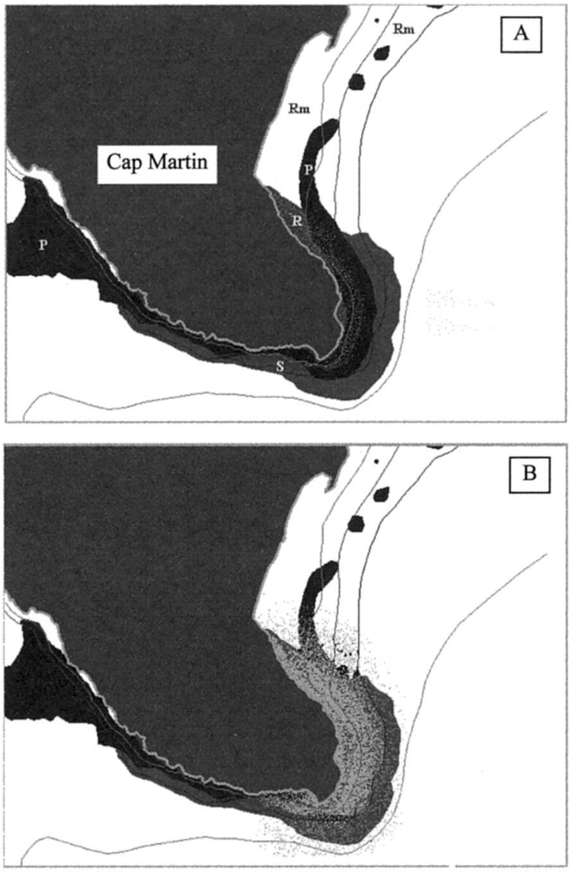

Fig. 8. Three year simulation on the Cap Martin site (3.5 m^2 resolution); P, *P. oceanica* beds; R, rocks; S, sediment (coarse gravel); Rm, unstable sand with ripplemarks. A. Initial data (1989). Isobaths lines correspond respectively to 10, 20, 30 and 50 m deep. B. Result for one replication.

depths of > 50 m). Back on the site, divers confirmed through careful investigations these settlements which had not been previously noticed. The model was also able to predict such 'hidden' settlements on the Passable site. Fig. 7 and Table

Table 4
Colonized surfaces predicted by 5 simulation years on the La Darse site

Surfaces (ha)	Minimum	Maximum	Mean
Total colonised surface (ha)	1.60	2.28	1.97 (± 0.13)
Surface densely colonized ($>80\%$) (ha)	1.04	1.49	1.31

A 90% confidence interval on the mean was obtained with ten replicates.

