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Review

Methods for identifying and tracking seaweed invasions

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Abstract

Tracking macroalgal invasions relies on a variety of approaches and techniques, including random sampling, active tracking near sources of introduction, and identification of alien species and their vectors of introduction using both classical means (based on taxonomical and biogeographical knowledge) and molecular tools. To identify the invaded ecosystems, and to describe the rate of spread and invasion dynamics, other approaches must be used, including mapping techniques and public awareness campaigns. In these endeavours, standardisation of geographical and density data is important. The tracking of alien species before eradication or control measures are instigated requires special cartographic techniques. This paper provides a general overview of these different approaches and the specific strategies adapted to the biological and ecological characteristics of particular species.

Keywords: introduced species; invasive seaweeds; mapping; monitoring; tracking.

Introduction

In recent decades, introductions of alien benthic algal species have increased dramatically in the oceans and in landlocked seas (Ribera and Boudouresque 1995, Ribera Siguan 2003). Rapid detection of a species new to a geographic region can be crucial for eradication or control operations. Rapid detection is also important for identifying sources of introduction so that transport vectors can be restricted. Furthermore, details on the invasive capability of an introduced seaweed indicated by rates of spread are needed to assess potential impacts on native ecosystems. Based on numerous case studies, clear directions are now emerging for optimal tracking strategies to (a) detect alien species as early as possible, (b) monitor their spread, and (c) assess their invasive potential.

Detecting alien invaders

Passive and random detection

The discovery of an alien species is often a matter of chance collection. Alien species occur perchance in sample collections, and are identified through the perspicacity of a phycologist. Detection is, thus, more frequent in areas that are most often visited by specialists, for instance in the vicinity of marine research stations or in marine protected areas.

This passive detection is aided by laypersons using the oceans for a living or for recreation (e.g., sailors, fishers, and divers), who often report any anomaly detected in the marine environment. When an introduced species has a size or shape very different from those of native species, they may be detected more quickly by amateurs than by professional biologists. This was the case for the green alga, *Caulerpa taxifolia* (Vahl) C. Agardh, initially identified in the Mediterranean Sea by SCUBA divers when it covered barely 1 m^2 of sea floor (Meinesz and Hesse 1991). However, early reporting is not always the case, even for large introduced and invasive species, where the first sighting is often reported only several years after introduction. Farnham (Farnham et al. 1973, Farnham 1974) first detected the brown seaweed *Sargassum muticum* (Yendo) Fensholt in 1973 on the Isle of Wight (south coast of Britain), two years before its discovery on the south side of the English Channel at Saint-Vaast-La-Hougue (France) (Cosson et al. 1977). The alga had probably been imported into Brittany or Normandy in the late 1960s from Japan on spat of the oyster *Crassostrea gigas* (Thunberg) (Gruet et al. 1976), but was not detected for many years in northern France. Similarly, in 2000, a SCUBA diving scientist working on marine phanerogams in California (San Diego) discovered *Caulerpa taxifolia* by chance. This was immediately identified as the well known invasive Mediterranean strain (Jousson et al. 2000, Woodfield and Merkel 2004). At the time of discovery in California, more than 1000 m^2 of the lagoon were already covered by this species. An invasion of *Caulerpa racemosa* (Forsskål) J. Agardh var. *cylindracea* (Sonder) Verlaque, Huisman *et* Boudouresque originating from Australia was discovered in Libya in 1990, thanks to the discerning eye of a phycologist sampling off Tripoli harbour (Nizamuddin 1991). The real date and site of introduction to the Mediterranean Sea are still not known.

Small algae whose invasive character is unspectacular, or algae that are difficult to distinguish from native species (cryptic invasions) often go unnoticed for long periods before detection and reporting. This is the case for a small member of the Ceramiales originating in Australia including *Acrothamnion preissii* (Sonder) E.M. Wollaston, which has invaded the Mediterranean Sea. Since this species is generally identifiable only with light microscopy, observations in the Mediterranean Sea have been spread widely in time and space, dependent on the collection and meticulous analysis of samples by specialists. Even though the site of first sighting for *A. preissii* was Leghorn in Italy (Cinelli and Sartoni 1969), the real site of first introduction cannot be known with certainty. Similarly, for *Codium fragile* (Suringar) Hariot ssp. *tomentosoides* (van Goor) P.C. Silva, a large green alga, long confused with *Codium tomentosum* Stackhouse, the site and date of first introduction into the North and Mediterranean Seas are unknown and debatable.

With so much uncertainty, it is clearly important to effectively monitor the arrival of introduced species, and this will depend on maintaining facilities with specialists in the taxonomy of algae and regional biodiversity. Investing in "outreach" activity, such as training members of the interested lay public about the shape and colour of native algae, and the potential impact of alien species, is also a means to ensure early detection of new alien species.

Active detection

Active detection is a dynamic process. When an invasive introduced algal species is reported, it is then sought in neighbouring regions or countries. The newly discovered species, once reported or given media exposure, usually then arouses interest in the local and regional scientific community.

Once the introduced alga has been properly described and recognised, it then becomes more easily identifiable, and an active search can be organised. A dynamic of detection is, thus, established, especially if the species is known to be potentially invasive with potentially deleterious impacts on the invaded environment. Numerous examples of this kind of "detection dynamics" may be cited, e.g., the introductions of *Sargassum muticum* (see the compilation of 300 publications concerning this invader by Critchley et al. 1990) and of the two invasive *Caulerpa* species (*C. taxifolia* and *C. racemosa* var. *cylindracea)*.

A revealing example is the tracking of *Caulerpa taxifolia* in some areas of the Mediterranean Sea. In Tunisia, this species had not yet been reported in the 1990s. A public awareness campaign about its possible arrival in Tunisia was organised in 1998 by local phycologists based on the distribution of well-illustrated brochures (Langar et al. 1998). Thanks to this information campaign, a fisherman reported the presence of the alga to an oceanographic centre in 2000 (Langar et al. 2000).

