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CHAPTER 5

The Spread of a Non-native Marine Species, *Caulerpa taxifolia*. Impact on the Mediterranean Biodiversity and Possible Economic Consequences

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**Introduction**

An introduced species is a species that colonizes a new area where it was not previously present. The extension of its range is linked, directly or indirectly, to human activity (Carlton, 1985). In addition, there is a geographical discontinuity between its native area and the newly invaded area (remote dispersal). This means that the occasional advance of a species at the frontiers of its native range (marginal dispersal) is not taken into consideration (Boudouresque and Ribera, 1994; Ribera and Boudouresque, 1995). Such fluctuations (advances or recessions) may be linked with climatic episodes. Finally, new generations of the non-native species are born *in situ* without human assistance, constituting self-sustaining populations: the species is said to be established, *i.e.*, naturalized (Williamson and Fitter, 1996). Based on the above definition, species such as maize (*Zea mays*), potato and tomato, found in European terrestrial environments and the sea mammal *Dugong dugon*, observed once along the Israeli coast (an isolated individual having entered the Mediterranean through the Suez Canal) (Por, 1978), are not considered to be introduced species.

The study of a large number of species introductions, in the terrestrial environment, has led to the conclusion that, on average, 10% of introduced species are invasive. This is the ‘tens rule’ (Williamson and Fitter, 1996). An invasive species is an introduced species the abundance of which is conspicuous, or threatens native species or communities, or which has economic consequences (Boudouresque, 1999a). Invasive species are also called ‘pests’. The zebra-mussel *Dreissena polymorpha* in the North American Great Lakes, the comb jelly *Mnemiopsis leidyi* in the Black Sea and the tropical green alga *Caulerpa taxifolia* in the Mediterranean are invasive species (Konovalov, 1992; Carlton, 1996; Meinesz and Boudouresque, 1996; Gesamp, 1997). It is difficult, or impossible, to predict whether or not an introduced species will become invasive: it is a matter of ‘ecological roulette’, a term coined by Carlton and Geller (1993).
The introduction of alien species and the biological invasions that may result from such an introduction, constitute an environmental problem of growing concern, especially in the marine environment. This is due to the fact that 1) the existing instruments, whose goal it is to protect the autochthonous biodiversity, are inadequate and 2) because the invasive phenomenon is still increasing in a linear, or even exponential manner, unlike other environmental problems. For example, the increase over time is still linear in British marine waters (Eno et al., 1997). In the Mediterranean, since the beginning of the twentieth century, the number of introduced species has nearly doubled every 20 years (Ribera and Boudouresque, 1995; Boudouresque, 1999a).

The Spread of *Caulerpa taxifolia* in the Mediterranean Sea

*Caulerpa taxifolia* is a green alga widespread in tropical seas, though usually uncommon (Boudouresque et al., 1995). A tropical sea is defined as a sea where the winter mean temperature is higher than 20°C. A strain of *C. taxifolia*, capable of surviving low temperatures (6-10°C), was cultured in a German public aquarium since the 1970s and in aquariums in France and Monaco since the early 1980s. It is now widespread in the world aquarist trade (Artaut, 1987; Boudouresque et al., 1995; Komatsu et al., 1997; Jousson et al., 1998). Since 1984, a strain of *C. taxifolia*, morphologically and genetically identical to the aquarium strain, has been present in the Mediterranean (Fig. 5.1). The first open sea site where the alga was

![Diagram of Caulerpa taxifolia](image)

*Figure 5.1. Morphology of the aquarium and Mediterranean strain of Caulerpa taxifolia.*
1. primary leaf; 2. secondary leaf (ramification); 3. pinnules; 4. rhizome (= stolons); 5. pillar of rhizoids; 6. bunch of rhizoids fixing sediment particles; 7. interruption in the distribution of the pinnules. Specimen from Cap Martin, French Riviera. From Meinesz et al. (1995).
observed is located a few meters off an aquarium in which it was actually present, which further supports the theory of an aquarium origin for its introduction (Meinesz and Hesse, 1991; Boudouresque et al., 1995; Meinesz et al., 1995; Meinesz and Boudouresque, 1996; Jousson et al., 1998).

