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INTRODUCED SPECIES IN THE MEDITERRANEAN: ROUTES, KINETICS AND CONSEQUENCES

by

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ABSTRACT

Introduced species are defined as species the expansion of which to a remote geographical area (not marginal area) is linked directly or indirectly to human activity, and which are naturalized, in the sense that they are able to reproduce in situ without human assistance. Nearly 75 species of plants and 330 species of animals can be considered as having been probably introduced to the Mediterranean Sea; this represents 4-5% of its known flora and fauna. The Mediterranean has a higher level of introduced species than any other major sea. Most of these species (67%) are of Lessessian origin (i.e. entered the Mediterranean through the Suez canal). Aquaculture is the second route of introduction to the Mediterranean: escape of aquaculture species as well as accidental introduction of species accompanying aquaculture species. The other vectors include fouling and clinging (transportation on ship hulls), ballast waters and aquaria. The kinetics of introduction is exponential. Since the beginning of the century, the number of alien species has nearly doubled every 20 years. Introduced species appear to be much more numerous in some regions and/or biotopes (e.g. Levantine coasts, French coasts, brackish lagoons) than in others. The kinetics of expansion (both geographical and ecological) comprises the arrival of the invader, a settlement phase, an expansion phase and a persistence phase. In the present paper, the effects on specific diversity and ecodiversity are reviewed: competitive displacement of native species, competitive substitution of native species, modification of the functioning of ecosystems (e.g. effect on native key-species, introduction of new key-species) and edification of new ecosystems. Secondly, negative economical consequences on tourism, diving activities, aquaculture and fisheries are also examined and the possible benefits (e.g. for some fisheries) are critically discussed. National legislation is an inadequate means of ensuring the protection of autochtonous biodiversity and is often unrealistic and always ineffective. In addition, introduced species do not respect national borders and international agreements are therefore of vital importance. Finally, the precautionary principle should always be applied with respect to these species.

RESUME

Une espèce introduite est une espèce dont l'arrivée dans une nouvelle aire géographique est liée, directement ou indirectement, à l'activité de l'homme, et qui est naturalisée (capable de se reproduire in situ sans l'aide de l'homme). Environ 75 espèces de plantes et 330 espèces animales peuvent être considérées comme probablement introduites en Méditerranée; cela représente 4 à 5% de sa flore et de sa faune connues. La Méditerranée constitue ainsi la mer la plus affectée au monde par les espèces introduites. La plupart d'entre elles (67%) sont dites lessepiennes (entrées en Méditerranée par le Canal de Suez). L'aquaculture est le second vecteur d'introduction : évacuation d'espèces aquacoles et introduction accidentelle d'espèces accompagnatrices des espèces aquacoles.
Les autres vecteurs d'introduction sont le fouling et le clinging (transport sur les coques des bateaux), les eaux de ballast et les aquariums. La cinétique des introductions est exponentielle : depuis le début du siècle, leur nombre double plus ou moins tous les 20 ans. Les espèces introduites sont plus nombreuses dans certaines régions et/ou biotopes (par exemple les côtes levantines, les côtes françaises, les lagunes littorales) que dans d'autres. La cinétique d'expansion (géographique et écologique) comporte l'arrivée, la phase d'installation, la phase d'expansion et la phase de persistance. Les conséquences sur la diversité biologique et sur l'écodiversité sont passées en revue : déplacement compétitif d'espèces indigènes, substitution compétitive à des espèces indigènes, modification du fonctionnement des écosystèmes (par exemple effet sur des espèces-clé et introduction de nouvelles espèces-clé) et édification de nouveaux écosystèmes. Enfin, les conséquences économiques négatives (tourisme, plongée sous-marin, aquaculture, pêche professionnelle) sont étudiées. Les bénéfices éventuels (par exemple pour certaines pêcheries) sont également discutés de façon critique. Les législations nationales constituent des instruments insuffisants pour assurer la protection de la biodiversité autochtone ; elles sont souvent peu réalisistes et toujours inefficaces. Par ailleurs, les espèces introduites ne respectent pas les frontières nationales, de telle sorte que les accords internationaux sont d'une importance capitale. Enfin, le principe de précaution devrait être systématiquement appliqué pour ces espèces.