Detection effort should also focus on the mode of introduction. For example, a site where several introduced species have been reported can become a focus of sustained interest for phycologists. In this case, it is the mode of introduction that justifies the active detection of introduced species. Certain sites are particularly favourable for the introduction of species, e.g., shipping harbours where deballasting takes place, or aquaculture facilities where juveniles of shellfish species are imported. Areas within the vicinity of public aquaria built on the coast may also be actively investigated. In fact, two cases of the introduction of *Caulerpa taxifolia*, in the Mediterranean Sea and in Japan, were reported in the vicinity of aquaria (Meinesz and Hesse 1991, Komatsu et al. 2003). Around potential sites of elevated risk of introduction, more intensive observation means that introduced species may be discovered more easily. A spectacular case is that of the Thau lagoon on the French Mediterranean coast, where there is a major oyster farming facility. Oyster spat has long been imported to Thau from Japan (from the Seto Inland Sea). After the discovery of several introduced species of Japanese origin in the early 1970s, phycologists organised tracking campaigns for new introduced species, and to date have discovered 45 introduced macroalgae, the majority of them (43 taxa) most likely originating from the Pacific region and including some large phaeophytes [e.g., *Saccharina japonica* (J.E. Areschoug) C. Lane, C. Mayes, Druehl *et* G.W. Saunders, *Sargassum muticum* and *Undaria pinnatifida* (Harvey) Suringar] (Verlaque 1994, 2001).

Determining the alien character of a species, its origin and vectors of introduction

Various criteria to recognise and designate a species as alien have been proposed, including:

- it should be new to the area studied (the original range should be clearly distinct);
- there should be identifiable invasion dynamics (temporal and geographical); and
- sources of introduction in the area of first sighting should be identifiable.

In the vast majority of cases of algal introduction, the designation as alien (either through range extension or anthropogenically mediated introduction) is not contested. Classical techniques of identification and biogeographical knowledge of the range of the natural populations of the introduced alga are usually sufficient to establish status as an alien. Similarly, in the vast majority of cases, the suspected vector has not been contested. However, in several cases outlined below, genetic tools have proven very useful in establishing alien invader status. The molecular tools to track and identify alien invasive species are described elsewhere in this issue (Booth et al. 2007).

Codium fragile* ssp. *tomentosoides This sub-species is a worldwide invader. In the management and control of such alien species, it is important to determine the frequency with which it was introduced into the different invaded areas and the subsequent pattern of spread. For *C. fragile* ssp. *tomentosoides*, several authors have demonstrated that the invasive strain is monophyletic and genetically homogeneous. This suggests that there are only a few (at least two) separate introductions from the native populations localised in the North Pacific Ocean (Goff et al. 1992, Coleman 1996, 1997, Provan et al. 2005).

Caulerpa taxifolia This green alga was first discovered as an invader in 1984 beneath a public aquarium in Monaco where it was cultivated. It had never been observed previously in the Mediterranean Sea (Meinesz and Hesse 1991). Its status as an introduced species and mode of introduction seemed obvious at the time, but two other hypotheses were formulated by scientists based in Monaco (Chisholm et al. 1995). These authors raised the possibility that the alga may have been carried from the Red Sea by currents (more than 2500 km from Monaco), or was native to the Mediterranean Sea as a "metamorphosis" of *Caulerpa mexicana* Sonder *ex* Kützing, known on the eastern shores of the Mediterranean Sea (nearly 3000 km from Monaco) since 1945. To settle the issue, Jousson et al. (1998) and Olsen et al. (1998) confirmed by genetic analysis that *C. taxifolia* and *C. mexicana* are two distinct species, as is readily observable from their morphological differences (Meinesz et al. 1994, Meinesz and Boudouresque 1996). Genetic analysis of samples of *C. taxifolia* from the Red Sea, other neighbouring oceans (Atlantic Ocean, Indian Ocean) and from aquaria, including those of Monaco and Stuttgart (which was the source of the strain cultivated in the Monaco aquaria since the 1980s), demonstrated that the invasive strain in the Mediterranean Sea is identical to strains cultivated in the Monaco Aquarium, but different from those originating in the Red Sea and the oceans neighbouring the Mediterranean Sea (Jousson et al. 1998).

Given the history of *Caulerpa taxifolia* as a (controversial) invasive species**,** its arrival in California (San Diego and Los Angeles) immediately prompted genetic analysis (Jousson et al. 2000). The genus *Caulerpa* was unknown on the Pacific coasts of the USA and *C. taxifolia* had never been reported off temperate and tropical coasts of the Pacific Ocean. Genetic knowledge accumulated during the debate about the introduction of *C. taxifolia* in the Mediterranean Sea made it possible to quickly identify the invasive strain in California as the one that had developed in the Monaco Aquarium and in the Mediterranean Sea (Jousson et al. 2000). This confirmation led the local authorities to attempt eradication of *C. taxifolia* in San Diego and Los Angeles and to ban trade in *Caulerpa* species for aquaria.

Knowing the temperature tolerances of the invasive strain of *Caulerpa taxifolia* in the Mediterranean Sea (Komatsu et al. 1997) helped to identify a population of this species in subtropical Australian waters (Meinesz 2001, p. 307). It was then established quickly, on the basis of various molecular analyses, that the invasive (Mediterranean, Japan and California) and aquarium strain did indeed originate in Moreton Bay, adjacent to the city of Brisbane, Australia (Jousson et al. 2000, Meusnier et al. 2001, 2002, 2004, Wiedenmann et al. 2001, Famà et al. 2002a,b, Schaffelke et al. 2002, Komatsu et al. 2003).

Finally, the appearance of new range extensions of *Caulerpa taxifolia* into southern Australia (Sydney, Adelaide) (Millar 2001) led to the realisation that transport of vegetative fragments by boat traffic from Moreton Bay was an important vector of introduction (Schaffelke et al. 2002).