Since then, the species has spread rapidly in the Northwestern Mediterranean. Spectacular progression has been observed on the French and Italian Rivieras, where the affected areas have increased from 1 m² in 1984, to 3 ha in 1990, 3,000 ha in 1996 and to more than 6,000 ha today (Meinesz et al., 1993; Boudouresque et al., 1995; Meinesz, 1997; Meinesz et al., 1998a, 1998b, 1998c, 1999; Cottalorda et al., 2000). To date, there is no sign of any slowing down in the spread of this species. Isolated colonies have also been discovered in French Catalonia (1991), Tuscany, the Balearic Islands (1992), Sicily (1993), Croatia (1994) and Tunisia (1999) (Pou et al., 1993; Fradà-ORESTANO et al., 1994; Meinesz and Boudouresque, 1996; Žuljević and Antolić, 2000). Finally, small colonies of the aquarium and Mediterranean strain of C. taxifolia have been discovered in a California lagoon (Dalton, 2000; Jousson et al., 2000; Kaiser, 2000). As in the Mediterranean, C. taxifolia has not been previously recorded on the Pacific American coasts. It is therefore highly probable that this species is a recent introduction.

Successful sexual reproduction has not been observed in the aquarium and Mediterranean strain of C. taxifolia: only male gametes are produced (Meinesz, 1992; Meinesz and Boudouresque, 1996; Žuljević and Antolić, 2000). The spreading over short distances (from a few metres to one kilometre or so) results from the small fragments transported along the bottom by water movement and which act as cuttings. The spreading over long distances seems to be the result of propagation of cuttings through fishing nets and anchoring systems. Under laboratory conditions, C. taxifolia cuttings survived up to 10 days out of water, when kept in the dark, at 18°C and at a high air humidity. These results indicate that the alga is able to survive long periods of time on board boats, e.g., in an anchor locker or in a heap of fishing nets (Meinesz, 1992; Boudouresque et al., 1995; Sant et al., 1996; Coquillard and Hill, 1997). Since 1991, public awareness campaigns in the Mediterranean region have been specially directed toward yachtsmen, fishermen, divers and the general public, including tourists. More than 100,000 leaflets were distributed in the local language as well as in English, with messages such as: “Yachtsmen – take care to inspect your anchors and chains when leaving an anchorage”; “Fishermen – check your nets and trawls”; “Divers, check your bags and equipment before each dive”; and “If you have accidentally picked up fragments of C. taxifolia, do not throw them back into the sea. Put them in a bag and throw it into a garbage can when you go ashore” (Anonymous, 1992; Castalia, 1993; GIS Posidonia, 1994; Cottalorda, 1996; Brozović, 1997; Cottalorda and Gravez, 1997; Cottalorda et al., 1998, 2000; Langar et al., 1998). Most of the remote spreading occurred before 1994. Its subsequent conspicuous slowdown can be attributed to the success of the awareness campaigns.
Impact on Species Diversity

In the Mediterranean, *C. taxifolia* colonizes all kinds of substrates: rock, sand, mud, sea grass beds and dead rhizomes of sea grasses (Meinesz and Hesse, 1991; Boudouresque et al., 1992, 1995). Both photophilic and sciaphilic biotopes are invaded. In fact, the photosynthesis compensation point for light is very low in the aquarium and Mediterranean strain: 0.3 μE m⁻² s⁻¹ (Gacia et al., 1996). No relationship has been detected between colonies of *C. taxifolia* and water quality (Belshcer et al., 1994). Moreover, its productivity is not nutrient-limited in summer (Delgado et al., 1994, 1996) when production of most Mediterranean native seaweeds is severely reduced by inorganic nutrient depletion in the water column (Ballesteros, 1989). Populations of *C. taxifolia* start from 1 m and 2-4 m depth in protected and exposed environments, respectively. In completely invaded sites, they form continuous and dense (up to 350 m of stolons and 14,000 leaves m⁻²) meadows down to 20-30 m, having a patchy distribution at greater depths. It has been observed attached to the seabed down to a depth of 100 m in the French Riviera (Meinesz and Hesse, 1991; Belsher et al., 1994; Meinesz et al., 1994; Belsher and Meinesz, 1995; Boudouresque et al., 1995).