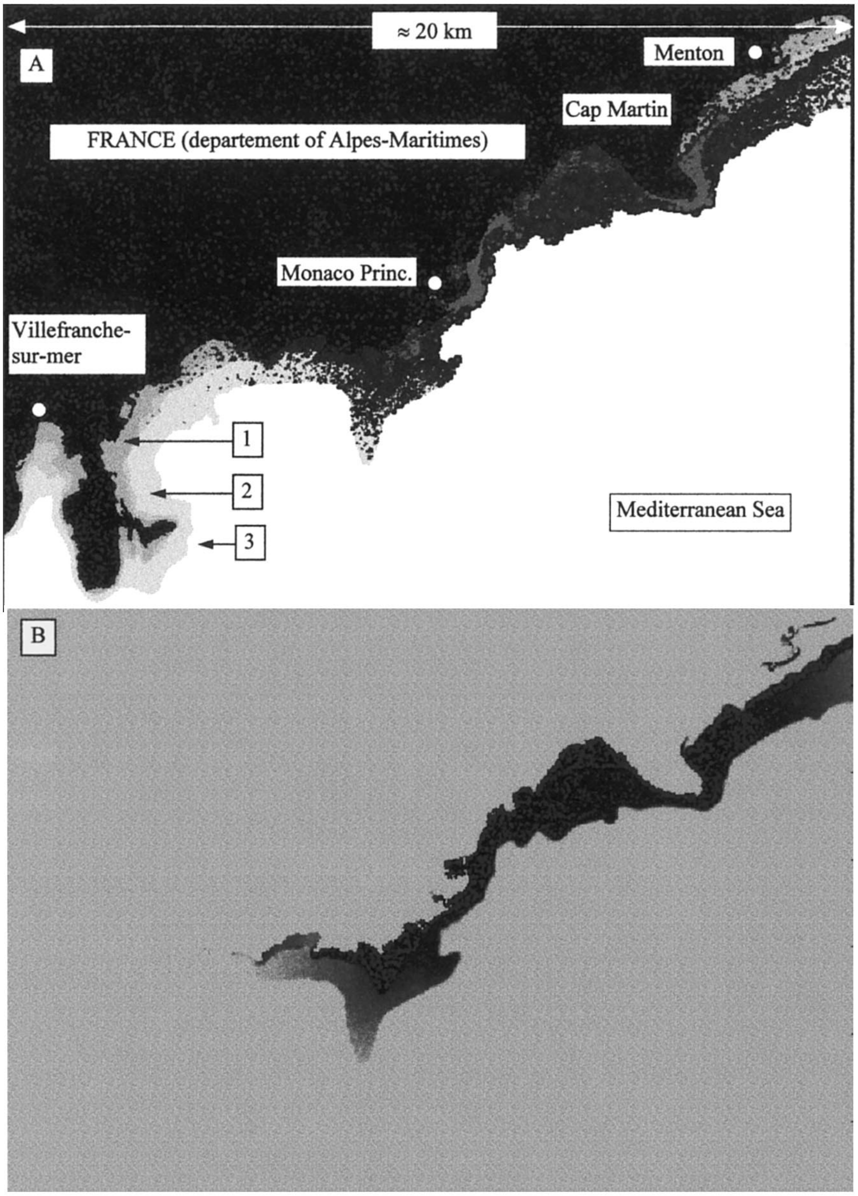

Fig. 9. Twelve years (1984–1996) simulation on Menton-to-Villefranche site (9 m^2 resolution). 1: 0–20 m deep; 2: 20–50 m deep; 3: >50 m deep. Same convention as for Fig. 5C and Fig. 6A. A. Results of a simulation. The model was initialized with two spots, one of 1 m diameter at Monaco in 1984 and one of 1 m diameter at Cap Martin in 1987. B. Result of a spectral analysis (255 replications).

4 show the results obtained about the colonized surfaces through the 5 simulation years.

2. Simulations of the Cap Martin (Fig. 8) and Menton-to-Villefranche-sur-Mer (Fig. 9) sites were engaged to follow the alga expansion on larger scales and test the third kind of validation technique (point 3, above). The comparison with real maps of the early 1990s gave encouraging results. The simulation maps are only samples of a stochastic process, however they are essential to

understand the spatial aspects of the colonization process. At this time on such large sites, the only possible validation consists of a graphical comparison with recent cartographic data provided by the French oceanographic research institute IFREMER (Belsher et al., 1994). Though statistical validations on those sites were not possible, graphical confrontation validations are encouraging. In September 1997, an IFREMER oceanographic ship will give a more precise sonar imagery of *C. taxifolia* settlement from 10 to 100 m deep, from Villefranche-sur-Mer to Italy. Substantial improvements of model validation are expected from this oceanographic campaign.

6. Conclusion

This simple and lumped model, taking into account the spatial effects, significantly increases the complexity and realism compared with usual analytic models, and appears robust and reliable enough to be considered as partially valid. Particularly, we can consider its ability to forecast some undetected *C. taxifolia* settlements as a good sign of its validity.

Some problems still remain. In essence they concern the evaluation of *C. taxifolia* biomass increase as a function of depth and time; the variations of surfaces occupied by *C. taxifolia* with respect to other species in competition, mainly *P. oceanica*; the settlement of fragments depending on the kind of substrate; and the direction, velocity and frequency of local currents. The possibility of providing a coupling of this simulation model with an oceanic circulation model influencing fragment distribution in direction and distance is envisaged but will require enormous data acquisition for each site.

Another extension of the model could be made concerning the spreading of *C. taxifolia* fragments through the anchors of boats and fisheries equipment (nets, trawls, etc.). The ability of the alga to survive for several days (up to 8 days) in the sheltered and wet anchor's case (Sant et al., 1994) allows us to suspect that these activities are one of the main factors of its extension on long distances.

