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Introduced marine plants, with special reference to macroalgae: mechanisms and impact

MARÍA ANTONIA RIBERA

Laboratori de Botànica, Facultat de Farmàcia,
Universitat de Barcelona, c/ Joan XXIII s/n,
08028 Barcelona, Spain

CHARLES-FRANÇOIS BOUDOURESQUE

Laboratoire de Biologie Marine et d'Ecologie du Benthos
(LBMEB; EP CNRS Nº 75), Faculté des Sciences de Luminy,
13288 Marseille cedex 9, France

1. INTRODUCTION

For any species, there occurs a natural phenomenon of expansion, which in geological times enabled it to attain its present distribution. A species' range of distribution is the result of its constant attempts to colonise new ranges. This new colonisation may occur either through marginal dispersal (progressive extension of the range into neighbouring areas), or by remote dispersal (with spatial discontinuity between the original range and the new range) (Crisp 1958). The process depends on the ecological requirements of the species, the characteristics of the colonisable environments and the mechanisms for crossing biogeographical barriers.

In any given biogeographical province, each species has normally occupied the whole of the accessible range, although there may be occasional fluctuations (advances or withdrawals) at the frontiers of its range, linked, for example, with minor climatic episodes. Fischer-Piette (1959, 1963) reported fluctuations of this kind in *Fucus spiralis* (Fucophyceae, Fucales) in southern Portugal. The arrival of *Laminaria ochroleuca* (Fucophyceae, Laminariales) in Great Britain from the continental coast may have been the result of a slight increase in the water temperature (Parke 1948; Farnham 1980). *Trichodesmium erythraeum* (Cyanobacteria, Oscillatoriales), which usually lives in the warm waters of the Caribbean, sometimes reaches the English

Channel when meterological conditions divert the Gulf Stream towards the south, then disappears when the stream resumes its normal course (Boalch 1994).

On the geological time scale, extensions of range (by remote or marginal dispersal) constitute a natural phenomenon which has played an important role in the history of the settlement of each region and in speciation. An archipelago such as the Azores, which has been isolated since its origins, has thus been progressively settled by species arriving more or less accidentally, most of them from the European coast (Feldmann 1946). A few of these species have already evolved (speciation) to give rise to endemic species, for example *Codium elisabethae* (Chlorophyta, Codiales) from its probable European ancestor *C. bursa* (Schmidt 1931; Feldmann 1946). Similarly, after the Messinian crises (5 to 6 million years ago), during which the Mediterranean partly dried up, with the consequent destruction of a major part of its flora and fauna, this sea was resettled by species arriving from the Atlantic (through the Straits of Gibraltar), and to a lesser extent from the Indo-Pacific (Por 1990). This explains why, for example, the marine flora of Sicily (Italy) is predominantly (47%) related to that of the Atlantic (Giaccone and Geraci 1989). In *Cladophora albida* (Chlorophyta, Cladophorales), a species that is now very widespread, DNA–DNA hybridization (Hoek *et al.* 1990) shows relatively recent divergences between the populations on either side of the Atlantic (2–4 Ma). These divergences are less ancient than the opening of the Atlantic Ocean, and can be interpreted either as corresponding to the date of the appearance of a barrier preventing genic flux, or the date of a crossing of the Atlantic in one direction or another. Nearer to home, the glaciations of the Quaternary contributed to extending the range of certain northern species into the Mediterranean. This is perhaps the case, for instance, for *Fucus virsoides*, very close (Forti 1931), if not identical (Sauvageau 1908a), to the Atlantic *Fucus spiralis*, and restricted to the Adriatic Sea (Boudouresque *et al.* 1990).

The extension of natural ranges, like the emergence by speciation or the natural extinction of species over the course of geological time, occurs at a very slow pace. If we accept that the average life-span of a species is 4 Ma (Chauvet and Olivier 1993), that at present we know of 1.5 million species, (but that the real number of existing species might be in the order of 5 million), then the average rate of natural extinction may be about one species a year for the earth as a whole. With the intervention of man, this rhythm is changing. If we accept that 2 to 8% of species will disappear between 1990 and 2015 (Reid *in* WCMC 1992), the rate of natural extinction will rise to 11–44 species a year on average. If we assume that planetary biodiversity is stable, the emergence of new species by speciation should occur at the same rate as the natural extinction of species. In fact, biodiversity has seen fluctuations over the course of geological time; overall, it has increased since the Antecambrian.

The rate of extension of natural ranges is undoubtedly much slower, except during periods of rapid climatic change and displacement of biogeographical frontiers, when it must accelerate (for periods ranging from a few centuries to several millenia). For example, the resettlement of the Baltic after the withdrawal of the ice and its opening into the North Sea, about 7,000 year ago, and the resettlement of the Mediterranean after the Messinian crises. Apart from these periods, calculations show that in the Mediterranean, one natural introduction every 125 years is compatible with the present composition of the flora and fauna (about 12,000 species listed; Fredj and Meinardi 1989; Boudouresque and Ribera in press), compared to that of the world's oceans (150,000 species listed), and with its biogeographical affinities (Giaccone and Geraci 1989) and degree of endemism (27%: Fredj *et al.* 1992).

The concept of introduction of a species is applied when the extension of a species range is linked, directly or indirectly, to human activity (Carlton 1985); this link may be only a probability, as we shall see below.

Since the most ancient times, man has been able to intervene in the distribution of species. Por (1978), for example, does not exclude the possibility that Red Sea species may have entered the Mediterranean two millenia ago through canals dug by the Pharaohs between the Red Sea and the Mediterranean: *Acanthophora najadiformis* (Rhodophyta, Ceramiales) may be an example of this.

Relatively recent introductions, although prior to the Linnean era (that is to say, the 18th century, when the modern system of botanical and zoological nomenclature was introduced by Linnaeus), may have occurred. *Cladophora sericea* (Chlorophyta, Cladophorales) on either side of the Atlantic are identical (DNA–DNA hybridization) (Hoek *et al.* 1990), which suggests that there has either been genetic mixing (permanent or intermittent), or more likely introduction on one or other side of the Atlantic prior to the Linnean period.

It was not however until the 20th century that our knowledge of systematics and biogeography became sufficiently developed for us to be able to affirm that a species was probably introduced (Ribera 1993). Even today, in genera whose systematics are particularly complex, or for species of very small size that can easily go unnoticed (Rhodophyta of the genus *Audouinella*, for example), the discovery of a station situated some distance away from the nearest known stations is interpreted, in the absence of alternative information, as representing a contribution to the knowledge of the range, rather than a case of introduction or extension of the range. An example of this is *Gelidiella antipai* (Rhodophyta Gelidiales), known from the Black Sea to the Pacific (Baja California, Mexico), and later discovered in the North-Western Mediterranean (Boudouresque 1972a; Ballesteros *et al.* 1986). In the future, molecular genetics may (?) make it possible to solve problems of this kind.

The particular case of gene introduction should be included in a discussion of the general phenomenon of species introduction. By introducing into a region where a species already occurs strains of the same species, but originating in a distant region, genes that do not normally occur there may be brought in. In the case of widely distributed species, geographical barriérs generally hinder gene flow and genetic mixing; a speciation process may thus be initiated.

Genetically modified organisms (GMOs) produced by aquaculture (including the polyploids) or hybridization (deliberate or accidental, *in vitro* or *in situ*), must also be taken into account. The strain of *Caulerpa taxifolia* (Chlorophyta, Caulerpales) which is colonising the Mediterranean may be a hybrid between races of different geographical origin brought together by chance in an aquarium (Alexandre Meinesz, per. com.). *Antithamnionella ternifolia* (=*A. sarniensis*; Rhodophyta, Ceramiales), which is highly variable morphologically, would appear to be the result of hybridization occurring at some point in its evolutionary history (L'Hardy-Halos 1986); since it is a species that is considered as introduced in Europe, and since its region of origin remains uncertain (see Section 2.2), the hypothesis that it is the result of recent hybridization linked to human activity must be considered. In the terrestrial domain, a similar case is the floating fern *Salvinia molesta* (Pteridophyta, Salviniales), which may be the result of hybridization occurring in the Rio de Janeiro Botanical Gardens (Brazil) (Barrett 1989). *Spartina anglica* (Spermatophyta, Poales) is the result of the hybridization of an introduced species and an indigenous species, followed by polyploidization.

2. CRITERIA FOR RECOGNITION OF AN INTRODUCED SPECIES

2.1 *The criteria*

The criteria for considering whether or not a species is probably introduced are as follows:

(i) *New species.*

The species is new to the area in question (according to the data in the literature).