The most drastic decrease in species diversity (alpha diversity; see Whittaker, 1965; Whittaker, 1972) is observed in photophilic algal communities of the sublittoral zone (0-35 m depth), when they are replaced by *C. taxifolia* meadows. Most of the large perennial species of algae, such as *Cystoseira* spp., disappear, especially in summer-autumn, when the vitality of *C. taxifolia* is at its highest (Boudouresque et al., 1992; Verlaque and Fritayre, 1994; Verlaque and Boudouresque, 1995, Table 5.1). The Mediterranean sublittoral communities harbor a high diversity of *Cystoseira* species (Ribera et al., 1992). Many of them, which are endemic, rare and ecosystem-engineers, are considered to be emblematic species. Furthermore, being long-lived and K-selected strategists, they are particularly vulnerable (Boudouresque et al., 1996b). In the long run, should the expansion of *C. taxifolia* continue, some of these *Cystoseira* species might be threatened with extinction. In the same way, there is a conspicuous decrease of polychaetes and crustaceans, both in terms of number of individuals and number of species (Bellan-Santini, 1995; Bellan-Santini et al., 1996). The parasites (Digenea) of the digestive tract of the labrid fish *Symphodus ocellatus* are significantly reduced in *C. taxifolia* meadows (2 species, prevalence = 1.5%) in comparison with control sites (6 species, prevalence = 46.3%) (Bartoli and Boudouresque, 1997). In contrast, gastropods and the sediment meiofauna (species smaller than 1-2 mm) do not show a decrease in the number of individuals or species in *C. taxifolia* meadows, though there is a great change in the species composition (Bellan-Santini et al., 1996; Poizat and Boudouresque, 1996).

As far as fishes are concerned, changes in alpha species diversity induced by *C. taxifolia* depend upon the initial structure and architecture of the habitats. When substrates with a high structural diversity (such as *Posidonia oceanica* beds, rocky areas with photophilic algae and coralligenous constructions) are colonized, there is a significant decrease in mean species richness, mean density of individuals and
Table 5.1. Comparison across seasons between the algal flora of a *Caulerpa taxifolia* meadow (means and, in parentheses, the standard deviation) and a control community dominated by native algae (minimum and maximum), 6-10 m depth, French Riviera. Sample surface: 400 cm². (From Verlaque and Boudouresque, 1995).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Winter <em>Caulerpa</em> meadow</th>
<th>Control site</th>
<th>Spring <em>Caulerpa</em> meadow</th>
<th>Control site</th>
<th>Summer <em>Caulerpa</em> meadow</th>
<th>Control site</th>
<th>Autumn <em>Caulerpa</em> meadow</th>
<th>Control site</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Caulerpa</em> biomass¹</td>
<td>13 (4)</td>
<td>-</td>
<td>24 (7)</td>
<td>-</td>
<td>18 (3)</td>
<td>-</td>
<td>17 (6)</td>
<td>-</td>
</tr>
<tr>
<td>Native biomass²</td>
<td>7 (2)</td>
<td>18-22*</td>
<td>3 (3)</td>
<td>18-22*</td>
<td>3 (3)</td>
<td>12-31*</td>
<td>1 (1)</td>
<td>4-15*</td>
</tr>
<tr>
<td>Macraalgae³</td>
<td>67 (4)</td>
<td>89-91*</td>
<td>59 (9)</td>
<td>86-111*</td>
<td>38 (6)</td>
<td>81-83*</td>
<td>30 (3)</td>
<td>66-74*</td>
</tr>
<tr>
<td>Macraalgae &gt;0.5%</td>
<td>14 (4)</td>
<td>35-40*</td>
<td>13 (3)</td>
<td>34-36*</td>
<td>12 (3)</td>
<td>32-39*</td>
<td>5 (1)</td>
<td>19-26*</td>
</tr>
<tr>
<td>Native covering⁵</td>
<td>82 (44)</td>
<td>341-366*</td>
<td>51 (36)</td>
<td>352-367*</td>
<td>53 (12)</td>
<td>208-273*</td>
<td>21 (16)</td>
<td>186-195*</td>
</tr>
<tr>
<td>Diversity index⁶</td>
<td>1.7-2.8*</td>
<td>3.7-3.9*</td>
<td>1.1-2.5*</td>
<td>4.0-4.2*</td>
<td>1.3-2.1*</td>
<td>3.8-4.7*</td>
<td>0.5-1.2*</td>
<td>3.1-3.7*</td>
</tr>
<tr>
<td>Evenness</td>
<td>0.36 (0.07)</td>
<td>0.51-0.56*</td>
<td>0.30 (0.09)</td>
<td>0.61-0.63*</td>
<td>0.31 (0.05)</td>
<td>0.60-0.73*</td>
<td>0.16 (0.06)</td>
<td>0.51-0.59*</td>
</tr>
</tbody>
</table>