1. INTRODUCTION

The introduction of alien species, and the biological invasions which may result, constitutes an environmental problem of growing concern, especially in the marine environment. This is due to the fact that existing instruments, whose goal it is to protect autochthonous biodiversity, are inadequate and also because the invasive phenomenon is still increasing in a linear, or even exponential manner, which is contrary to other environmental problems.

An introduced species is a species which 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. They are reported, for example, in Fucus spiralis from southern Portugal and in Laminaria ochroleuca De la Pylaie from Great Britain (Parke, 1948; Fischer-Piette, 1959, 1963). 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, the corn Zea mays Linnaeus found in European terrestrial environments, and the sea mammal Dugong dugon Müller, observed once along the Israeli coast after an isolated individual having entered the Mediterranean through the Suez canal (Por, 1978), are not introduced species.

2. CRITERIA USED TO DETERMINE IF A SPECIES IS INTRODUCED

A set of criteria can be used to consider whether or not a species is probably introduced (Boudouresque, 1994; Boudouresque and Ribera, 1994; Ribera and Boudouresque, 1995).
• The species is new to the area in question, according to the data in the literature.

• There is a geographical discontinuity between the species' known range and its new locality. This is, for example, the case of the brown algae Laminaria japonica Areschoug and Undaria pinnatifida (Harvey) Suringar, discovered in a French brackish lagoon (Thau), and whose nearest habitat is in Japan (Perez et al., 1981; Boudouresque et al., 1985).

• The new locality is very localised. Biotopes similar to the one that has been colonized, and which are situated in the vicinity of this locality, are devoid of the invader. This was the case for the green alga Caulerpa taxifolia (Vahl) C. Agardh, which was discovered in Monaco and along the Cap Martin (French Riviera), where it formed dense meadows in the sublittoral on rocks and sand and in beds of Posidonia oceanica (Linnaeus) Delile (Spermatophyta). Similar biotopes in the region had not been colonised, although they have been since then (Meinesz and Hesse, 1991; Meinesz et al., 1993; Meinesz and Boudouresque, 1996).

• There is a potential introduction source close at hand, for example an aquaculture farm, a harbour, a laboratory, or an aquarium. This is the case for the numerous species of Japanese algae introduced into the Thau lagoon, where oyster farmers imported Crassostrea gigas (Thunberg) spat from Japan: e.g. Sargassum muticum (Yendo) Fensholt, Undaria pinnatifida, Laminaria japonica and Chrysomenia wrightii (Harvey) Yamada (Perez et al., 1981; Critchley et al., 1983; Knöpfle-Péguy et al., 1986; Ben Maiz et al., 1987; Verlaque, 1996).

• From an initial localised station, the kinetics of range extension follows a logical pattern. The spread of the brown alga Sargassum muticum along the Atlantic and Mediterranean coasts of Europe is a good example (Fig. 1). Another example is the local spread of Caulerpa taxifolia along the French and Italian Rivieras (Meinesz and Boudouresque, 1996).

• Some introduced species have a tendency to pullulate, at least for a certain period. Examples are Colpomenia peregrina (Sauvageau) Hamel (Fucophyceae) in Brittany, Caulerpa taxifolia in the Western Mediterranean and the jellyfish Rhopilema nomadica Galil et Spanier 1990 in Israel (Sauvageau, 1906; Meinesz and Hesse, 1991; Spanier and Galil, 1991; Boudouresque et al., 1995).

• The new population only possesses part of the genetic variability of the species in its original range (Occipinti-Ambrogi, 1994). This is known as "founder effect". Prud'Homme van Reine (1993) thus observed that Sphacelaria cirrosa (Roth) C. Agardh (Fucophyceae) occurs in the North Atlantic and in the Mediterranean under a variety of forms. Yet only one of these forms has been reported in Australia, where the species also occurs. The species might therefore have been introduced into Australia from the North Atlantic (Ribera and Boudouresque, 1995). In certain cases, the normal life cycle does not run its course. This is perhaps the case for Caulerpa taxifolia in the Mediterranean, in which only the male gametes have so far been observed. The plants therefore only reproduce vegetatively (Meinesz, 1992; Meinesz and Boudouresque, 1996).