Caulerpa racemosa* var. *cylindracea This species was first recognised as an invader in the Mediterranean Sea off Tripoli harbour, Libya (Nizamuddin 1991). However, there is no certainty regarding the date and location of first introduction, and the vector is unknown. The problem posed by this species, which rapidly invaded the coasts of most Mediterranean countries, and even the Canary Islands in the Atlantic Ocean (Verlaque et al. 2003a,b, Piazzi et al. 2005), was to determine whether it was derived by hybridisation between several different varieties of *C. racemosa*, known since 1925 on the southern coasts of the Mediterranean Sea (Hamel 1926), or whether it came from the Red Sea or from other oceans. Several contradictory genetic analyses were published, but it was finally determined that the invasive strains were genetically close to a population developing in a temperate region of Western Australia near Perth (Famà et al. 2000, Verlaque et al. 2000, 2003a, Durand et al. 2002).

***Grateloupia* species** Another example of the utilisation of genetic tools to elucidate the origin of an introduced and invasive alga is that of a rhodophyte identified initially as *Grateloupia doryphora* (Montagne) Howe, originally described from Pacific South America. This species was reported as introduced and invasive since 1973 in western Europe, since 1997 in eastern North America and since 1982 in the Mediterranean Sea. However, genetic analysis demonstrated clearly that this *Grateloupia* was misidentified, and that it corresponds to *G. turuturu* Yamada, originally described from Japan (Gavio and Fredericq 2002, Verlaque et al. 2005).

Undaria pinnatifida Debate on this species is often focussed on the vector. It has invaded coastlines worldwide, being first observed outside its native Asian range in the Mediterranean Sea in 1971 and later in the eastern North Atlantic Ocean in Brittany, with subsequent establishment in the United Kingdom, Spain and the Netherlands. This alga has also established in New Zealand, Australia, Argentina and the American north Pacific coast (Silva et al. 2002, Valentine and Johnson 2003). It is often queried whether it arrived in ship ballast water, from hull fouling, or from aquaculture facilities where this edible alga is cultivated (under the name of wakame). Genealogical analyses point to aquaculture as a major vector of introduction and spread in Europe, but implicate maritime traffic in promoting recurrent migration events from the native range to Australasia (Uwai et al. 2005, Voisin et al. 2005). These analyses also make it possible to estimate the number of sources of introduction or distinct origins within an affected area.

***Acanthophora spicifera* (Vahl) Børgesen** Genetic tools were used to investigate the geographic origin of Hawaiian populations of this alga believed to have been introduced 50 years ago by way of a biofouled barge from Guam. Subsequently it reached most of the islands of the archipelago and became the most invasive alien macroalga on coral reefs throughout the main Hawaiian Islands. DNA sequencing revealed no variation for the two markers, even when collections from other areas of the Pacific Ocean and Australia were included. This genetical analysis can neither confirm the supposed origin nor secondary introductions in Hawaii. In contrast, ISSR analyses revealed highly structured Hawaiian populations of *A. spicifera* with a substantial range of both within- and among-population variation, with individual plants forming discrete clusters corresponding to geographic locality (Sherwood 2005, O'Doherty 2007).

***Asparagopsis armata* Harvey and *A. taxiformis* (Delile) Trevisan** Genetic tools were used to differentiate these introduced species in the Mediterranean Sea [the tetrasporophyte stages ("*Falkenbergia*") are difficult to distinguish] and to describe genetic variability within native and introduced strains (Andreakis et al. 2004, 2005, Ní Chualáin et al. 2004, Procaccini et al. 2005).

For some introduced species, genetic analysis has not been able to resolve disagreements regarding sites and modes of introduction. A certain number of species introduced into the Mediteranean Sea and referred to as Lessepsian (coming from the Red Sea via the Suez canal, built by Ferdinand de Lesseps in 1855–69) by Por (1978), call for genetic investigation since they may represent relics of an algal flora originating in the tropical Atlantic Ocean. This is the case for *Caulerpa mexicana* Sonder *ex* Kützing, *C. scalpelliformis* (Brown *ex* Turner) C. Agardh and certain varieties of *C. racemosa* developing in the southern Mediterranean Sea. Similarly, genetic tools would provide a basis for testing the opinions of Cormaci et al. (2004) who contested the status of 14 taxa considered by other authors as introductions into the Mediterranean Sea.

In summary, these different cases demonstrate that, where there is debate, genetic analyses usually support initial observations that use classical morphological and biogeographical criteria indicating that the species is indeed introduced. Genetic analysis may inform us on the status of a species of interest (its identity and origin), may confirm or identify the mode of introduction, assess the genetic diversity of introduced populations, and thus, enable estimates of the number of secondary independent introductions. Finally, genetic studies of alien algae can elucidate some evolutionary and genetic consequences for native and invading species (see Booth et al. 2007).

Tracking alien algae to determine their spread and invasiveness

As soon as an alien species is detected and reported, its spread and invasion dynamics must be determined. In the first instance, this requires a good knowledge of patterns of reproduction and habitat use of the introduced alga, and then the application of a variety of monitoring techniques, depending on the biological and ecological characteristics of the species.

Importance of knowledge of the biology of the alga

Basic biological knowledge is important to estimate the potential for natural or anthropogenic dissemination. For example, knowledge of the production pattern of spores or zygotes or of vegetative fragments or propagules that may be spread by currents or by man, and a clear understanding of the phenology, is essential to define the potential for spread. A variety of case studies underline the importance of this kind of knowledge.

Caulerpa taxifolia At the time of its initial discovery at Monaco and the first studies of this species (Meinesz and Hesse 1991), the question of whether sexual reproduction occurs was raised. The reproductive cycle of the genus *Caulerpa* involves production of gametes. All the nuclei are associated with chloroplasts and when the gametes are released the thallus, emptied of its content, disintegrates (this is a process of holocarpy). Species are dioecious or monoecious. *C. taxifolia* was known to be monoecious (Goldstein and Morall 1970). However, observations of the reproduction pattern of the strain introduced into the Mediterranean Sea showed that it is exclusively dioecious, producing only male gametes (without eyespots) (Meinesz et al. 1994, Zuljevic and Antolic 2000). This characteristic had already been observed in *Caulerpa prolifera* (Forsskål) J.V. Lamouroux on the French Mediterranean coast (Meinesz 1979). Since then, numerous phases of gamete production have been observed, without any female gametes being detected. Thus, all the signs are that sexual reproduction does not occur. Reproduction appears to be solely vegetative. If we consider that the introduced strain has a single origin, then all the populations of *C. taxifolia* that have developed in the Mediterranean Sea are clonal. Genetic analyses would appear to support this notion, since there is very little genetic differentiation among populations. In the Mediterranean Sea, the only one that appears to differ from the others is the population of *C. taxifolia* that has developed in Tunisia, but the only sample examined was in poor condition (Jousson et al. 1998). On this basis we may predict a slow rate of dispersal attributable solely to "secondary" anthropogenic dispersal, e.g., by boats with fragments attached to their anchors. In this case, tracking *C. taxifolia* can be undertaken in the immediate vicinity of already identified sites to assess natural rates of vegetative spread, and searches for the alga can be undertaken within a wider radius where human activities are likely to have transported fragments, such as to harbours and fishing or mooring areas.