1. Biomass (g dry weight) of *Caulerpa taxifolia*.
2. Total biomass (g dry weight) of native species.
3. Total number of species of macroalgae (Chlorophyta, Phaeophyceae, Rhodophyta).
4. Number of species of macroalgae with covering >0.5%.
5. Total coverage of native species.
7. Evenness.
8. * = minimum and maximum.

mean biomass. However, coexisting species may react differently. Some species, such as *Diplodus sargus* and *Serranidae cabrilla*, are very sensitive to the modification of their environment and present lower density and biomass in *C. taxifolia* meadows. The mean density of *D. sargus*, a target species for fishermen, is 0.5 individuals/10 m² in the reference sites and only 0.2 individuals/10 m² in *Caulerpa* meadows. Other species, like *Serranidae scriba*, do not present any consistent difference in the reference and colonized sites (Francour et al., 1994, 1995; Harmelin-Vivien et al., 1996, 1999; Table 5.2). In contrast, when substrates with a low structural complexity (such as *Cymodocea nodosa* and *Zostera noltii* meadows, dead

Table 5.2. Decrease in mean species richness, mean density and mean biomass of fish assemblages in sites colonized by *C. taxifolia* compared to reference sites at Cap Martin (French Riviera), expressed as percentage of reduction. (From Harmelin-Vivien et al., 1999).

<table>
<thead>
<tr>
<th></th>
<th>Shallow sites</th>
<th>Deep sites</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean species richness (number of species/transect)</td>
<td>-23%</td>
<td>-31%</td>
</tr>
<tr>
<td>Mean density (number of fishes/10 m²)</td>
<td>-36%</td>
<td>-31%</td>
</tr>
<tr>
<td>Mean biomass (g wet weight10 m²)</td>
<td>-57%</td>
<td>-42%</td>
</tr>
</tbody>
</table>
‘matte’ of Posidonia oceanica, or sandy or muddy areas) are colonized by C. taxifolia, there is a moderate increase in species richness, density and biomass of fishes, though species that are specific to these habitats (e.g., Soleidae and Mullus) disappear (Relini et al., 1998a, 1998b; Harmelin-Vivien et al., 1999). In fact, the colonization of all these habitats by C. taxifolia results in a homogenization of microhabitats and a decrease in the diversity of microhabitats offered to fishes on a regional spatial scale. A variety of fish faunas, be they rich, moderately rich, moderately poor, or poor, are replaced by a uniformly moderately poor fauna, resulting in a conspicuous decrease in gamma species diversity (sensu Whittaker, 1965) (Harmelin-Vivien et al., 1999).