• Finally, when two populations of the same species, with geographically discontinuous ranges, are genetically identical, then it is probable that one of the two populations is
introduced. Indeed, the occurrence of geographically discontinuous ranges would otherwise lead one to expect differences.

The above criteria, that are rarely all met, offer a means of assessing the probability (very high, high or medium) that a species has been introduced.

![Map of Sargassum muticum expansion](image)

Fig. 1 Chronology of *Sargassum muticum* (Fucophyceae) expansion along the Atlantic and Mediterranean coasts of Europe. Starting from the (hypothetical) date of introduction, the curves cover successively the 1960s, 1970s, 1980s and 1990s. From Boudouresque and Ribera (1994), Verlaque (1994) and Ribera and Boudouresque (1995).

3. **HOW MANY SPECIES HAVE BEEN INTRODUCED TO THE MEDITERRANEAN?**

Nearly 75 species of plants (macrophytes and microphytes) and 330 species of animals can be considered as having been probably introduced to the Mediterranean (Por, 1978, 1990; Zibrowius, 1991, 1994; Boudouresque and Ribera, 1994; Verlaque, 1994; Ribera and Boudouresque, 1995; Boudouresque, 1996; Golani, 1996).

There is a wide disparity in the number of introduced species from one sea to another. In the Mediterranean, introduced species represent 4-5% of its known flora and fauna. In New-Zealand, on the Atlantic coast of Europe and in Australia, the percentage of introduced macro-algae ranges from 2 to 3%. In the other regions of the world, introduced
species only appear to account for an insignificant proportion of the flora (Ribera and Boudouresque, 1995).

For certain regions, these differences can be an artefact. However, it is reasonable to assume that certain regions are more receptive to introductions of species (that is to say that they accept potential alien species more easily). Another possibility is that certain regions are subject to a greater pressure from the vectors of immigration.

4. THE ROUTES OF SPECIES INTRODUCTIONS

Routes of access for species introduction are (Por, 1978; Zibrowius, 1991; Carlton and Geller, 1993; Boudouresque and Ribera, 1994; Ribera and Boudouresque, 1995; Boudouresque, 1996; Eno et al., 1997):

- Transportation of species on ship hulls (fouling and clinging).

- Transportation of ballast water. Hundred of ships of all sizes ply the oceans of the world, taking on water as ballast in one ocean, with its accompanying planktonic flora and fauna, including the meroplankton (planktonic larvae of benthic organisms), and unloading it in another ocean (Fig. 2). In all, millions of cubic metres of seawater are transported each year from one ocean to another. The survival time in ballast water for some species may exceed 18 days (Salt, 1992; Carlton and Geller, 1993). This vector of introduction is a source of considerable concern and has no equivalent on land. Ballast waters are responsible for the introduction of the zebra mussel *Dreissena polymorpha* (Pallas) in North America and of the comb jelly *Mnemiopsis leidyi* to the Black Sea (Carlton, 1993; Carlton and Geller, 1993; Carlton, 1996a, 1996b; GESAMP, 1997).

![Fig. 2 Ballast water capacity (in black) of ships. From Durnil et al. (1990).](image)

- Escape of non-indigenous species bred or reared for aquaculture purposes. This is the case in the Mediterranean of the Japanese oyster *Crassostrea gigas* and of the Japanese carpet shell *Ruditapes philippinarum* (Adams et Reeve) (Zibrowius, 1991).
Accidental introduction of species accompanying aquaculture species. The importation from Japan of spat of the Japanese oyster *Crassostrea gigas* (more than 10,000 t between 1971 and 1977) is responsible for the introduction to the Mediterranean of a variety of species which occur naturally in association with this mollusc. For example, the Fucophyceae *Sargassum muticum*, *Undaria pinnatifida* (Fig. 3) and *Laminaria japonica*, and the Rhodophyta *Chrysymenia wrightii* and *Antithamnion nipponicum Yamada et Inagaki* (Perez et al., 1981; Ben Maiz et al., 1987; Verlaque and Riouall, 1989; Verlaque, 1996).