(ii) *Geographical discontinuity.*

There is geographical discontinuity between the species' known range and its new station (Williamson *et al.* 1986). This is, for example, the case for *Undaria pinnatifida* (Fucophyceae, Laminariales) and for *Chrysymenia wrightii* (Rhodophyta, Rhodymeniales), discovered in the Thau lagoon

(France, Mediterranean; Perez *et al.* 1981; Ben Maiz *et al.* 1987), whose nearest stations are in Japan (Okamura 1915). Similarly, *Discosporangium mesarthrocarpum* (Fucophyceae, Sphacelariales), which has been described from the Adriatic and the Gulf of Naples (Falkenberg 1879; Hauck 1885) and is widespread in the Mediterranean (Boudouresque 1972b; Ribera *et al.* 1992), at Madeira and the Canaries (Haroun *et al.* 1993), has been discovered in Southern Australia on artificial reefs formed of tyres (Womersley 1987).

(iii) *Very localised new station.*

The new station is very localised; similar biotopes to the one that has been colonised, situated in the vicinity of this station, have not been colonised (yet?). This was the case for the first report of *Sargassum muticum* (Fucophyceae, Fucales) in Europe: thirty or so specimens were discovered at the Isle of Wight (England) (Farnham *et al.* 1973; Boalch and Potts 1977). Another example is *Caulerpa taxifolia*, which was discovered at Cap Martin (Alpes-Maritimes, France) and at Monaco (Meinesz and Hesse 1991), where it formed very dense meadows in the infralittoral on rock and sand and in the beds of *Posidonia oceanica* (Spermatophyta, Najadales); similar biotopes in the region had not then been colonised, although they have been subsequently (Meinesz *et al.* 1993, 1994).

(iv) *Logical range extension kinetics.*

From an initial localised station, the kinetics of extension of the range follows a logical pattern: the progression is from station to neighbouring station. The spread of *Sargassum muticum* along the Atlantic and Mediterranean coasts of Europe is a good example (Figs 1, 5). In the Mediterranean, after its discovery in the Thau lagoon (Knoepffler and Perez in Critchley *et al.* 1983; Perez *et al.* 1984; Belsher *et al.* 1985), the species was observed in the open sea, to the east and especially to the west of the Thau lagoon (Knoepffler-Péguy *et al.* 1985). Subsequently, the range of *Sargassum muticum* continued its spread westwards, in the direction of the Liguro-Provençal-Catalan current, to reach Banyuls-sur-Mer, near the Franco-Spanish frontier (Knoepffler *et al.* 1990). Similarly, *Acrothamnion preisii* (Rhodophyta, Ceramiales) has mainly extended its range in the Mediterranean in the direction of the prevailing current (Boillot *et al.* 1982; Cinelli *et al.* 1984; Thelin 1984) (see Section 5.3).

(v) *Pullulation.*

The introduced species has a tendency to pullulate, at least for a certain period. Examples of this are *Biddulphia sinensis* (Bacillariophyceae, Centrales) in the North Sea (Ostenfeld 1908), the brown alga *Colpomenia sinuosa* (Scytosiphonales) in Brittany (France) (Sauvageau 1906) and the green alga *Caulerpa taxifolia* in the North-Western Mediterranean (Meinesz and Hesse 1991). In the Leghorn region (Italy), *Acrothamnion preisii* occurs in all communities between the surface and 40 m depth, with coverage that is sometimes as high as 60% (Cinelli *et al.* 1984).

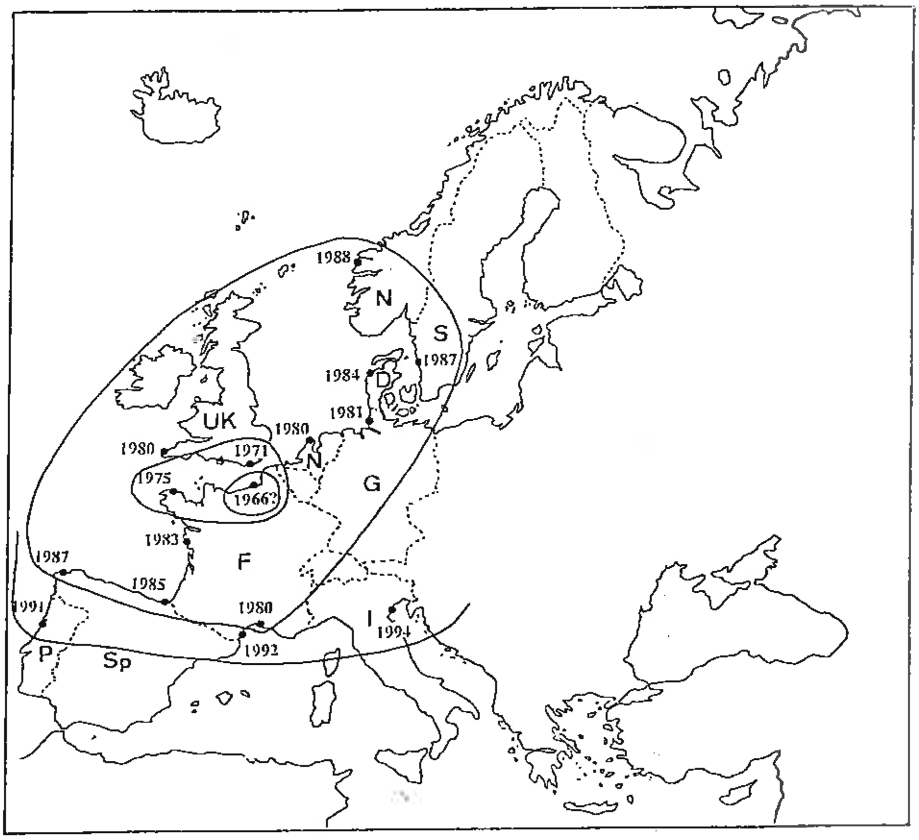

Fig. 1. Chronology of the expansion of *Sargassum muticum* along the Atlantic coast of Europe (from Verlaque in Boudouresque1994, modified with additions). Starting from the (hypothetical) date of introduction, the curves cover successively the 1960s, 1970s, 1980s and 1990s.

(vi) *Proximity of potential introduction source.*

There is a potential introduction source in proximity, e.g. aquaculture farm, harbour, laboratory, aquarium. This is the case in particular for the numerous species of Japanese algae introduced into the Thau lagoon, where oyster farmers imported spat of *Crassostrea gigas* from Japan: *Sargassum muticum* (Critchley *et al.* 1983), *Undaria pinnatifida* (Perez *et al.* 1981), *Chrysymenia wrightii* (Ben Maiz *et al.* 1987), etc. The red alga *Acrothamnion preisii* was first observed in the Mediterranean in proximity to the harbour of Leghorn (Italy) (Cinelli and Sartoni 1969); similarly, in New Zealand, *Undaria pinnatifida* made its appearance inside Wellington harbour (Hay and Luckens 1987).

(vii) *Incomplete genetic variability.*

The new population only possesses part of the genetic variability of the species in its original range (Occhipinti Ambrogi 1994), which is knows as "foundation effect"; this genotype may even be rare and marginal in its original range. Prud'Homme van Reine (1993) thus observed that *Sphacelaria cirrosa* (Fucophyceae, Sphacelariales) occurs in the North Atlantic and in the Mediterranean under a variety of forms (or ecads). 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. The differences in physical factors (temperature and daylength) that control the tetrasporogenesis of *Asparagopsis armata* (Rhodophyta, Bonnemaisoniales) in Italy (Mediterranean) and in Ireland (Atlantic) have led Guiry and Dawes (1992) to consider that it is likely that the Mediterranean and Irish populations represent separate introductions in the Northern Hemisphere; the foundation effect would appear to be different in the two regions. Another explanation however could be a difference in genetic drift, subsequent to the introduction, between the two regions. The morphological differences that are often observed between an introduced population and an original population (see Section 6) may, in fact, be due either to the ecological conditions in the host environment (chemical and physical factors, interspecies competition), or to genetic differences linked to the foundation effect. In certain cases, the life span may be incomplete. An example of this is *Codium fragile* which is only represented by female parthenogenetic gametophytes (Feldmann 1956; Delépine 1959) in the Mediterranean, Brittany (France) and the Bay of Biscay. In other 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 (Meinesz 1992), and the plants therefore only reproduce vegetatively.

(viii) *Genetic identity between distant populations.*

When two populations of the same species with geographically discontinuous ranges are genetically identical, whereas their separation and the probably long-standing nature of their genetic isolation might lead one to expect differences, this is an indication that one of the two populations is introduced. Molecular analysis (restriction fragment length patterns and hybridization data on organellar DNA) revealed that populations of *Gymnogongrus* sp. (possibly *G. leptophyllus*, Rhodophyta, Gigartinales) on both sides of the North Atlantic Ocean show little morphological variation, identical Rubisco spacer sequences and the same plasmid; it is very likely that this species was introduced from one side of the North Atlantic to the other by shipping during the early 19th century (Maggs *et al.* 1992).