Caulerpa racemosa For this species, two modes of reproduction that might explain its very rapid spread have been described. The alga reproduces sexually (Panayotidis and Zuljevic 2001), and there is a highly efficient system of vegetative reproduction in which the spherical branchlets of the thallus can break off and form vegetative propagules. This production of specialised propagules more easily disseminated than fragments of thallus increases the colonisation potential of an affected site (Renoncourt and Meinesz 2002). These mechanisms can account for the very rapid spread of this alga at some sites. Tracking of *C. racemosa* should reveal a more rapid progression of cover over a more extensive area than has been demonstrated for *C. taxifolia*.

Other invasive introduced algae Other invasive introduced algae have a variety of reproductive modes that influence invasion dynamics. *Codium fragile* var. *tomentosum* reproduces parthenogenetically (Feldmann 1956, Chapman 1999), which must have favoured its dissemination. In contrast, some Rhodophyta introduced into the Mediterranean Sea [*Womersleyella setacea* (Hollenberg) R.E. Norris (=*Polysiphonia setacea* Hollenberg) and *Antithamnionella elegans* (Berthold) Price *et* John)] appear to be sterile (Cormaci et al. 1994, Athanasiadis 1996, Rindi et al. 1999), so their dissemination occurs only through natural (currents) or anthropogenic (mainly fishing nets in the case of these two algae) dispersal of thallus fragments.

Knowledge of the ecology of introduced species

Understanding a species' autecology is also essential for efficient tracking of range extension. Knowing whether a species is able to colonise a large or small range of habitats determines the choice of monitoring techniques for the alga. Similarly, knowledge of the bathymetric limits attainable by an introduced species is useful to define the "search space" for tracking. For the two invasive species most extensively mapped in the Mediterranean Sea, *Caulerpa taxifolia* and *C. racemosa*, it was soon established that they are able to invade most benthic habitats from the surface to 50 m depth. Conversely, *Sargassum muticum* and *Undaria pinnatifida* develop just at the level of the lowest tides with a vertical distribution range of <5 m. These algae are, thus, more easily detected from aerial photographs or teledetection images.

In some cases, the isothermic limits characteristic of certain species offer a basis for predicting the limits of spread. However, this kind of prediction can also fail. This was the case for *Undaria pinnatifida*, the cultivation of which in Brittany (France) was permitted on the basis that low water temperatures would not allow reproduction by spores. However, estimates of the thermal threshold for this species proved inaccurate, since the alga spread rapidly in the natural environment, invading further to the North (on the southern shores of the United Kingdom) than had been anticipated. Responses to requests to cultivate other large phaeophytes have been more conservative. Cultivation of the giant kelp *Macrocystis pyrifera* (L.) C. Ag. was banned in Normandy (France) on the basis of evidence that the alga could complete its reproductive cycle in the temperatures of the English Channel and the North Sea. If this were the case, then its development may have become uncontrolled (Boalch 1981).

Collection of cartographic data through community observation

Although discovery and monitoring of small or cryptic algae usually depends on observations by professional phycologists, tracking large algae has been greatly assisted by the community at large (e.g., SCUBA divers, fishers, bathers, sailors and other lay persons). Brochures or posters to inform the public helped monitor the spread of *Sargassum muticum* in various countries on the coasts of the north-eastern Atlantic Ocean, the English Channel and the North Sea.

Important public awareness programmes were intitiated in New Zealand to track *Undaria pinnatifida*. Several government agencies have distributed brochures to the public including the Department of Conservation, Ministry of Fisheries and Biosecurity of New Zealand. Brochures have generally been made available both in hard-copy and more recently on the Internet (M. Stuart personal communication).

Properly informing the public made it possible to identify most of the Mediterranean sites affected by *Caulerpa taxifolia* and *Caulerpa racemosa*, and to monitor their development. More than 300,000 brochures have been distributed since 1991 in six Mediterranean countries (Spain, France, Italy, Croatia, Tunisia, Turkey), with similar brochures written in several languages in some countries (Cottalorda et al. 2001). This effort to collect cartographical data with the assistance of an informed public was also supported by the mass media (we estimate that 2000 press articles relating to the invasion by *C. taxifolia* and *C. racemosa* have been published by the media in Mediterranean countries). Finally, numerous Internet websites have been developed to raise public awareness and collect information (almost 1500 press articles and 36 websites are listed on the website http://www.caulerpa.org). Keeping the public informed has proven to be an effective means of collecting the information needed to estimate the overall extent of invasion in a region as vast as the Mediterranean Sea.

Collection of cartographic data by systematic monitoring

Monitoring marine species involves two distinct types of observation (Meinesz et al. 1981). The first allows the localisation of populations (or individuals) from information obtained through a distributed (but usually haphazard) collection of point samples (by divers or by using a grab), or linear samples (i.e., using transects), e.g., by the passage of SCUBA divers or towed or autonomous video cameras (ROV). The second involves collecting and analysing two-dimensional images of the seabed, usually at large scales, using aerial photographs, spectral responses obtained from satellite teledetection, by compact airbone spectographic imaging (CASI), or sonograms of the seafloor obtained by side scan sonar. These monitoring techniques always require confirmation by divers since the spectral responses of different communities or species are often very similar and vary with depth (in the case of spectrographic images) or type of bottom (in the case of side scan sonar sonograms).