![Fig. 3 Undaria pinnatifida (Fucophyceae), accidentally introduced to the Mediterranean (French coast and Venice lagoon, Italy). Its introduction is linked to the importation of spat of the Japanese oyster Crassostrea gigas. From Boudouresque et al. (1985).](image)

Species used as fishing bait and species escaping from markets. One example is *Fucus spiralis* (Fucophyceae), a species used as packaging for bait which (in France) comes from Brittany. It is by this means that it was introduced to the Gruissan lagoon (French Mediterranean coast) (Sancho, 1988).

Escape from aquaria. In the North-Western Mediterranean Sea, the green tropical alga *Caulerpa taxifolia* was introduced in this way (Meinesz and Hesse, 1991; Boudouresque et al., 1995; Meinesz and Boudouresque, 1996; Jousson et al., 1998).

Scientific research. Many scientists working in the field of ecology, in addition to those working in disciplines distantly related to ecology (aquaculture, physiology, etc.) and who use non-indigenous strains or species, are completely unaware of or underestimate the possible impact of the introduction of the species they are working on. They thus fail to take the elementary precautions necessary to prevent these species from escaping from their cultures or breeding sites (Ribera and Boudouresque, 1995).
An additional and recent route (last century), specific to the Mediterranean, is the Suez canal. The species which have entered the Mediterranean from the Red Sea via the Suez canal are named "Lessepsian aliens", from Ferdinand de Lesseps who built the canal (Por, 1978, 1990; Boudouresque, 1996).

Unintentional introductions associated with aquaculture, fouling and ballast waters are usually the main methods of introduction. This is the case, for example, in British waters (Fig. 4) (Eno et al., 1997).

![Pie chart showing the probable primary route of introduction of non-native marine flora and fauna in British waters. Numerals indicate the number of species involved, and the percentage of total introductions. From Eno et al. (1997).](image)

**Fig. 4** Probable primary route of introduction of non-native marine flora and fauna found in British waters. Numerals indicate the number of species involved, and the percentage of total introductions. From Eno et al. (1997).

In the Mediterranean, the main routes of plant introductions are the Suez canal, fouling on ship hulls and accidental introduction of species accompanying aquaculture species. If the fauna is considered, however, the percentage of Lessepsian aliens is even greater, and can reach a value as high as 77 %, although this may be an over-estimation (Table 1).

**Table 1**

Routes of access to the Mediterranean of probably introduced species
(expressed as a percentage of the number of species).

<table>
<thead>
<tr>
<th>Routes of access</th>
<th>Flora</th>
<th>Fauna</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fouling or clinging on ship hulls</td>
<td>25 %</td>
<td>10 %</td>
<td>13 %</td>
</tr>
<tr>
<td>Ballast water</td>
<td>3 %</td>
<td>1 %</td>
<td>2 %</td>
</tr>
<tr>
<td>Escape of species bred for aquaculture purposes</td>
<td>-</td>
<td>1 %</td>
<td>1 %</td>
</tr>
<tr>
<td>Accidental introduction of species accompanying oyster spat (aquaculture)</td>
<td>23 %</td>
<td>4 %</td>
<td>8 %</td>
</tr>
<tr>
<td>Fishing bait, escape from markets</td>
<td>3 %</td>
<td>+</td>
<td>1 %</td>
</tr>
<tr>
<td>Escape from aquariums</td>
<td>1 %</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>Suez Canal</td>
<td>38 %</td>
<td>77 %</td>
<td>67 %</td>
</tr>
<tr>
<td>Unknown</td>
<td>7 %</td>
<td>7 %</td>
<td>7 %</td>
</tr>
</tbody>
</table>
5. THE KINETICS OF SPECIES INTRODUCTIONS

In certain parts of the world, the phenomenon of marine species introduction is still in a phase of linear increase, e.g. in British waters (Eno et al., 1997). In the Mediterranean, the kinetics of species introduction is even exponential: since the beginning of the century, the number of introduced species (fauna and flora, Lessepsian and non-Lessepsian) has nearly doubled every 20 years (Fig. 5, 6).