2.2 *Reliability of the criteria*

The above criteria, that are rarely all met, offer the means to judge the probability of a species having been introduced. The fact that a species is of large size, and therefore does not easily go unnoticed, and has a clear taxonomic status, makes diagnosis easier. It is no accident that groups with complex and more or less confused systematics, such as *Ulva*, *Enteromorpha*, *Cladophora* (Chlorophyta), the Ectocarpaceae (Fucophyceae) and *Audouinella* (Rhodophyta), do not include species assumed to have been introduced.

Certain species may be considered with certainty to be introduced species: examples in Europe include the three large-sized algae, known to be endemic in Japan, i.e. *Sargassum muticum*, *Undaria pinnatifida* and *Laminaria japonica*; it is impossible that they could have occurred previously without being noticed.

Certain species have been considered from the time of their discovery as being very probably or definitely introduced, while their geographical origins were uncertain or even unknown. This is the case for *Colpomenia peregrina*, considered ever since its discovery on the Atlantic coast of Europe (Brittany in France, Great Britain) as an introduced species; it was initially attributed to the Mediterranean species *C. sinuosa* (Sauvageau 1906, 1908b, 1912). Subsequently, it became clear that it was a distinct taxon that had not yet been described in its native region, and Sauvageau (1927) described it under the name of *C. sinuosa* var. *peregrina*. It was finally Blackler (1963) who identified it in its native region, the Pacific.

By contrast, certain species were not considered as introduced at the time of their discovery. An example of this is *Antithamnionella ternifolia*, described at Guernsey (English Channel) as a new species by Lyle (1922); it was not until later that the hypothesis of introduction was postulated (Westbrook 1930; Farnham 1980). Nevertheless, its origin remains uncertain: no doubt somewhere in the Southern Hemisphere (Farnham 1980). A similar case in the Mediterranean is *Antithamnion algeriense* (Rhodophyta, Ceramiales), described recently for Algeria (Verlaque and Seridi 1991), then rediscovered in the Alboran Sea (Ribera-Siguan and Soto-Moreno 1992) and along the Medes islands (Spain) where it is abundant (Ballesteros *in* Ribera 1994). The flora of these islands had been thoroughly studied previously, and there is little likelihood that this species could have gone unnoticed; Ribera (1994) therefore considers that it is an introduced species, although its region of origin is not yet known.

Finally, the status of certain species has altered with time. This is the case for *Polyphysa parvula* (Chlorophyta, Dasycladales). At the time of its discovery in the Mediterranean, it was considered as an endemic species, under the name of *Acetabularia wettsteinii* (Schussnig 1930). Subsequently, it was synonymized with *Acetabularia moebii*, then with *A. parvula* (=*Polyphysa parvula*), and considered as a "Lessepsian species", that is to say an Indo-Pacific species that had entered the Mediterranean through the Suez Canal (Por 1978). Its occurrence in the West Indies, then its discovery at the Canaries and Madeira (Valet 1969; Prud'Homme van Reine *et al.* 1984) suggest that it may be a pantropical species whose occurrence in the Mediterranean is of long standing; it is worth noting that it was reported in the Western Mediterranean (Schussnig 1930) before being reported in the Eastern Mediterranean (Aleem 1948), which is not the normal case with the Lessepsian species. Similarly, *Acetabularia calyculus* (Chlorophyta, Dasycladales), considered by Por (1978) as a Lessepsian immigrant in the Mediterranean, but also occurring in the tropical Atlantic, in the Azores and at Madeira (Valet 1969), is now considered as indigenous to the Mediterranean (Ribera 1994).

3. PRESENT STATE OF SPECIES INTRODUCTIONS

In some regions of the world, relatively comprehensive inventories of flora are too recent for it to be possible to attempt to identify in them the species that were probably introduced, without the risk of error being unacceptably high. Often, the authors of inventories have not specified that certain species that are mentioned were probably introduced, either because they do not attach much importance to the question, or because the feel that this assumption is too hypothetical. Certain authors, such as Lawson and John (1982) in West Africa and Millar (1990) in Australia (New South Wales), have contented themselves with pointing out the discontinuous distribution of certain species, with the implicit suggestion that it is an indication of introduction. Overall, it is thus difficult to produce an accurate inventory of marine plant introductions, region by region. We have therefore decided to focus on a few specific regions.

3.1 *Mediterranean*

We have inventoried (Table I) 61 species of macrophyte[1] probably introduced into the Mediterranean: 40 Rhodophyta, 12 Fucophyceae, 8 Chlorophyta and 1 Spermatophyta. This list, which includes species of varying degrees of probability of introduction, corresponds to the present state of knowledge (see Section 2.2); it is therefore likely to require modification, even without taking into account the new introductions that will be discovered in the years to come.

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[1]By macrophyte, we understand the marine Phanerogams (= Spermatophyta) and the macroalgae (multicellular Rhodophyta, Fucophyceae and Chlorophyta).

Table I. Macrophytes introduced into the Mediterranean (including Lessepsian species). The date of the first observation is the date of publication, when an earlier date is not proposed by the author of the first report. Probability of introduction: H = high, M = medium, L = low. Mode of introduction: AQ = aquarium, S = Suez Canal, G = Gibraltar (species previously introduced along the Atlantic coast of Europe, then entering the Mediterranean through the Straits of Gibraltar), FB = fishing bait, FO = fouling on hull of ship, O = oyster farming. Origin: A = Atlantic, BS = Black Sea, IP = Indo-Pacific, J = Japan, PT = pantropical, RS = Red Sea, SH = Southern Hemisphere. By "biotope colonised in the Mediterranean", we understand the biotope that was the site of the first report: BL = brackish lagoon, H = harbour, Ph = infralittoral photophilous biotopes in open sea, POM = *Posidonia oceanica* bed, Scia = sciaphilous open sea biotopes, Medio = mediolittoral, Pol = polluted. Data according to Aleem (1948, 1950, 1993), Anonyme (1982), Ardré *et al.* (1982), Belsher *et al.* (1984), Ben Maiz (1986), Ben Maiz *et al.* (1987), Bidoux and Magne (1989), Boudouresque and Ribera (1994), Boudouresque *et al.* (1985), Cinelli and Sartoni (1969), Cormaci *et al.* (1991, 1992), Cormaci and Furnari (1988), Diapoulis *et al.* (1985), Dubois and Lauret (1991), Feldmann (1931, 1939, 1956), Feldmann and Feldmann (1938), Forti (1928), Fritsch (1895), Gómez Garreta *et al.* (1979), Hamel (1926, 1930a, 1930b), Lipkin (1972), Meinesz and Hesse (1991), Méndez Domingo (1957), Ollivier (1926), Perez *et al.* (1981), Perrone and Cecere (1994), Petersen (1918), Por (1978), Ramon and Friedmann (1965), Rayss (1941), Ribera (1994), Riouall (1985), Riouall *et al.* (1985), Sancholle (1988), Schiffner (1916), Verlaque (1981, 1989), Verlaque and Boudouresque (1991), Verlaque and Riouall (1989), Verlaque and Seridi (1991), Verlaque (1994).

Species	Date of first observation	Probability of intro-duction	Mode of intro-duction	Probable origin	Biotope colonised in Mediterranean
Rhodophyta					
Acanthophora najadiformis	1813	M (1)	?	RS, IP	Ph
Acrothamnion preissii	1969	H	FO	IP	Ph, POM
Agardhiella subulata	1987	L	?	A	BL
Aglaothamnion feldmanniae	1976	L	FO	A	H
Antithamnion algeriense	1989	H	FO	?	Ph
Antithamnion nipponicum	1988	H	O	J	BL
Antithamnionella spirographidis	1914	M	FO	IP	H
Antithamnionella ternifolia	1926	H	FO	SH	Ph
Asparagopsis armata	1926	H	G	A	Ph, Scia
Audouinella sargassicola	1950	M	S	IP	?
Audouinella spathoglossi	1950	M	S	IP	Ph
Audouinella subseriata	1950	M	S	IP	Ph