However these last points do not prohibit additional simulations on other sites and the model would gain in reliability with complementary studies. We are now looking at simulations on other sites from the colonization velocity point of view, producing time-series of spectral analysis. Substantial responses about the following points and questions are expected:

1. natural speed of *C. taxifolia* colonization of a site from one or several initial places of settlement,
2. what consequences on speed and spreading could be predicted when starting simulation with virtual eradications (analogous to the already used manual rooting-up and chemical treatments (Riera et al., 1994), especially within protected areas such as natural parks and reserves, and what are the optimized locations for such operations in order to preserve the richest zones?

Lastly, some technical points can be improved:

1. Spectral analysis helps to predict the most probable colonized areas. However this technique is not able to detect some multiple spatial attractors due to spatial correlations. Consequently, in some cases the system could significantly diverge from the predicted results. Unfortunately, no reliable mathematical or statistical techniques are available at this time to detect such circumstances. Accurate knowledge and the functional analysis of the ecosystems seem to be the only ways to avoid any wrong forecasts and interpretations.
2. Simulation on very large sites cannot yet be considered on isolated computers (even on supercomputers). In order to reduce the computing time and increase the accuracy (scale and grid resolution), distributed interactive simulations (DIS) on a set of networked computers, each one managing a part of a site, is being set up and promises interesting results (Fujimoto, 1990).

```
General Algorithm for Caulerpa Expansion
Begin
     // Experiment initialization
     Read and check experiment File
     Initialize every parameters
     Load GIS bathymetry map into memory
     Load GIS Substrate map into memory
     Initialize statistical results and compute spatial scale parameters depending on maps
     Initialize the long range random number generator
     While (we have not finished all the replicates)
     Begin
            Load GIS info concerning initial Caulerpa settlement
            Initialize graphics and display initial situation
            Compute Caulerpa growth for one replicate                       // see below
            Update the Bernouilli matrix for spectral analysis
            Compute intermediate Min & Max statistics concerning biomass & surface growth
            next Simulation
     end
     Finalize experiment and compute final statistical results (confidence intervals etc.)
end
```

```
Caulerpa growth algorithm (for one replicate)
Begin
     Year = first simulation year
     While (current Simulation year < Date of simulation end)
     Begin
            Set initial simulation month according to experiment context
            While (current simulation month <= December)
            begin
                  Initialize Total surface & biomass variables
                  For every Caulerpa position in the current set of Caulerpa positions
                  Begin
                        Get the Characteristic of this (X,Y) position using GIS maps
                        // this returns the substrate, sea depth, current colonized surface
                        // and current biomass at this X,Y position depending on the
                        // current scale (imposed by the selected map resolution)

                        Modify the Caulerpa surface and biomass at this position
                        // This depends on the current spatial and time context.

                        If    (the colonized surface at this position is wide enough
                              and
                              the current month is favourable to stolon growth )
                        Then
                              Compute stolon growth
                        Endif
                        Next Caulerpa position in the current set of colonized positions
                  End
                  Spread of cuttings depending on the current simulation month  // See below
                  // Stolon growth and spread of cuttings are implemented with
                  // stochastic algorithms and can generate new colonized
                  // positions which are added to the current set of positions
                  // and taken into account for next simulation month (respect of parallelism)
            End
            Compute intermediate statistics
            Next simulation month
     End
     Next simulation year
End
```

```
Spread of cuttings (Algorithm for current simulation month)
Begin
     Compute the number of cuttings depending on the current colonized surface and exper. ratio
     For this number of cuttings
     Begin
             Random selection of a (X,Y) Caulerpa position
             Get substrate information at this position
             Set the cutting distribution radius following the experiment parameters
                   depending on the substrate (distribution radius is smaller inside Posidonia
                   or inside a harbour)
             Random draw of an angle (uniformly) and compute the cutting position
                   depending on : (i) Caulerpa position selected, (ii) the previous radius and
                   angle, (iii) the current strength and direction if specified
             Check for geometric collision using GIS maps (i.e. cuttings are not spread over a
                   headland or over pieces of concrete composing a harbour = we use a
                   fast integer Bresenham algorithm for discrete differential line drawings)
             If (the cutting position is already colonized by Caulerpa)
             Then  Increment this position surface & biomass
             Else  Try to Add a new (X,Y) Caulerpa position to a set of new colonized positions
                   Success depends on sea depth and substrate colonization probabilities
                   (which are introduced as experiment parameters)
             Endif
     End
End
```

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