![Graph showing the number of introduced plants (Lessepsian and non-Lessepsian macrophytes and microphytes) into the Mediterranean from 1870 to 1990. Species introduced after 1990 are not taken into account. Cumulative data.](image)

Fig. 5 The number of plants (Lessepsian and non-Lessepsian macrophytes and microphytes) introduced to the Mediterranean, from 1870 to 1990. Species introduced after 1990 are not taken into account. Cumulative data.

Introduced species appear to be conspicuously more numerous in some regions or in some biotopes, than in others. For example, Lessepsian aliens are, logically, more or less confined to the eastern basin, most of them along the Levantine coast (Fig. 7). In contrast, non-Lessepsian species appear to be concentrated in the western basin, in particular along the French coast (Fig. 8). For non-Lessepsian species, the pattern is even more contrasting if we consider the countries where the introduced species were first reported rather that their present day distribution (Fig. 9). It is probably no coincidence that 51% of marine macrophytes introduced into Europe were first introduced in France. The reason resides in the fact that legislation and current practices are particularly lax in France (Boudouresque and Ribera, 1994; Ribera and Boudouresque, 1995). Indeed, once introduced in one country, an alien species has little respect for national borders.
Fig. 6 The number of Lessepsian aliens (flora and fauna) introduced to the Mediterranean, from 1870 to 1990. Species introduced after 1990 are not taken into consideration. Cumulative data. From Boudouresque (1996), modified.

Fig. 7 Number of Lessepsian alien species (macrophytes) present in the different regions of the Mediterranean and in the Black Sea. Regions correspond to countries, with the exception of the Balearic Islands, Corsica + Sardinia, Sicily, the Adriatic Sea and the Levantine coast (Syria, Lebanon and Israel).
Fig. 8 Number of non-Lessesian alien species (macrophytes) present in the different regions of the Mediterranean and in the Black Sea. Regions correspond to countries, with the exception of the Balearic Islands, Corsica + Sardinia, Sicily, the Adriatic Sea and the Levantine coast (Syria, Lebanon and Israel).

6. PROCESSES INVOLVED IN SPECIES INTRODUCTIONS

There are four successive phases in the introduction of a species: the arrival, the settlement phase, the expansion phase and the persistence phase (Fig. 10).

Introduction processes involve (i) a donor region (or source region), (ii) a corridor, (iii) a vector, (iv) a recipient region, that is to say the region where the candidate may become established, (v) and of course a candidate species (Fig. 11). The first question which arises is: why does an introduction occur when it does? Why, if a corridor has been in place for over one hundred years, would the species newly appear at the end of that corridor only in year 101? (Carlton, 1996a).

The cause of an introduction may be a change in the donor region. For example, pollution may increase the population numbers of a native species, such that more individuals would be available to interface with a corridor and a vector. The change in the donor region can also be the arrival of a non-native species. This non-native species can then interface with an existing transport mechanism. This is the "hub and spoke model". For example the zebra mussel Dreissena polymorpha was formerly endemic to the Caspian Sea. It was initially introduced to a new area where it interfaced with a vector (ship ballast water) and a corridor to reach the Northern American Great Lakes. The cause of an introduction may also be the opening of a new corridor with an accompanying new donor region. Other causes can be new vectors, or increase in vector speed, for example faster ships (Fig. 11).
A recipient region with a low biodiversity, and vacant ecological niches, may substantially help the alien species to become established. It is worth noting that the end of most of the spokes, i.e. the corridors, are harbours or brackish lagoons, that is to say areas with a low diversity (naturally or artificially). Of course, once they have arrived and after having profited from these conditions to become established, some introduced species spread to neighbouring areas, even if these are neither polluted nor characterized by a low biodiversity. Indeed, in the Mediterranean, most of the introduced species were initially observed in brackish lagoons, harbours and other polluted biotopes (Table 2). Such biotopes are both localised at the end of a corridor and characterized by a rather low biodiversity.

Along the way from the donor region to the recipient region, numerous filters (or windows) can be opened or closed (Fig. 11). These include the period of egg and larval production, resistance to transport, an appropriate temperature and salinity, the availability of trophic resources at the time of arrival and a drop in the abundance of predators at the time of arrival. Thus, an appropriate timing in its arrival is absolutely essential to a candidate species.