Species	Date of first observation	Probability of introduction	Mode of introduction	Probable origin	Biotope colonised in Mediterranean
Bonnemaisonia hamifera	1910	H	G	A	Scia
Chondria pygmaea	1991	H	S	RS	H
Chrysymenia wrightii	1978	H	O	J	BL
Gracilaria arcuata	1931	M	S	RS, IP	Pol
Gracilaria disticha	1926	H	S	RS, IP	?
Grateloupia doryphora	1982	L	O?	J ou A	BL
Griffithsia corallinoides	1984	M	O	A	BL
Hypnea cervicornis	1977	M	?	PT	Ph
Hypnea cornuta (2)	1948	M	S	RS	H
Hypnea esperi	1972	H	S	RS	Ph
Hypnea harveyi	1993	M	S	IP	?
Hypnea nidifica	1928	M	S	RS	?
Hypnea valentiae (3)	1898	M	S ou FO	RS	?
Laurencia coronopus	1984	M	O?	BS	BL
Lomentaria hakodatensis (4)	1979	H	O	J	BL
Lophocladia lallemandii	1938	L	S ou FO	RS	Ph
Pleonosporium caribaeum	1974	L	FO	PT	?
Plocamium secundatum	1991	L	?	SH	Scia
Polysiphonia nigrescens	1988	M	FB	A	BL
Porphyra yezoensis	1975	H	O	J	BL
Rhodophysema georgii	1978	M	O	A	BL
Rhodothamniella codicola	1952	H	G	A	Ph
Rhodymenia erythraea	1948	H	S ou FO	RS,IP	H
Sarconema filiforme (5, 6)	1948	H	S	RS	Ph
Sarconema scinaioides (7)	1980	H	S	IP	Pol
Solieria dura	1950	H	S	RS	?
Solieria filiformis	1922	L	?	A	BL
Womersleyella setacea	1987	H	FO?	PT	Scia
Fucophyceae					
Chorda filum	1981	H	O	A ou J	BL
Colpomenia peregrina	1956	H	G	A	Ph
Fucus spiralis	1987	H	AP	A	Medio
Laminaria japonica	1976	H	O	J	BL
Leathesia difformis	1979	M	O	A	BL

Species	Date of first observation	Probability of intro-duction	Mode of intro-duction	Probable origin	Biotope colonised in Mediterranean
Padina boergesenii (8)	1965	M	S	RS	Ph
Padina boryana	1993	H	S	IP	?
Sargassum muticum	1980	H	O	J	BL
Spathoglossum variabile	1950	H	S	RS	?
Sphaerotrichia divaricata	1981	M	O	J ou A	BL
Stypopodium schimperi	1982	H	S	RS	Ph
Undaria pinnatifida	1971	H	O	J	BL
Chlorophyta					
Caulerpa mexicana	1941	H	S	RS	Ph
Caulerpa racemosa (5)	1926	L	S	RS	Ph
Caulerpa scalpelliformis	1930	M	S	RS	Ph
Caulerpa taxifolia	1984	H	AQ	⸗PT	Ph, Scia
Cladophora cf *patentiramosa* (9)	1992	M	S ou FO	IP	Ph
Cladophoropsis zollingeri	1948	H	S	RS	Ph
Codium fragile subsp. *tomentosoides*	1950	H	G	A	Ph
Ulvaria obscura	1986	M	O	A	BL
Spermatophyta					
Halophila stipulacea (10)	1894	H	S	RS	Pol

(1) It is probably either a relic of the Tethys (Cormaci *et al* 1982; Verlaque 1994), or a pre-Lessepsian immigrant that may have entered the Mediterranean through the canals dug by the ancient Egyptians (Aleem 1948). (2) According to Mayhoub (1976), a synonym of *H. hamulosa*. (3) Includes *Hypnea hamulosa*, which according to Mayhoub (1976), is a synonym of *H. valentiae*. (4) Occurs in the Thau lagoon (France) according to Ben Maiz and Boudouresque (unpubl.). (5) Rayss (1963) has proposed that it might be a relic of the Téthys. (6) Reports of *Sarconema furcellatum* are included under *S. filiforme*, the two species having been synonymized (Papenfuss and Edelstein 1974). (7) Sightings of *Sarconema scinaioides* and *S. filiforme* in the Mediterranean may in fact correspond to the same species. (8) Synonym of *Padina gymnospora*. (9) Sampled at Cyprus by Hadjichristophorou (Verlaque 1994; Verlaque, unpubl.). (10) It has been suggested that it may perhaps be a pre-Lessepsian species (Pérès 1967), but this is highly unlikely.

Various species that have been assumed to be introduced by certain authors have not been included here. (i) We have eliminated dubious or insufficiently well-established reports. For example, *Cystoseira myrica* (Fucophyceae, Fucales), a Red Sea species, was reported in the

Mediterranean (Alexandria, Egypt) by Muschler (1908); this single report was considered dubious by Lipkin (1972). *Scytosiphon dotyi* (Fucophyceae, Scytosiphonales), a Pacific species, was reported from Trieste (Italy, Adriatic) by Giaccone (1978); in the absence of any description of specimens, Verlaque (1994) considers that its occurrence in the Mediterranean requires further investigation. (ii) We have also eliminated species that have been newly reported in the Mediterranean, but that are very close to an already reported species with which it may have been previously confused. For example, *Goniotrichopsis sublittoralis* (Rhodophyta, Porphyridiales), known on the North American Pacific coast, has been reported by Magne (1992) at Roscoff (Brittany, France) and Mallorca (Balearics, Spain, Mediterranean); it is a microscopic species that closely resembles a species that is assumed to be indigenous, i.e. *Stylonema cornu-cervi* (Rhodophyta, Porphyridiales), with which it may have been confused; for this reason, we do not follow Verlaque (1994), who considered it as introduced in Europe, since we do not feel that the probability of introduction is strong enough. Similarly, *Botryocladia madagascarensis* (Rhodophyta, Rhodymeniales), which is known in Madagascar and South Africa, and which has recently been reported in the Mediterranean (Cormaci *et al.* 1992), is very close to *B. botryoides*; it is considered as introduced by Verlaque (1994). (iii) Finally, certain species were probably introduced into one area of the Mediterranean from extra-Mediterranean populations, whereas they already occurred in other Mediterranean areas. Although these should be taken into account with regard to introductions of genes, we have not included them in Table I. This is the case for *Pilayella littoralis* (Fucophyceae, Ectocarpales) and *Desmarestia viridis* (Fucophyceae, Desmarestiales) in the Thau lagoon.

Including invertebrates and fishes (Por 1978, 1990; Zibrowius 1991; Fredj *et al.* 1992; Boudouresque and Ribera 1994), the total number of species introduced into the Mediterranean may be estimated at 340. They already represent 4 to 20% of numbers of species, depending on the taxonomic group (Table II).

3.2 *Atlantic coast of Europe*

We list 28 probably introduced taxa occurring along the Atlantic coast of Europe (Table III): 18 Rhodophyta, 4 Fucophyceae, 4 Chlorophyta and 2 Spermatophyta. The comments cited above also apply here with regard to the choice of species. In addition, a certain number of species, which have been or are used for marine aquaculture operations, and which are mentioned by Wallentinus (in press) or by Farnham (1994), but which have not been observed as wild populations, have been excluded, e.g. *Caulacanthus* *ustulatus* (Rhodophyta, Gigartinales) and *Laminaria longicruris*, *L. ochotensis*, *Macrocystis pyrifera* (Fucophyceae, Laminariales).

Table II. Relative proportion of introduced species, in particular Lessepsian immigrants, in certain groups of Mediterranean flora and fauna.

Taxon	Lessepsian species	Other introduced species	Total introduced species	Total species	% of introduced species	Source of data
Fucophyceae	4	8	12	265	5%	Table I and Ribera *et al.* (1992)
Chlorophyta	5	3	8	214	4%	Table I and Gallardo *et al.* (1993)
Phanerogams	1	0	1	5	20%	Hartog (1972)
Molluscs	71	16	87	1376	6%	Por (1978, 1990), Fredj *et al.* (1992)
Fishes	44	0	44	648	7%	Por (1990), Fredj *et al.* (1992)
Total Fauna	239	42	281	7241	4%	Por (1978, 1990), Fredj *et al.* (1992)

There are a few regional inventories. In the Netherlands, Hartog and Van Der Velde (1987) have listed 35 species in marine and brackish waters. In the Baltic Sea, 35 species (including only two macrophytes) are considered as introduced (Leppakoski 1994), but because of the very low salinity, the list includes some fresh water species.

Table III. Macrophytes introduced along the Atlantic coast of Europe (including the Canary Islands). The date of first report is the date of publication when no prior date has been proposed by the author of the first report. Probability of introduction: H = high, M = medium, L = low. Mode of introduction: BW = ballast water or sediment, FO = fouling, O = oyster farming, PC = phycoculture, S = scientific research. Probable origin: AU = Australia, E = Europe, EA = European Atlantic, IP = Indo-Pacific, J = Japan, M = Mediterranean, NA = North America, NAA = North American Atlantic, P = Pacific, SA = Southern Atlantic, SH = Southern Hemisphere, WA = Western Atlantic. "Colonised biotope" is the first biotope colonised, or in the absence of specific data, the biotope colonised subsequently: AS = artifical substrate, H = harbour, IR = intertidal rocks, OP = oyster bed, Ph = photophilous sublittoral, Pol = polluted, PT = pantropical, Scia = sciaphilous sublittoral, TP = tidal pools. Data from: Ardré *et al.* (1982), Castric-Fey *et al.* (1993), Cabioch and Magne (1987), Cabioch *et al.* (1990), Farnham (1980, 1994), Guiry and Irvine (1974), Guiry and Maggs (1991), Hartog (1964), Hylmö (1933), L'Hardy-Halos (1968), Luther (1979), Maggs and Guiry (1987), Maggs and

Hommersand (1990, 1993), Mathiesen and Mathiesen (1992), Sansón *et al.* (1991), Sauvageau (1918), Silva (1955, 1957), Wallentinus (in press), Westbrook (1934).