Mapping using point samples For most introduced species, plotting the dynamics of population expansion has been limited to drawing up a list of scattered sightings on relatively small scale maps (more than 1/5000). This kind of monitoring effort can produce maps of the distribution of invasive algae over large areas (e.g., Figure 1). This is the case for *Sargassum muticum* and *Undaria pinnatifida*, which have been relatively easy to map, reflecting the fact that they are readily located and identified because of their large size, tendency to form dense aggregations in a narrow depth range and, in the case of *S. muticum*, floating thalli that often reach the surface. For these algae that are easy to see and identify, most sightings have been recorded as occurrences (plotted as points on distribution maps) without any estimation of the areas covered or concerned (e.g., Farnham 1997, Stuart 2004). Considering the timing of reports of species occurrences at different points in space can enable production of useful maps of the rate of spread, i.e., the temporal component of the dynamics (Figure 2).

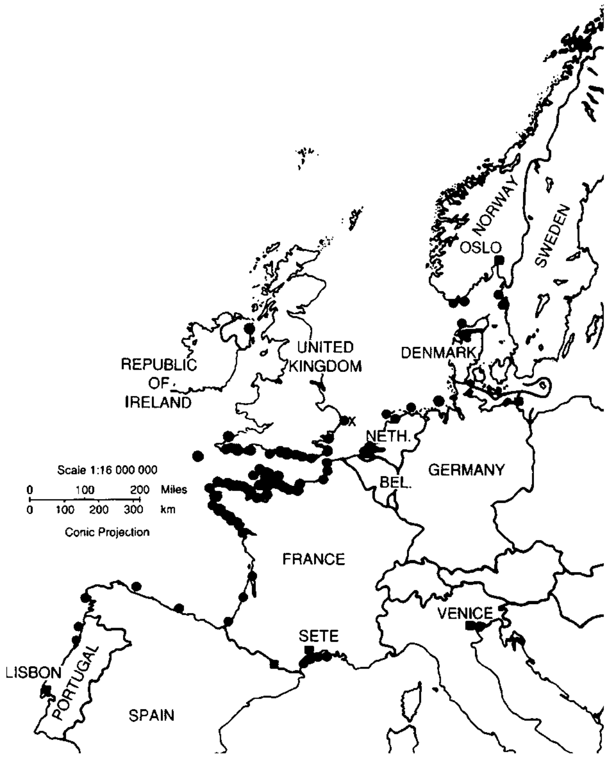

Figure 1 Example of a map of sightings of invasive species on small scales.
Scattered sighting (dots) of *Sargassum muticum* with no data on density or colony sizes (area). From Farnham (1997).

In a minority of cases, where there is high confidence that detection is soon after initial establishment, efforts to describe the density or coverage of invading algae are limited to relatively localised areas. The abundance and spread of the invasive red alga *Kappaphycus* sp. in Hawaii was followed by monitoring 15 sites within a single bay (using quadrats of 0.25 m^2) (Conklin and Smith 2005).

Mapping using linear observations For invasive species with large populations, other types of assessment enable spread to be estimated and reported on larger scale maps (e.g., scales between 1/500 and 1/5000). This has been the case for *Caulerpa taxifolia*, where major mapping operations have been undertaken on the coasts of all the countries affected in the Mediterranean Sea (26 cartographic publications were cited by Meinesz et al. 2001). This species occurs in large, often very dense and extensive perennial populations, albeit with marked seasonal fluctuations. Several methods have been used to describe the extent of its colonisation. The simplest and least costly strategy is to involve those members of the public who routinely observe the seabed in shallow waters, including fishers, divers, swimmers and sailors. Most of the 130 independent infested areas known to date along the French Mediterranean coasts were discovered by amateurs, but were subsequently checked and verified by scientists. To find reported colonies, or to locate the alga in the vicinity of colonised areas, free divers can be towed on a surface buoy with a GPS device to continually record position. With this method, transects 200–500 m in length (according to depth) can be readily explored to search for or localise invasive *Caulerpa*.

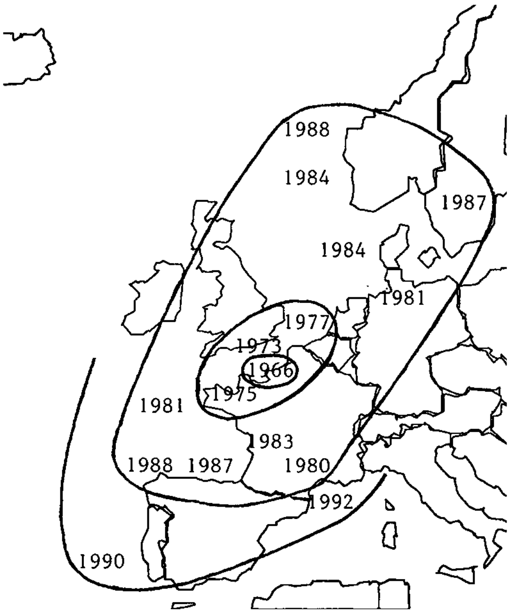

Figure 2 Example of a map of sightings of invasive species on small scales.
Isocontours indicate the rate of spread of *Sargassum muticum* in the northeastern Atlantic Ocean, the English Channel and the North Sea (from Boudouresque 1994).

For more severely affected areas (mostly in the form of multiple scattered colonies), divers seek to delimit the area over which the colonies are dispersed. For this, using a small boat towing a diver at the surface or underwater provides a suitable means. This technique is also used to actively search for algae in areas where there have been no previous sightings. In the Mediterranean Sea, visibility is often more than 10 m, which means the diver can detect colonies in a 20 m swath bisected by the transect. A GPS can be used to localise the area covered by the diver, and each population observed can be localised with precision. A diver can cover 2–5 km in 2 h while observing from the surface in this way, often in water depths to 20 m.

These techniques have been used extensively in monitoring the spread of *Caulerpa racemosa* var. *cylindracea* in the Mediterranean Sea (see the 23 cartographic publications cited by Piazzi et al. 2005).