Fig. 9  Distribution by country of the number of first reports of introduced macrophytes in Northern and Western Europe (the appearance in a country of an introduced species previously reported in another European country is not included). The diameter of the black circles is in proportion to the number of introduced species. From Ribera and Boudouresque (1995).
Table 2

Biotope and communities where introduced non-Lessepsian macrophytes and invertebrates were first reported (later on, other kinds of biotope or communities may have been colonized).

<table>
<thead>
<tr>
<th>Biotope or Community</th>
<th>Percentage</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brackish lagoons</td>
<td>44%</td>
</tr>
<tr>
<td>Estuaries</td>
<td>1%</td>
</tr>
<tr>
<td>Harbours</td>
<td>25%</td>
</tr>
<tr>
<td>Other polluted biotope</td>
<td>4%</td>
</tr>
<tr>
<td>Photophilous communities</td>
<td>7%</td>
</tr>
<tr>
<td>Sciaphilous communities</td>
<td>2%</td>
</tr>
<tr>
<td><em>Posidonia oceanica</em> meadows (seagrass)</td>
<td>1%</td>
</tr>
<tr>
<td>Pelagic ecosystems</td>
<td>2%</td>
</tr>
<tr>
<td>Unknown</td>
<td>14%</td>
</tr>
</tbody>
</table>

Fig. 10 Successive phases in the introduction of a species. Model B (above) and model A (below).
Fig. 11 Processes involved in a species introduction: the donor region, the corridor, the vector, the recipient region and the candidate species.

The "proper" combination of all these features, that is to say the simultaneous opening of all the windows, is clearly an event of uncommon occurrence: even one closed window would hinder a candidate species arrival, or, upon arrival, its establishment. As a result, the successful introduction of a candidate species must be considered to be an exceptional event. However, the exponential increase in the rate of introductions demonstrates both a human-mediated opening of the windows, and a conspicuous increase in invading pressures.

After the arrival of a candidate species, the settlement phase begins. This phase ends either in its elimination, or its naturalization (Fig. 10). The "naturalization" is the definitive integration of the candidate among the flora or fauna of the region. Of course, "definitive" means: as far as it is known. "Integration" means: the constitution of populations of individuals born in situ, without human assistance (see § 1).

Once naturalized, the introduced species starts its expansion phase. It will try to occupy the whole of the biotopes and the whole of the geographical range to which it may have access.

The persistence phase means that the introduced species occupies all of the accessible biotopes and the entire accessible geographical range. The persistence phase, however, rarely resembles like a plateau. The abundance fluctuates to a varying degree, in much the same manner as do most native species (model B, see Fig. 10). Such fluctuations are linked to predator-prey relationships, parasite-host relationships, unevenness in recruitment, etc.

It is often claimed that, at the end of the expansion phase, the abundance of an introduced species will naturally decline (model A, see Fig. 10). A good example of such a decline is constituted by the Lessepsian Gastropod Cerithium kochi Philippi. First reported in
the mid-1960s, this Gastropod became one of the dominant species of the Levantine coast in the late 1970s. It has now stepped back into the ranks (Por, 1978; Galil and Lewinsohn, 1981; Spanier and Galil, 1991). However, not only is such a natural decline not a rule, but on the contrary it has proved to be a rather rare event. This conclusion can be drawn from the careful examination of introduced species for which accurate historical data are available, both in marine and terrestrial environments (Ribera and Boudouresque; 1995; Boudouresque, 1996; Eno et al., 1997; GESAMP, 1997).

Several reasons may explain why data have been mis-interpreted, leading to the generalization of the rare model A (natural decline). In some cases, the occurrence of a decline can be easily explained: an introduced specialized parasite, or an introduced specialized predator, wipes out its native host, or its native prey, and of course then declines. For example, in the last century, a parasite of the European vine, Phyloxera, was introduced from America. Once the European strains of vine were all destroyed, or replaced by resistant American strains, of course, the parasite declined. In fact, in most cases, the so-called "natural decline" comes from a mis-interpretation of the first decline occurring within the first fluctuation cycle of the persistence phase (model B). For example, in the Thau lagoon (France), the decline of Sargassum muticum (Fucophyceae) in the late 1980s and early 1990s was considered to be typical of model A (Boudouresque and Ribera, 1994). Subsequently (late 1990s), however, its abundance increased, reaching previous levels.