Species	Date of first observation	Probability of intro-duction	Mode of intro-duction	Probable origin	Biotope colonised in Europe
Rhodophyta					
Agardhiella subulata (1)	1973	H	?	WA	TP
Antithamnion densum	1960	M	?	SA ou IP	Scia
Antithamnionella spirographidis	1931	M	FO	P	H
Antithamnionella ternifolia	1906	H	FO	SH	H
Asparagopsis armata	1922	H	FO	AU	Ph
Bonnemaisonia hamifera	1890	H	FO	J	Ph
Cryptonemia hibernica	1971	M	?	IP	H
Dasya baillouviana	1950	M	FO ou O	M?	Pol
Grateloupia doryphora	1969	M	O?	J	Ph et H
Grateloupia filicina var. *luxurians*	1947	H	?	IP	TP
Laurencia brongniartii	1989	H	O	PT	Ph
Lomentaria hakodatensis	1984	H	O	J	TP
Mastocarpus stellatus	1970	H	S	EA	IR
Pikea californica	1967	H	FO	IP	Ph
Pleonosporium caribaeum	1967	L	FO	PT	?
Polysiphonia harveyi	1976	L	?	NAA	TP
Porphyra yezoensis (2)	1984	H	S	J	H
Predaea huismanii	1980	L	?	AU	AS
Fucophyceae					
Colpomenia peregrina	1905	H	O	IP	OP
Fucus evanescens	1924(3)	H	?	P	H
Undaria pinnatifida	1990	H	PC	M	Ph
Sargassum muticum	1971(4)	H	O	P	TP
Chlorophyta					
Chara connivens	1850	H	BW	E	Ph
Codium fragile					
subsp. atlanticum	1895	H	?	IP	Ph
subsp. scandinavicum	1919	H	?	IP	Ph
subsp. tomentosoides	1900	H	?	IP	Ph
Spermatophyta					
Elodea canadensis (5)	1870	H	BW	NA	Ph
Myriophyllum sibiricum (5)	1990	?	BW	?	Ph

(1) This species was initially identified as *Neoagardhiella gaudichaudii* (Farnham 1980). (2) The alga was recorded on the island of Helgoland (Germany) in 1984 (Kornmann 1986);

however, the species has not been reported in the area subsequently (K. Lüning *in* Wallentinus, in press). (3) According to Bokn and Lein (1978), *Fucus evanescens* was introduced to southern Norway about 100 years ago. (4) Verlaque (1994) considers that the introduction of this species along the French coast of the Channel probably dates from 1966. (5) These fresh water species occur in the Baltic Sea, where the water in some areas is perfectly fresh.

3.3 *Southern Australia*

In Southern Australia, the following species are considered as having probably been introduced (Womersley 1984, 1987; Gordon-Mills and Womersley 1987): *Antithamnionella spirographidis*, *Chondria arcuata*, *Polysiphonia brodiaei* and *P. pungens* (Rhodophyta, Ceramiales), and the Fucophyceae *Arthrocladia villosa* (Dictyosiphonales) (probably not persistent), *Asperococcus compressus* (Dictyosiphonales), *Discosporangium mesarthrocarpum* (Sphacelariales), *Elachista orbicularis* (Chordariales), *Sorocarpus micromorus* (Ectocarpales), *Sphacella subtilissima* (Sphacelariales), *Stictyosiphon soriferus* (Dictyosiphonales), *Striaria attenuata* (Dictyosiphonales). One might add a few species of Chlorophyta whose Australian populations are highly localised and distant from the species' main range, which suggest that they may have been introduced into Australia, although Womersley (1984) does not say so in so many words: *Derbesia tenuissima* (Bryopsidales), *Rosenvingiella polyrhiza* (Prasiolales) and some Cladophorales *Anadyomene stellata*, *Chaetomorpha melagonium*, *Cladophora dalmatica*, *C. laetevirens*, *C. lehmanniana*.

In the present state of our knowledge, the percentage of possibly introduced macrophyte species (less than 2%) remains very low in relation to the flora of Southern Australia (Womersley 1984, 1987): 800 Rhodophyta, 231 Fucophyceae and 123 Chlorophyta. The situation in the marine environment thus appears to be very different from that on land, where the number of introductions has been considerable. For Australia as a whole, Pollard and Hutchings (1990) record 55 introduced marine species (algae and invertebrates).

3.4 *Other regions*

As indicated above, the data available for other regions of the world are generally very sketchy.

In California (USA), no species is mentioned as introduced by Abbott and Hollenberg (1976), even *Sargassum muticum*, which we know from other sources to have been introduced into the region (Thom and Widdowson 1978). This species, which is endemic to Japan, was first observed in British Columbia (Canada), at least as early as 1944 (Scagel 1956), often in proximity to areas with imported Japanese oysters. Subsequently, it colonised a substantial stretch of the North American Pacific coast, from Alaska (Scagel *et al.* 1989) to Baja California (Mexico) (Espinoza 1990). The Japanese seagrass *Zostera japonica* (Spermatophyta, Najadales) was reported in 1957 from Washington state; it was probably introduced with the oyster *Crassostrea gigas* imported from Japan, either from spat or from being used as packing material around the oysters (Harrison and Bigley 1982); it was first reported from Oregon in the mid-1970s (Posey 1988). Recently, another Japanese species was observed in British Columbia: the *Gelidium vagum* (Rhodophyta, Gelidiales) (Renfrew *et al.* 1989). If the number of introduced macrophytes does not appear to be very high, the same is not true of the fauna: in the Bay of San Francisco (California) alone, 255 species of invertebrates are thought to have been introduced (Carlton 1979 *in* Hedgpeth 1993).

In Brazil, Oliviera (1984) reported two species introduced for aquaculture, a *Porphyra* originating in Japan and an *Eucheuma* from the Philippines. In the tropical American Atlantic, no introduced species is mentioned by Taylor (1960). Further north, along the Atlantic coast of North America, a few introduced species have been reported: *Furcellaria lumbricalis* (Rhodophyta, Gigartinales), which probably arrived from Europe during the last century with ballast water (Novaczek and McLachlan 1989), *Lomentaria clavellosa* (Rhodophyta, Rhodymeniales), originating in Europe or the Mediterranean, first observed in Boston harbour (USA), and with a range later extending from Connecticut to New Hampshire (Wilce and Lee 1964; Schneider *et al.* 1979), *Polysiphonia breviarticulata* (Rhodophyta, Ceramiales) (Kapraun and Searles 1990), *Colpomenia peregrina* (Bird and Edelstein 1978), *Fucus serratus*, which no doubt arrived from Europe in the 19th century with ballast water and has today spread to several Canadian provinces (Edelstein *et al.* 1972; Novaczek and McLachlan 1989), and *Codium fragile* subsp. *tomentosoides*, first observed at Long Island Sound, and later extending from North Carolina to New Hampshire (Carlton and Scanlon 1985). Finally, the possibility that *Lomentaria orcadensis* (Rhodophyta, Rhodymeniales) may have been introduced into Nova Scotia is discussed by Bird (1978).

The Japanese *Undaria pinnatifida*, introduced into the Mediterranean and Brittany (France), was also introduced into New Zealand (Hay and Luckens 1987; Hay 1990) and Tasmania (Sanderson 1988; Hay 1990). In New Zealand, Adams (1994) mentions 21 species of macrophyte algae that were probably introduced, which represents 3% of the flora: the Rhodophyta *Champia affinis* (Rhodymeniales), *Deucalion levringii* (Ceramiales), *Grateloupia prolifera* (Gigartinales) and the Ceramiales *Ceramium rubrum*, *Chondria harveyana*, *Griffithsia crassiuscula*, *Medeiothamnion lyallii*, *Polysiphonia brodiaei*, *P. constricta*, *P. sertularioides*, *P. subtilissima*, *Pterothamnion simile*, the Fucophyceae *Asperococcus bullosus*

(Dictyosiphonales), *Colpomenia durvillaei* (Scytosiphonales), *Hydroclathrus clathratus* (Scytosiphonales), *Pilayella littoralis* (Ectocarpales), *Punctaria latifolia* (Dictyosiphonales), *Sargassum verruculosum* (Fucales), *Striaria attenuata* (Dictyosiphonales), *Undaria pinnatifida* (Laminariales) and the Chlorophyta (Codiales) *Codium fragile* subsp. *tomentosoides*. Most of these species seem to have been introduced by shipping; *Polysiphonia subtilissima* is often associated with oyster and mussel farms.