For *Sargassum muticum*, estimates of invaded areas at a regional scale together with assessments of density have been recorded on large scale maps (1/500–1/5000), based on density data for a series of transects (Thomsen et al. 1998).

Another method of linear observation consists of towing a camera mounted on a benthic sled or hovering device that maintains an approximately fixed distance off the seafloor. The coverage depends on the lens used, but given the variations in the height of the camera above the bottom, a band of only 2–4 m width can usually be monitored effectively. This method has been utilised successfully in monitoring *Caulerpa taxifolia* in large bays at depths of 10–40 m. Belt transects several tens of km long can be filmed in one day using this methodology (Belsher et al. 1994, 2001, 2003).

Mapping based on two-dimensional images of the seabed When invasive species densely cover large areas in shallow waters (particularly between 0 and -10 m), they can be detected by aerial photography or by using a compact airbone spectographic imager (CASI). Since the responses of several species of the same genus are similar, interpretation usually requires diving to "ground truth" the remotely sensed data.

CASI is rarely used in detecting underwater alliens. Its efficacy was tested on only one occasion in the case of *Caulerpa* in the Mediterranean Sea, in some densely covered areas. No new records have been indicated by this costly method, which was unable to delineate the total area of infestation (Jaubert et al. 2003). Comparison of the densely covered areas detected by CASI with larger areas that have been invaded and observed previously by divers in the same region is not possible.

Satellite teledetection has been used to estimate the spread of *Sargassum muticum* (Belsher and Pommellec 1988) but, again, this technique is likely to prove useful for detecting and estimating the area occupied by thalli at relatively high densities**,** and it is also very costly.

Standardisation of cartographic data

Once monitoring techniques have been implemented, the information collected must be recorded and visualised appropriately, usually as maps or tables. To compare data from one year to another and between neighbouring countries that have invested in monitoring the invasion, standardised criteria for the geographical assessment of the invasion are required.

In the vast majority of cases, sites of observation are recorded in point fashion (one point per area where occurrence has been observed) on maps, as was the case, for example, in monitoring the invasion of *Sargassum muticum* in Europe (Critchley et al. 1983, Farnham 1997; see Figure 1), and in monitoring the invasion of *Acrothamnion preissii* and *Codium fragile* in the Mediterranean Sea (Ferrer et al. 1994, Ribera 1994).

If the boundaries of the invasion can be described with reference to time, it is possible to estimate the invasion dynamics of an alga (e.g., *Sargassum muticum*, Figure 2). Numerous examples of invasions by introduced species in the terrestrial environment have been described by dividing the landscape into a large number of discrete cells of similar or identical size, and indicating those cells that are colonised. The use of isocontours for invasive species based on densities is frequently utilised in conjunction with temporal wave fronts of the invasion (Hengeveld 1989). Other representations are based on presence/absence within square grids of highly variable size, each containing information on the incidence of the invasive species. Each sighting of the alien species within a square, irrespective of density, is seen as a basis for considering the entire square invaded (and coloured uniformly on maps or recored as "present" in tables). Other spatial conventions have been proposed such as presence/absence within broader polygons, such as states, regions or other administrative subunits (county, city, country). For the sea, this form of demarcation is less relevant, but it has been used in the Mediterranean Sea to indicate the number of countries affected by the invasion of the two species of *Caulerpa*. For example, as regards *C. taxifolia*, at least six Mediterranean countries are affected (in 2001) while *C. racemosa* is established in 12 countries (in 2005).

Since the beginning of the invasion in the Mediterranean Sea, several international teams have been involved in monitoring the spread of *Caulerpa taxifolia* in several countries. In order to standardise the mapping, an international pool of experts (from France, Spain, Monaco, Italy, Tunisia and Croatia) established a standardised method (Vaugelas et al. 1999, Meinesz et al. 2001) (Figure 3). These guidelines for mapping *C. taxifolia* define three levels of invasion and associated descriptive terms for assessing an impacted area (Figure 4):

(1) Level I is the first stage of colonisation, in which one or more colonies occurring less than 100 m apart occupy a total surface area of less than 1000 m^2. Under these conditions, it is relatively easy to estimate the surface area covered by the alga (referred to as the *covered area*) and to delimit the exact perimeter of the area of dissemination by SCUBA diving (the *concerned area*).

(2) Level II refers to the next step of spreading. It is characterised by several colonies that occur within 250 m of each other, that cover a total area of more than 1000 m^2, and that are dispersed over an area $<$10 ha. During this stage of the invasion, it is both time-consuming and futile to measure the *covered area*, as the alga grows and spreads very quickly. The best method to estimate the extent of coverage is to delimit the perimeter enclosing all colonies (i.e., the *concerned area*).

(3) Level III is attained when dozens or hundreds of colonies of various sizes are dispersed over a surface area $>$10 ha, with a total *covered area* of more than 1000 m^2. At this stage, it becomes impossible (and in any case not very useful) to map the location of each colony with any precision, or to measure the covered areas. Rather, the outer boundary, or *concerned area*, is estimated by identifying the positions of the peripheral colonies.

By summing the colonised areas (Levels I, II and III), an evaluation of the overall status of a given region in terms of the area affected by the colonisation is obtained.

For *Caulerpa racemosa* var. *cylindracea* in the Mediterranean Sea, invasions proceed so rapidly that only the linear coastal extent of colonies is a valid criterion for description. Thus, maps summarising the invasion of this alga typically show only the lineal extent of the invaded area along the shoreline (Piazzi et al. 2005, Ruitton et al. 2005) (Figure 5).