7. ECOLOGICAL CONSEQUENCES OF SPECIES INTRODUCTIONS

The study of a large number of species introductions, in the terrestrial environment, has led to the conclusion that, as a mean, 10% of arriving species try to settle, 10% of them actually become introduced, and 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 has economic consequences. Invasive species are also called "pests". The zebra-mussel Dreissena polymorpha in the North American Great Lakes (Kiernan, 1993; Carlton, 1996b), the comb jelly Mnemiopsis leidyi in the Black Sea (Konovalov, 1992; Carlton, 1996b; GESAMP, 1997) and the tropical green alga Caulerpa taxifolia in the Mediterranean (Meinesz and Hesse, 1991; Boudouresque et al., 1995; Meinesz and Boudouresque, 1996; Boudouresque, 1997, 1998) are invasive species. It is difficult, or impossible, to predict whether or not an introduced species will become invasive: it is a matter of "ecological roulette", as coined by Carlton and Geller (1993).

Most attention has focused on environmentally damaging consequences resulting from alien invasive species in terrestrial and freshwater environment. Most of the neo-extinction of species, that is to say modern extinctions, are due, when the cause is identified, to species introductions.

In contrast, the marine environment has been very little studied. Nothing is known about the possible impact of most of the 400 species introduced to the Mediterranean. Available information concerns mainly the green alga Caulerpa taxifolia in the Western Mediterranean (Meinesz and Hesse, 1991; Verlaque and Fritayre, 1994; Villècle and Verlaque, 1995; Bellan-Santini et al., 1996; Boudouresque, 1997), the brown alga Sargassum muticum in the Thau lagoon, France (Gerbal et al., 1985), a few Lesserian aliens (Por, 1978), and the comb jelly Mnemiopsis leidyi in the Black Sea (Konovalov, 1992; GESAMP, 1997). A few additional data are available about the red algae Acrothamnion preissii (Sonder) Wollaston in Western Italy (Piazzi et al., 1996), Asparagopsis armata
Harvey in the north-western basin (Sala and Boudouresque, 1997) and Womersleyella setacea (Hollenberg) Norris in Western Italy and in the Aegean Sea (Airoldi et al., 1995a, 1995b; Athanasiadis, 1997).

The conclusions which can be drawn from the available studies show that each introduced species constitutes a special case. According to species, the following has been observed: (i) Zero or slight impact. (ii) More or less drastic changes in the number and/or abundance of native species (Ruitton and Boudouresque, 1994; Verlaque and Fritayre, 1994; Bellan-Santini et al., 1996). For example, along the French Riviera coasts, 6 species of parasites (Digenea) are present in the digestive tract of the fish Symphodus ocellatus (Forsskål) (cumulative prevalence = 46%); At sites colonized by the introduced green alga Caulerpa taxifolia, only 2 digenean species are present (cumulative prevalence = 2%) (Bartoli and Boudouresque, 1997). (iii) Displacement of a native species occupying a close ecological niche. For example in the Thau lagoon (France), the introduced brown alga Sargassum muticum has replaced another brown alga, Cystoseira barbata (Gerbal et al., 1985). Along the Levantine coasts, the introduced asteroid Asterina wega Perrier appears to have locally replaced the native, ecologically similar Asterina gibbosa (Pennant) (Por, 1978). The native prawn Penaeus kerathurus (Forsskål), which supported a commercial fishery throughout the 1950s, has now nearly disappeared; it is replaced by P. japonicus Bate (Geldiad and Kocatas, 1972, Spanier and Galil, 1991). (iv) Several native species along the Levantine coasts have been competitively displaced towards deeper waters by introduced competitors, e.g. the red snapping shrimp Alpheus glaber (Oliv), the red mullet Mullus barbatus Linnaeus and the bake Merluccius merluccius (Linnaeus), have been displaced by the shrimp Alpheus rapacida De Man, the goldband goatfish Upeneus moluccensis (Bleeker) and the brushtooth lizardfish Saurida undosquamas (Richardson), respectively (Por, 1978). (v) Changes in the functioning of native ecosystems, due to an introduced species which acts as a key-species. For example, the presence among Lessesian aliens of large herbivore fishes, Siganus luridus (Rüppell) and S. rivulatus Forsskål, makes highly probable a strong impact on the functional processes of the ecosystems of the Eastern Mediterranean. Indeed, the Mediterranean is a sea characterised by a rather low level of herbivory.