In China, two species have been deliberately introduced for aquaculture: *Laminaria japonica*, originating in Japan, and *Macrocystis pyrifera* (Tseng 1981; Neushul 1983). The Rhodophyta *Acanthophora spicifera* (Ceramiales) and *Hypnea musciformis* (Gigartinales) have been introduced at Hawaii (Russell 1992).

In West Africa, Lawson and John (1982) point out two species of the Rhodophyta (Gigartinales) with discontinuous distribution: *Corynomorpha prismatica* occurs in Ghana and in the Indian Ocean, *Halymenia actinophysa* occurs in Ghana and on the American Pacific coast.

3.5 *Species introductions: contrasting patterns worldwide*

Examination of the literature on species introductions reveals a wide disparity from one region to another. In the Mediterranean, 4 to 5% of algal species are introduced. On the Atlantic coast of Europe, in Australia and in New Zealand, the percentage 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. For certain regions, these differences are probably an artefact resulting from differences in the degree of knowledge of the flora; in addition, introductions dating from a very long time ago of species that are today considered as being more or less cosmopolitan are not taken into account (see Section 4.1). It is reasonable to think, however, that certain regions are either more "receptive" to introductions of species (i.e. they accept potential alien immigrants more easily), or are subject to greater pressure from the vectors of introduction (shipping, aquaculture, etc.). The relatively high rate of introductions of species in the Mediterranean and in New Zealand may be due to the isolation of these regions (semi-landlocked sea or insularity), separated from neighbouring regions by natural biogeographical barriers, with a high level of endemism. The Levantine basin in the Eastern Mediterranean has in addition inherited a low level of biodiversity from its recent history (cutting of communications with the Red Sea and quaternary glaciation). After the opening of the Suez Canal, the Red Sea species (Lessepsian immigrants) found ecological niches in the Mediterranean that were sparsely occupied and interspecies competition that was not intensive. If the Lessepsian species, which represent about half of the introduced species in the Mediterranean, are not taken into account, the rate of species introduction would be of the same order as in New Zealand. As more and more species are introduced, the "receptivity" of a region probably declines. On the other hand, the pressure from the vectors of introduction no doubt varies widely over time, increasing or decreasing with fluctuations in shipping, aquaculture, etc.

3.6 *Species introductions: a phenomenon on the increase*

Up until the 1950s, introductions appeared to occur at a relatively slow rate. But from the 1960s on, an increase in the rate of introductions is apparent.

It will be noted that 50% of introductions of marine plants along the Atlantic coast of Europe occurred after 1960 (Table III, Fig. 2B). The phenomenon is even more marked in the Mediterranean, where more than 50% of introduced macrophytes (including the Lessepsian species) being recorded after 1970 (Fig. 2A). The same pattern is apparent if we examine introductions of marine macrophytes for Western Europe as a whole (Atlantic and Mediterranean coasts): more than 55% of introduced species were observed after 1970 (Fig. 2C). Of course, these figures are to be taken with some caution, since the first observation of an introduced species nearly always occurs some time after its real introduction. In addition, these figures may be indicative of an increase in the intensity of observation and of our improved knowledge of biogeography.

What are the causes of this increase in the rate of introduction? Firstly, it must be pointed out that human activities involving a movement of goods and/or people have also increased both qualitatively and quantitatively. Fish and shellfish farming, for example, are undergoing constant expansion in most countries in the world; there are more and more trials aimed at widening the range of species farmed, regardless of their geographical origin. The increasing ease of movement across European frontiers and the intensification of movements of people means that living material can circulate freely (whether legally or illegally); it is today possible to transport virtually anything virtually anywhere in the world. Finally, there has been an increase in maritime traffic (size and number of vessels, including pleasure craft); the use of sea water as ballast in ships, added to the speed of the ships, means that an infinite number of organisms can be transported from one ocean or one latitude to another. Ballast water is the least selective means of transport of species from the ecological or taxonomic points of view (Carlton and Geller 1993). The question of the vectors of introduction is dealt with in Section 4.

If we assume that the current trend of an increase in the rate of species introductions continues, extrapolation on the basis of the data in Fig. 2A suggests that in 2050, the number of introduced species of marine macroalgae in the Mediterranean may be between 250 and 1,000 (Fig. 3); in

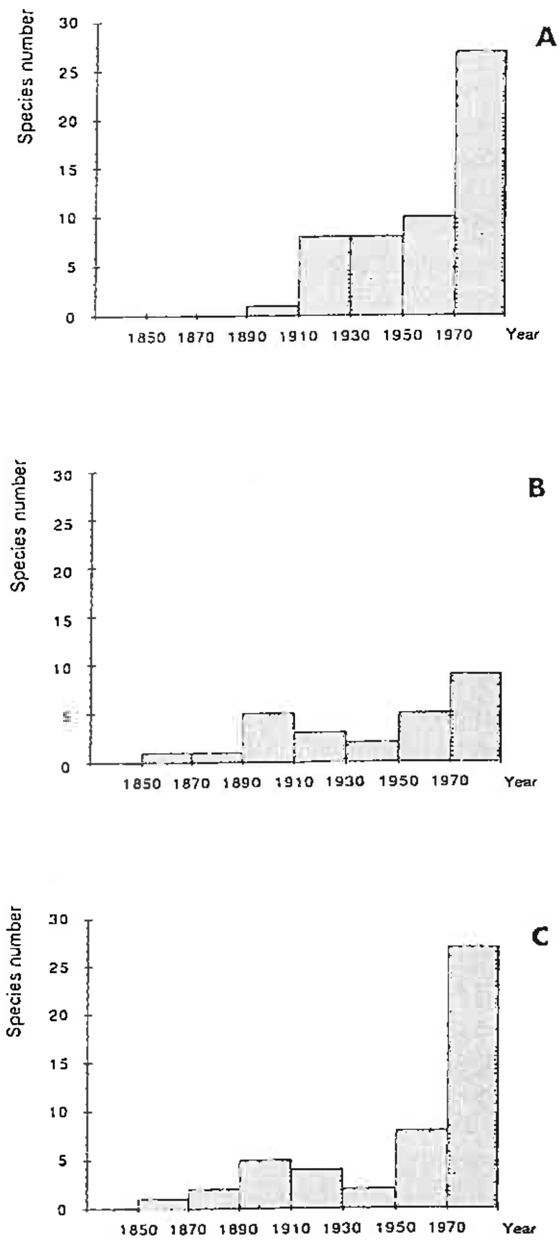

Fig. 2: Number of species of probably introduced marine macroalgae and marine phanerogams, by periods of 20 years (data not cumulative) according to the date of first observation (or when this is not specified, the date of publication). Introductions prior to 1850 are not included. A: Number of introduced species in the Mediterranean (based on the data in Table I). B: Number of introduced species along the Atlantic coast of Europe (based on data in Table III). C: Number of introduced species in Western Europe (including the Mediterranean) and Northern Europe (see Fig. 9 for the countries included; based on data in Tables I and III).

the latter case, the number of introduced species would be of the same order as the number of indigenous species (Boudouresque and Ribera 1994). Extrapolations of this kind are not too far-fetched, given that the stock of species that might potentially be introduced, that is to say, living in regions of the world where environmental conditions are similar to those of the Mediterranean (or one area of it), consists of at least 3,000 species (Boudouresque and Ribera 1994). Similar extrapolations (that we do not present) may be made on the basis of the data in Fig. 2B (number of introduced marine macrophyte species in Atlantic Europe). Nevertheless, there are no grounds for thinking that the rate of introductions is constant over time: the impact of certain vectors of introduction may diminish with time, while others take over. An example of this is fouling, which would appear to have played a more important role in the past than is the case nowadays (see Section 4.1). In fact, most of the species that attach themselves to the hulls of ships have probably long since become cosmopolitan. On the other hand, transportation by ballast water (see Section 4.2) is at present a vector that is on the increase. Similarly, Lessepsian migrations will in the long run reach a plateau, as has been predicted by Por (1978, 1990). Finally, genetic manipulations may in the future become a new source of introductions of a particular type. Overall, although the extrapolations that we present (Fig. 3) are based on models that have a very good fit with the available data (r = 0.94 in both cases), they should nonetheless be taken with considerable caution: the aim is not to offer predictions, but to draw attention to the gravity of present trends, and to demonstrate what might be the hypothetical consequences should these continue.