**Impact on Ecodiversity**

More than twenty suplittoral photophilic and sciaphilic communities of the hard-bottom realm, dominated by algae and/or by gorgonians, together with soft-bottom communities, can be replaced by homogenous C. taxifolia meadows. The resulting decrease in ecosystem diversity (ecodiversity) and uniformization of the underwater landscape (seascape) are probably the more conspicuous ecological impacts of the spread of C. taxifolia (Verlaque and Fritayre, 1994; Boudouresque et al., 1995; Romero, 1997).

The meadows of the sea grass Posidonia oceanica constitute both a key and emblematic ecosystem in the suplittoral zone of the Mediterranean Sea, from a biological, physical equilibria and natural heritage perspective. In addition, they harbor a very high species diversity and constitute a spawning place and/or nursery for fish species of great economic value (Molinier and Picard, 1952; Boudouresque and Meinesz, 1982; Boudouresque et al., 1994a, 1994b). The P. oceanica ecosystem, especially when shoot density is very high, seems to be able to better resist invasion of C. taxifolia than photophilic algal communities. However, evidence of stress and decline were detected in meadows densely colonized by C. taxifolia: increase in the number of tannin cells, loss in shoot density, regression of the border, fragmentation into isolated patches and overgrazing. This overgrazing may be due to the shift of large herbivores (the sea-urchin Paracentrotus lividus and the fish Sarpa salpa) away from the avoidable C. taxifolia, which is rich in toxic metabolites, to the more palatable leaves of Posidonia oceanica (Guerriero et al., 1993; Villèle and Verlaque, 1994, 1995; Boudouresque et al., 1996a; Boudouresque, 1997; Amade and Lemée, 1998). Long-term monitoring of P. oceanica meadows is required to accurately assess their trend in areas colonized by C. taxifolia: either pinpointed and only local decline, or slow but widespread regression.

**Possible Economic Impact**

Some introduced species are now of economic importance in the Mediterranean, being exploited by local fisheries (Oren, 1957; Galil, 1986; Spanier and Galil 1991; Zibrowius, 1991). The crab Portunus pelagicus has become the dominant crab in
commercial catches all around the eastern Mediterranean, especially in Egypt. The prawns *Penaeus japonicus* and *P. monoceros* are also commercially exploited. In Israel and Egypt, they make up most of the shrimp catches. Off the Israeli coast, Lessepsian fishes constitute a third of the trawl catches. It is unclear, however, whether total stocks or even annual catches have actually increased in these regions, or if the introduced species have simply replaced native ones of equal economic value (Boudouresque, 1996, 1999b). At any rate, the economic benefits of a species introduction should not be assessed simply on the basis of strict sale price, but on the basis of a wider view, taking into account the losses to other business activities and the costs of any damage that may result: these losses are usually ‘externalized’. This means that benefits are for some people, whereas the costs are ‘externalized’, that is to say paid by other people (e.g., McNeely, 1992, 1994, 1996a, 1998; Bayon et al., 1998).

Species introduction may have harmful consequences for several sectors of human activity (e.g., Kiernan, 1993; Boudouresque, 1999a; IUCN, 2000):

- **Fisheries.** In the Black Sea, the dramatic drop in fish catches is considered to be a consequence of the introduction of the comb jelly *Mnemiopsis leidyi* (Gesamp, 1997).
- **Aquaculture.** Most of the new diseases of bacterial or parasitic origin that strike marine cultures in many parts of the world (e.g., oyster culture) probably result from species introduction (Mazzola, 1992; Barber, 1997). In the same way, the worldwide increase in blooms of unicellular algae producing paralytic shellfish poisoning (PSP), diarrheic shellfish poisoning (DSP) and amnesic shellfish poisoning (ASP) toxins may be due to the transportation of millions of cubic metres of seawater by ships (ballast water) from one ocean to another (Carlton and Geller, 1993; Hallegraeff, 1993; Belin and Martin-Jezequel, 1997; Carlton, 1998). Such blooms often result in the temporary prohibition of the shellfish trade, with dire economic consequences for sea farmers. Finally, introduced species may prove to be successful competitors of oysters, as in the case of the mollusc *Crepidula fornicata* in Europe (Blanchard, 1995).
- **Public health and tourism.** Along the coast of Israel, painful stings are inflicted by the introduced jellyfish *Rhopilema nomadica* and nets strung along the bathing beaches have proved to be ineffective (Galil et al., 1990; Spanier and Galil, 1991).