Spread modelling

Numerous theoretical and empirical approaches for assessing and predicting the spread of invasive terrestrial species have been proposed based on the characteristics of the invasion dynamics observed during the first years of colonisation of an environment (Hengeveld 1989, Hastings et al. 2005). These studies suggest that long range dispersal events from initial points of establishment have a strong influence on the rate of the overall range

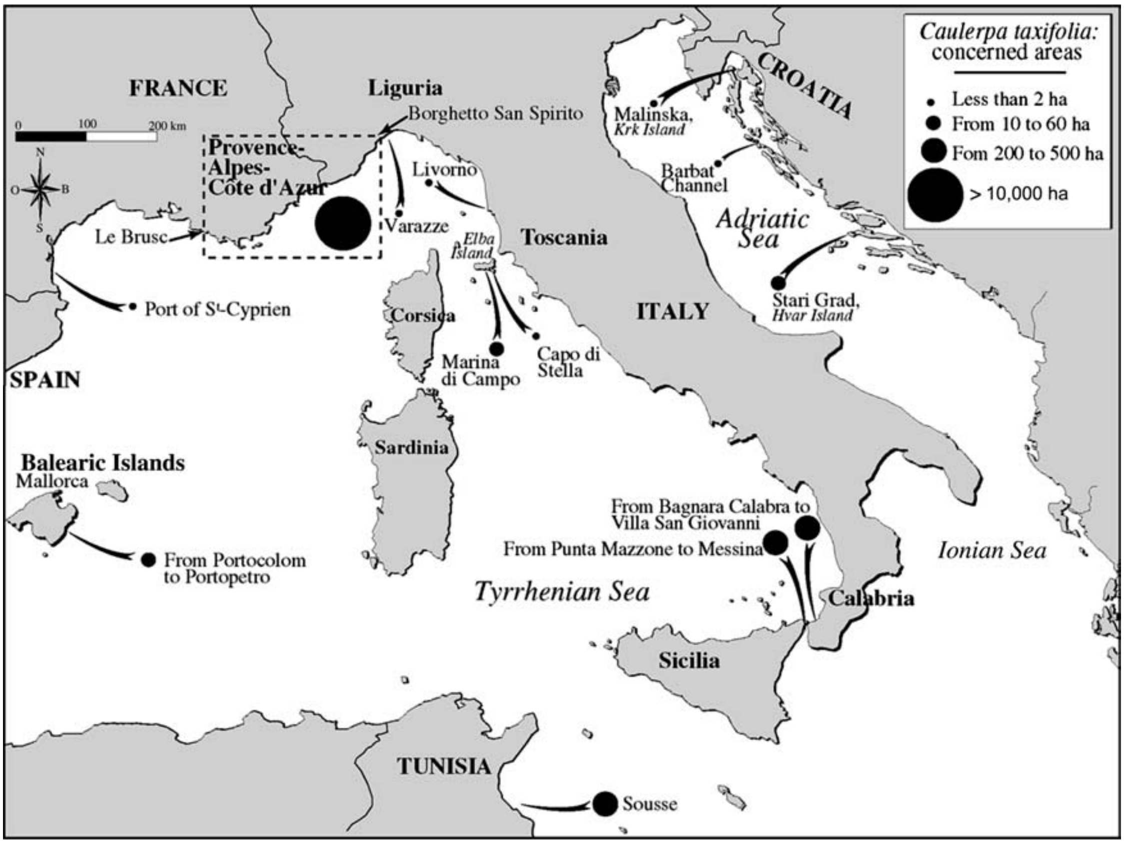

Figure 3 Example of a map of sightings of invasive species on small scales.
Report of occurrences with spatial extension for each spot. Invasion of *Caulerpa taxifolia* in the Mediterranean Sea (from Meinesz et al. 2001).

expansion. For invasive algae, a predictive spread model has been developed only for *Caulerpa taxifolia* (Vaugelas et al. 1997, Hill et al. 1998, 2001, 2002) at a particular site. In the marine domain, predictions are hampered by poor knowledge of both coastal currents and the spatial distribution of the subtidal habitats that an introduced species is likely to colonise.

Tracking for eradication purposes

In a few rare cases, monitoring invasive algae must be carried out with a high level of precision. Very precise monitoring is required if it is necessary to completely eradicate either the whole of an introduced population or all of a particular sub-population of developing colonies within a restricted area.

The eradication of *Caulerpa taxifolia* in southern California, near San Diego (Agua Hedionda lagoon) and near Los Angeles (Huntington Harbor), where more than 1000 m^2 of *C. taxifolia* were discovered in 2000 (Jousson et al. 2000, Williams and Grosholz 2002, Woodfield and Merkel 2004), is a useful example. The success of eradication operations usually depends more on the precision of monitoring than on the eradication technique itself, since if a few colonies have not been detected, the whole eradication investment may be rendered worthless within a few years. Commencing in summer 2001, different methods of tracking the algae for eradication purposes were tested in the turbid waters of these areas (visibility is typically <2 m in Agua Hedionda lagoon), and included towed divers, towed cameras and laser line scan, and divers using a guide-line deployed by a small boat using differential GPS. The latter technique appeared to be the most effective in locating very small fronds of *C. taxifolia* (Woodfield and Merkel 2004). This method seeks to ensure 100% coverage of the afflicted area. Agua Hedionda lagoon near San Diego was covered several times by SCUBA divers along hundreds of transects 1 m apart. Permanent grids of ropes were deployed in the colonised areas in the third year of quarterly surveys. This technique made it possible to detect all colonies, which were then successfully eradicated.

Off the French Mediterranean coast, the Parc National de Port-Cros authorities decided in 1994 to control the spread of *Caulerpa taxifolia* by eradicating the colonies as soon as they became established. Each year since 1994, between 40 and 60 SCUBA divers or skin divers combed the waters of the national park for three days to detect developing colonies. Each year, colonies were discovered and eradicated. Even if the detection of the colonies is less than exhaustive, the occurrence of the alga at Port Cros has since been highly restricted, whereas in an uncontrolled neighbouring island (Porquerolles) the invasion spread to cover several tens of hectares by 2004. At Port-Cros, the extensive area of seabed favourable for the development of *C. taxifolia* cannot be monitored in its entirety during each campaign. Therefore, those particular sites most favourable for the introduction (mooring areas in sheltered bays or areas where fishing