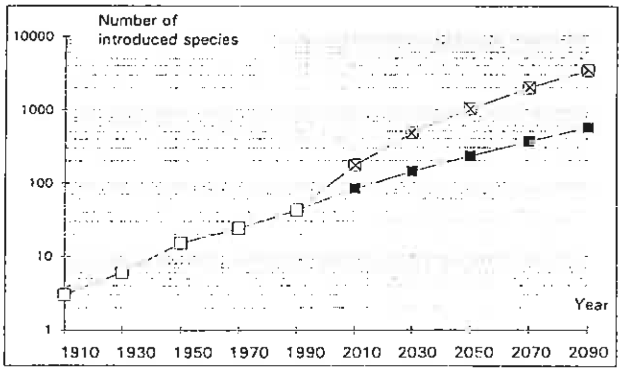

Fig. 3: Total number (cumulative data; logarithmic ordinates) of introduced marine macroalgae species in the Mediterranean. From 1910 to 1990 (white squares), data based on Fig. 2A. From 2010, values extrapolated by an exponential model Y = exp(a+bX). Black squares: all data included (a = –36.2; b = 0.02; r^2 = 90%). Crossed squares: only data after 1900 included (a = –52.9; b = 0.03; r^2 = 89%); these data are in fact more reliable than those prior to 1900 (from Boudouresque and Ribera 1994).

4. THE VECTORS OF SPECIES INTRODUCTIONS

In the marine environment, species introductions may result from a variety of causes (vectors): the transportation of species on the hulls of ships (fouling and clinging), deballasting of water (or solid matter) transported by ships, fishing bait, scientific research, aquaculture, aquariology and, in the Mediterranean, the construction of the Suez Canal. All these vectors result in indirect (or accidental) introductions; in aquaculture, however, introductions may sometimes be deliberate.

4.1 *Transportation on ships' hulls*

Historically, the transportation on the hulls of ships of fixed (fouling) or non fixed (clinging) species is certainly the most ancient vector of species introduction. One might suppose that most of the species that were potential candidates for introduction by this means have by now been introduced, and that this source of introduction is now on the decline, especially since anti-fouling paint now limits fouling on ships' hulls. It is also probable that certain species that are regular components of fouling and clinging, and that today have world-wide distribution (the species known as "cosmopolitan") correspond to ancient introductions, although they are not considered as such. Molecular genetics may eventually offer evidence on this point. Examples that come to mind include certain Serpulidae among the Polychaeta, the wood-boring Isopods of the genus *Limnoria* among the Crustaceans, and among the algae, the Acrochaetiales, the Ectocarpaceae and *Cladophora*.

Among the introduced species that are probably linked to fouling, for the Mediterranean one might mention the Rhodophyta (Ceramiaceae) *Antithamnion algeriense*, *Aglaothamnion felmanniae* and *Acrothamnion preisii* (Ribera 1994). The introduction in Australia of *Arthrocladia villosa* (Fucophyceae, Dictyosiphonales) from Europe (Skinner and Womersley 1983) can also be noted.

Fouling generally concerns small-sized species; nevertheless, large species whose life history includes a microscopic stage may be disseminated by this vector. Examples of this include microscopic gametophytes of *Undaria pinnatifida* (Hay 1990). Furthermore, Hay demonstrates that even the very large sporophytes (measuring more than a metre) of this species may remain fixed onto the hull of a boat after sailing hundreds of miles. It was perhaps by this means that the species arrived in New Zealand with the fishing fleets from Korea, Japan or Taiwan (Adams 1994).

Certain seas with very distinct physical or chemical characteristics in relation to the neighbouring regions enjoy some protection against introductions by fouling and clinging. This is the case in the Baltic, where the water is virtually fresh; the ships that arrive in the Baltic have generally sailed through thousands of miles of waters with much higher salinity (Leppakoski 1994).

4.2 *Deballasting of ships*

Deballasting (water or solid matter) from ships is a vector of introduction that is a source of considerable anxiety, and that has no equivalent on land (Carlton and Geller 1993). Hundreds of ships of all sizes ply the oceans of the world, taking on water as ballast in one ocean, with all its planktonic flora and fauna, including the meroplankton (planktonic larvae of benthic organisms), and unloading it in another ocean (Fig. 4). 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), so that many of these organisms are still alive after their intercontinental voyage at the time of deballasting: 367 species (mainly crustaceans, Polychaeta and Turbellaria) were recorded in the ballast water of a Japanese ship on arrival in Oregon (USA) (Carlton and Geller 1993). Incubation of sediment transported with the ballast water has resulted in the proliferation of various diatoms, Dinophyta and Chrysophyta; this results from the presence of spores, cysts and other surviving forms in these sediments (Kelly 1993). Hallegraeff and Bolch (1991) estimate that 300 million cysts are brought into Australian harbours by ships. Carlton and Geller (1993) note that ballast water is the least selective means of transportation of species from the ecological and taxonomic points of view.

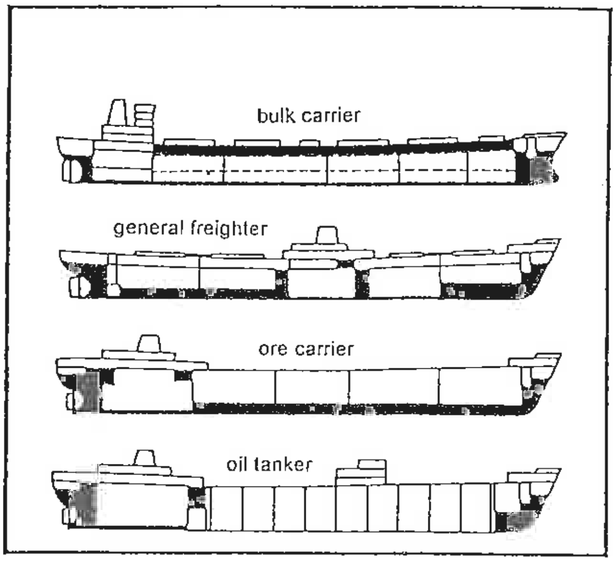

Fig. 4: Ballast water capacity (in black) of ships. A ship can transport more than 3 000 m^3 of ballast water, usually in its ballast tanks, but sometimes also in its cargo tanks (from Durnil *et al.* 1990).

The unloading of ballast water from ships was the cause of the introduction in Europe of the planktonic Bacillariophyceae *Biddulphia sinensis* (Centrales) (Ostenfeld 1908; Carlton 1985; Boalch 1987), *Thalassiosira angstii* (Centrales) (Boalch 1987), *Coscinodiscus wailesii* (Centrales) (Boalch and Harbour 1977b) and *Pleurosigma planktonicum* (Pennales) (Boalch and Harbour 1977a). This was probably also the case for the introduction in Australia of the toxic *Dinophyta* (Gymnodinales) *Gymnodinium catenatum* (Hallegraeff *et al.* 1988; Pollard and Hutchings 1990). A unicellular alga that has recently been reported on the Atlantic coast of France, *Fibrocapsa japonica* (Raphidophyceae), may have arrived with ballast water rather than with the spat of the oyster *Crassostrea gigas*, as Billard (1992) had hypothesized. Ballast water has also been responsible for the introduction of numerous animal species, including the zebra mussel *Dreissena polymorpha* in North America; this species, that originated in the Caspian Sea, arrived from a European port (where it had previously been introduced) into the Great Lakes in North America in ballast water in about 1988 (Dorchada *et al.* 1990; Carlton 1993). In all, 27 of the 69 exotic organisms introduced into the North American Great Lakes arrived there with ballast water (Dorchada *et al.* 1990).

4.3 *Fishing bait*

Fishing bait is a minor cause of species introduction. One example is *Fucus spiralis*, which is used as packaging for bait and which (in France) comes from Brittany; it was by this means that this alga was introduced into the Gruissan lagoon (Aude, French Mediterranean coast) (Sancholle 1988). Along the Atlantic coast of the United States, the use of *Codium fragile* to accompany fishing bait has probably contributed to its dissemination (Carlton and Scanlon 1985).

4.4 *Scientific research*

Many scientists working in the field of ecology or 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, and fail to take the elementary precautions that are required to prevent these species from escaping from their cultures or breeding sites.

The Atlantic red alga *Mastocarpus stellatus* (Rhodophyta, Gigartinales) was introduced into Germany (Helgoland, North Sea) at the end of the 1970s by a visiting scientist who needed it for his research. The species has since colonised the whole of the west coast of the island of Helgoland (Luning *in* Wallentinus, in press). Similarly, Koch (1951) suggested that some of the populations of *Bonnemaisonia hamifera* (Rhodophyta, Bonnemaisoniales) on Helgoland may have originated from discarded material sampled on scientific expeditions to Norway. The cultivation in open sea in the the West Indies of strains of *Eucheuma spinosum* (Rhodophyta, Gigartinales) from the Philippines, without quarantine procedures, for the purpose of comparing their growth rate with that of the indigenous *Eucheuma* (Barbaroux *et al.* 1984) may have resulted in the introduction of the species or of a disease of which it is the carrier (see Section 7.2).