In USA, alien plants and animals have caused damage costing at least US$ 97 billion from 1905 to 1991. This is a very conservative estimate since data were available for only 79 species out of the 4,500 introduced (Kiernan, 1993; OTA, 1993; McNeely, 1996b). On a world scale, the direct economic costs of alien invasive species run into many billions of dollars annually (IUCN, 2000).

In areas colonized by *C. taxifolia* (hard bottoms and meadows of *Posidonia oceanica*), fish biomass declines significantly, especially that of target fishes and there is a decrease in their mean size (Harmelin-Vivien et al., 1999; Table 5.2). In addition, fishing nets are clogged up with *C. taxifolia* and can be spotted by fishes, which escape (Cottalorda et al., 2000). As a result there is a conspicuous decrease in catch-
es, according to the fishermen. They therefore move to more distant sites, which involves extra costs: more diesel fuel, more time and more powerful fishing boats (Durin, 2000). If the decline of the meadows of Posidonia oceanica were to be confirmed in the long term and considering the major role they play as spawning sites and nurseries for fishes, the negative impact of C. taxifolia on fish catches might further increase.

A large proportion of the Mediterranean economic activity is based on tourism. For example, the Provence and French Riviera region hosts each year over 24 million tourists, who are mainly attracted by the sea: swimming, pleasure boating, scuba-diving and snorkeling. Scuba-diving is currently one of the driving forces that is contributing to the development of tourism. In the Mediterranean, increase rates of more than 10% per year are not uncommon. The uniformization of the underwater landscape due to C. taxifolia spread is repellent rather than appealing for divers—they hope to find gorgonians and fishes, a richly coloured fauna and flora, a variety of species and not a sea floor carpeted with C. taxifolia. As a result, this alga has a negative impact on the development of scuba-diving. Indeed, managers of the diving clubs on the French Riviera say that only beginners are still willing to dive to bottoms carpeted with C. taxifolia. To keep other divers, both local divers and tourists, they have to move on to more distant sites still free of this seaweed, with extra costs (Boudouresque, 1999a; Durin, 2000). At the moment, only two diving clubs, located in front of the most densely colonized coast, are concerned (Durin, 2000). However, this behavior could be the harbinger of more serious problems.

Unfortunately, only preliminary data are available on the impact of C. taxifolia on non-merchant values, e.g., the existence value (Bec, 2000).

Conclusions

The issue of invasive species has been primarily addressed by biologists. The conclusions that can be drawn from the available studies show that each introduced species constitutes a special case. According to the species, the ecological consequences range from zero or slight impact to the extinction of native species and/or major changes in the functioning of native ecosystems. However, we are only beginning to realize the magnitude of the changes that mankind has unleashed through the spread of thousands of alien species around the planet (Clout, 1995). Clout (1998) suggested that, as a result of this widespread homogenization of flora and fauna, the Earth might now be entering a new era – the ‘Homogocene.’

At the present time, international conventions and most national legislation are somewhat inadequate, often unrealistic and usually totally ineffective in stopping or even slowing down the flow of introduced species (IUCN, 2000). The fact that, beyond harmful ecological impact, the introduction of alien species could result in economic damages, should lead decision-makers and politicians to feel more concerned about this problem and prompt them to implement existing regulations and above all to improve legislation. The case of the marine alga C. taxifolia, introduced
to the Mediterranean Sea, deserves their attention. This species has had a rather spectacular impact on indigenous species and, more particularly, on ecosystem diversity, as well as having lead to negative economic consequences. Furthermore, economic consequences affect tourism, a field of activity that has yet to be properly addressed by researchers studying the impact of biological invasions.

References


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Chapter 5 – The Spread of a Non-native Marine Species, *Caulerpa taxifolia*