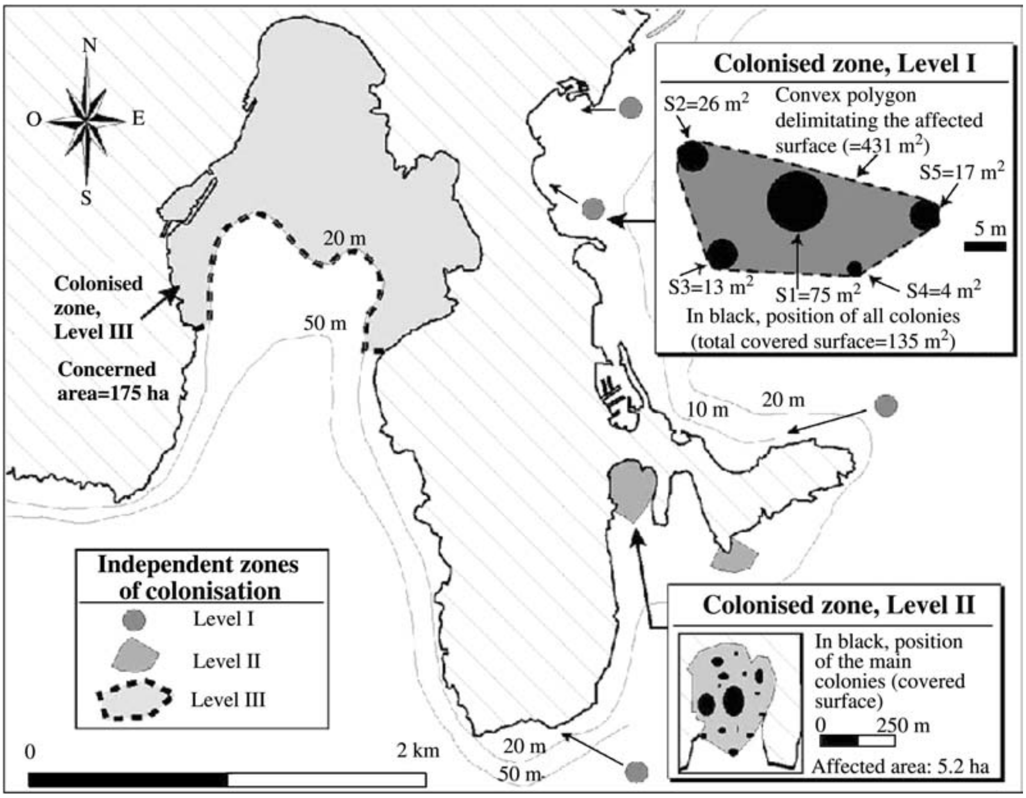

Figure 4 Configuration of the three levels of colonisation of *Caulerpa taxifolia* on large scale maps.
In Level III the position of the dozen or hundred main colonies involving more than 100 ha and covering much more than 1000 m^2 is not presented. Example: the rade of Villefranche (France, Mediterranean Sea; 43°41′58″N, 7°18′58″ E), (after Vaugelas et al. 1999 and Meinesz et al. 2001).

nets are placed underwater) have been most closely inspected. Monitoring methods based on groups of 6 to 10 divers swimming in line on a pre-established course holding a rope have been used. Since the waters at Port-Cros are very clear (visibility often more than 10 m), the distance between divers is 5 m. A buoy attached to a weight by a rope is placed at each of the colonies detected. Their position can, thus, be easily determined with a GPS, with subsequent eradication (Cottalorda et al. 1996, Robert 1996, Robert and Gravez 1998).

Conclusion

The manner of discovery of new invasions and their subsequent monitoring provides a basis for assessing the effectiveness of several different tracking protocols that have been attempted. In the majority of cases, the activity of phycologists with a good knowledge of the algal flora of their region, plus informing the lay public about potential invaders, led to relatively rapid detection of alien algal species.

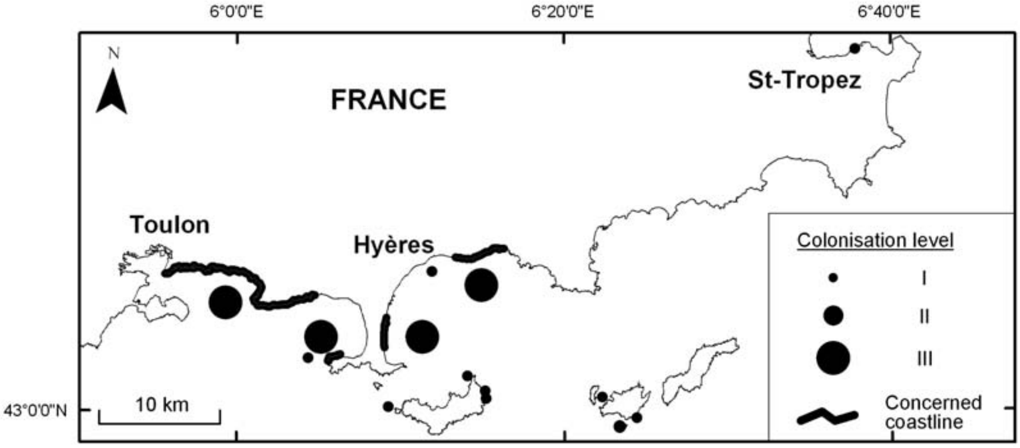

Figure 5 Representation of the invasion of *Caulerpa racemosa* var. *cylindracea* on large scale maps in terms of the linear extent of coast line affected (from Ruitton et al. 2005).
Colonisation Levels I–III are as outlined in Figure 4.

To assess spread, it is necessary to match appropriate marine environmental monitoring techniques to the biology and ecology of the alga. Comparing standardised cartographic data over time and between different areas has proven extremely useful in this context. Although in a majority of cases classical identification and biogeographical knowledge provides an adequate basis for determining that particular individuals represent an alien algal species, and often to ascertain their mode of introduction, genetic tools can be particularly helpful in illuminating the likely history of a given introduction. Above all, cartographic methods make it possible to measure the extent of the spread of an invasive alga and can assist in helping to predict potential impacts. Early discovery of major invaders followed immediately by exhaustive monitoring is the exception rather than the rule, and so successful prevention of spread as a result of early detection and tracking, such as that of the eradication of *Caulerpa taxifolia* in California, are relatively rare.

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