There is a common empirical opinion that species introductions do not result in species deletion but instead in species enrichment: "one species more! what good news for biodiversity!" As a matter of fact, this opinion is not supported by scientific data. The fate of most native species is generally not studied. This simplistic interpretation (likely to appeal to politicians), whose long-term result would be the world-wide standardization of underwater landscapes (such a standardization is referred to as "mcdonaldization") is diametrically opposed to both the concept of biodiversity and the ethics of nature conservancy. If this were in fact the case, zoos and botanical gardens would be the paradigm of biodiversity.

Another common opinion among politicians, is: "don't worry! it will become integrated into native ecosystems". Of course: an introduced species always becomes integrated into an ecosystem, a "native" one or a completely new ecosystem: it participates in new food webs, establishes new predator-prey relationships, etc. Were we to introduce the lion to Spain, it would also become integrated into native ecosystems; it would prey on red deers, cows, etc. The question is: is it still a native ecosystem?

Other politicians are in the habit of saying: "don't worry! a new equilibrium will occur". Of course a form of equilibrium exists even in a heavily polluted harbour community. The question is: do we want this new equilibrium?
8. ECONOMIC CONSEQUENCES OF SPECIES INTRODUCTIONS

Some introduced species are now of economic importance in the Mediterranean, being exploited by local fisheries (Gaill, 1986; Oren, 1957; Spanier and Galil 1991; Zibrowius, 1991). The crab Portunus pelagicus (Linnaeus) has become the dominant crab in commercial catches all around the eastern Mediterranean, especially in Egypt. The prawns Penaeus japonicus and P. monoceros (Fabricius) 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 (Boudouresque, 1996). 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 (McNeely, 1992, 1994, 1996, 1998; Bayon et al., 1998).

Harmful consequences of species introduction may affect several sectors of human activity (Kieman, 1993): (i) 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). (ii) Aquaculture. Most of the new diseases of bacterial or parasitic origin that strike marine cultures in many parts of the world (for example oyster culture) probably result from species introduction. (iii) Public health and tourism. Scuba diving is currently one of the driving forces that is contributing to the development of tourism. The uniformisation of the underwater landscape may have a negative impact on the development of scuba diving. Along the Israeli coast, 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).

Finally, species introduction cannot be considered solely as an ecological and economic problem. We are also faced with an ethical and cultural problem.

9. CONCLUSION

There are various reasons why species introductions are today a cause of growing concern. Firstly, unlike some other environmental problems, the phenomenon of species introduction is still in a phase of increase. The vectors of introduction have been identified, but they are far from being brought under control. Indeed, it is difficult or impossible to predict whether or not an introduced species will become invasive: it is the "ecological roulette".

Furthermore, the ecological consequences of a species introduction, a dynamic phenomenon by definition, are often not immediately discernible. And the assessment of these consequences cannot be generalized, since each introduction is a special case. In addition, assessing the impact takes time, and by the time a sufficiently accurate assessment has been made, it is generally rather late to take suitable remedial measures. As far as economic consequences are concerned, these are even more difficult to anticipate and it can take some time before the full impact is felt. It must be emphasized here that economic consequences are probably always underestimated, due to the externalization of costs.
Finally, the national legislation of the Mediterranean countries is somewhat inadequate, often unrealistic and always totally ineffective (Kneopfler and Kneopfler-Peguy, 1996). Fortunately, international agreements provide a good basis for cooperation and for the development of new instruments for that purpose. Such an international cooperation is absolutely vital as, once it has been introduced in one country, an alien species has no respect of national borders.

The introduction of species is clearly a field where the precautionary principle, adopted by the Convention on Biological Diversity, must be implemented: the impact of species introduction may be impossible or extremely costly to control once the species has become established. Prevention is consequently of the utmost importance.

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