Many laboratories work on toxic or potentially toxic unicellular algae (mainly Dinophyta); the strains come from various regions of the world. Some of these laboratories are situated beside the sea; yet no special precautions are taken to destroy the strains after experimentation or to prevent possible contamination of the environment. Of course, it might be assumed that material disposed of in a washbasin will spend a certain amount of time in a sewage depository, will generally be processed through a sewage treatment plant and is therefore unlikely to reach the marine environment. But can one be sure of this? The survival capacity of such species in fresh water is poorly known (and one specimen in a million would be enough); sewage treatment plants are occasionally out of order or temporarily short-circuited by the sewage; some laboratories dispose through their own direct outfalls (for sea water). Of course, it might be assumed, in the case of exotic tropical species, that the chances of acclimatization to temperate waters, in the event of contamination, are virtually nil. But what do we know of experimentally or accidentally produced interspecific or interpopulational hybrids and of their ecological requirements, that are often different from those of the parent strains? The example of *Caulerpa taxifolia*, a tropical alga that should not have been able to survive in the Mediterranean, but which nonetheless has survived there, should not be forgotten.

4.5 *Aquaculture*

If aquaculture (deliberate introduction of aquacultural species, as well as accidental introduction of species accompanying aquacultural species) is not the main source, directly or indirectly, of species introduction, it is certainly the best documented. We shall also include in this section deliberate introductions of non-aquacultural species destined for exploitation in the sea as wild populations. The few examples given below only represent a very small proportion of the species introduced through aquaculture; many other will be mentioned in passing in other sections by way of illustration of various points.

The brown alga *Undaria pinnatifida* (known under its Japanese name Wakame) was deliberately introduced into Brittany (France, Atlantic) from the Thau lagoon for aquacultural purposes (Perez *et al.* 1988, 1991; Floc'h *et al.* 1991; Castric-Fey *et al.* 1993). On the basis of work by Akiyama (1965), experts had established that the species could not reproduce in open sea under the thermal conditions prevailing in Brittany. Nevertheless, it succeeded in escaping from the aquaculture farms (Floc'h *et al.* 1991), as might have been predicted on the basis of less naive or more thorough analysis of the wealth of available literature (Wallentinus 1994). Another brown alga *Macrocystis pyrifera*, was deliberately introduced into China for the production of alginates (Neushul 1983). There were introduction schemes for this species in Europe in the 50s and 70s (Boalch 1981). This giant alga, *M. pyrifera*, which may reach a length of 40m and forms dense and spectacular underwater forests, is exploited for the production of alginates, in particular in California (Foster and Schiel 1985). In 1950, the Scottish Research Association suggested that it be introduced in Scotland, but governmental approval was refused (Boalch 1981). In the early 1970s, strains from Chile were cultivated by the ISTPM in the open sea at Roscoff (Brittany, France), with a view to testing the feasibility of introducing the species; it appeared that *M. pyrifera* was perfectly capable of surviving in Brittany. Strong protests in France and other European countries (Boalch 1981), as well as the unfavourable opinion (which only had the force of a recommendation) from the ICES (Wallentinus 1994), induced the ISTPM to put an end to this experiment and to give up its plans for introduction of the species. Had *M. pyrifera* been introduced in France, it might have colonised the European Atlantic coast from Spain to Norway (Boalch 1981), with consequences that are difficult to predict for the currents, coastal shipping, fishing and of course the coastal ecosystems. In Chile, transferance of *Gracilaria* sp. (Rhodophyta, Gigartinales) from one region to another for the purposes of *in situ* aquaculture were undertaken on a large scale (Santelices 1989); according to Santelices, these practices have altered the original geographical range of the species.

The importation of spat of the Japanese oyster *Crassostrea gigas* (Mollusca) in Washington state (USA) and British Columbia (Canada) was the cause of the introducion of the Fucophyceae (Fucales) *Sargassum muticum* in the late 1930s – early 1940s (Scagel 1956). The species' range subsequently expanded to include much of the Pacific coast of North America (from Mexico to Alaska) (De Wredde 1983) (Figs 1, 5). *Crassostrea gigas* was later introduced in France from 1966 onwards, initially to make up for the drop in productivity of the Portuguese oyster *C. angulata*, and then to replace it when it was decimated (in 1967 and in 1970–72) by a disease of viral origin (Comps *et al.* 1976; Grizel and Heral 1991; Grizel 1994). Between 1971 and 1977, more than 10,000 t of oyster were imported from Japan (Bay of Sendai). On their arrival in France, the oyster spat were subjected to a veterinary inspection, and were immersed for an hour in fresh water (instruction ISTPM of 30 April 1971), in order to destroy the fouling organisms and predators, mainly the Turbellaria *Pseudostylochus*

(Grizel and Heral 1991; Grizel 1994). The duration of this immersion in fresh water does not appear to have been chosen on the basis of any thorough scientific study, and its efficacy was questioned by Gruet *et al.* (1976), who identified on similarly treated oyster spat about thirty living species: algae, Actinia, Turbellaria, Polychaeta, Bryozoans, Molluscs, Crustaceans and Ascidians. In addition, the procedure was entrusted to the oyster farmers themselves, who apparently did not carry it out as thoroughly as they should. Under these conditions, it is easy to understand why accidental introductions of species associated with the Japanese oyster have been so frequent (Table IV). In the Thau lagoon (France, Mediterranean), there are at least 9 species of algae whose introduction is linked to the introduction of oyster spat of *Crassostrea gigas* (Perez *et al.* 1981; Riouall 1985; Riouall *et al.* 1985; Ben Maiz *et al.* 1987; Verlaque and Riouall 1989): *Laminaria japonica*, *Undaria pinnatifida*, *Sargassum muticum*, *Sphaerotrichia divaricata*, *Antithamnion nipponicum* (Rhodophyta, Ceramiales), *Chrysymenia wrightii* (Rhodophyta, Rhody-meniales), *Grateloupia doryphora* (Rhodophyta, Gigartinales), *Lomentaria hakodatensis* (Rhodophyta, Rhodymeniales) and *Porphyra yezoensis* (Rhodophyta, Bangiales) (Table I). It has long been asserted that *Crassostrea gigas* was introduced to make good the decline, then disappearance of *C. angulata* (Grizel 1983). Another hypothesis is that the opposite was the case: *C. gigas*, imported into France in 1966 for aquaculture trials, may have been responsible for bringing in the *Bonamia* and the virus (as "healthy" carriers) that decimated the *C. angulata* (Balouet and Poder 1985). A third possibility is that the virus may have come from Portugal with adult *C. angulata* (Grizel and Heral 1991).

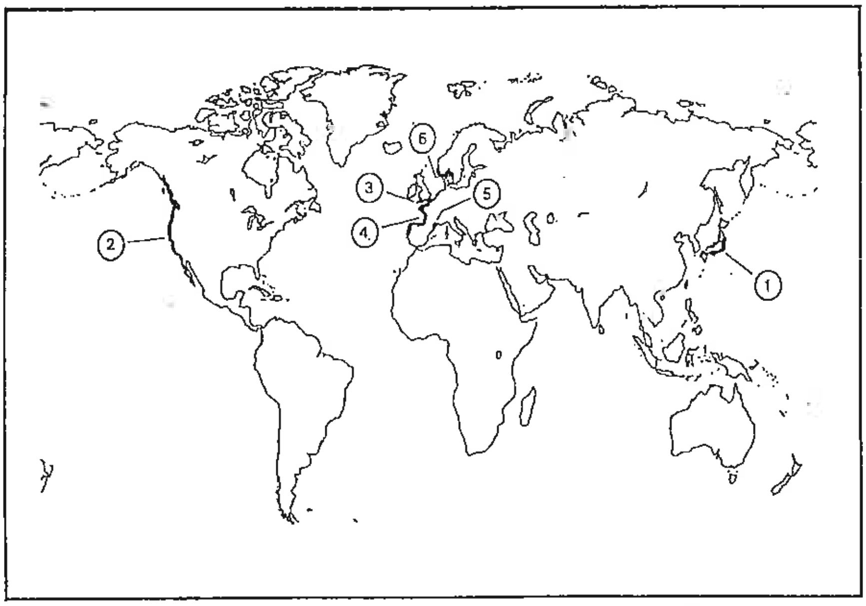

Table IV. Vectors of introduction of marine macrophytes in the Mediterranean, according to the data in Table I. "Gibraltar" refers to species previously introduced along the Atlantic coasts of Europe, which then entered the Mediterranean through the Straits of Gibraltar.

Vectors of introduction	Number of species
Suez Canal	22 to 26
Gibraltar	5
Aquaculture (oyster beds)	14 to 15
Fouling	5 to 10
Fishing bait	1
Aquariums	1
unknown	5 to 7

In the United States, the dissemination of *Codium fragile* along the east coast may have been facilitated by transfers of oysters (Carlton and Scanlon 1985).

4.6 *Aquariology*

With a few exceptions (see Section 10), the importation, sale and possession of marine species are not subject to any specific regulations. For example, the French-based company *Europrix* offers in its catalogue 102 species of marine algae, exotic and non-exotic, which include *Caulerpa taxifolia* and *Sargassum muticum.* Many aquaria have water supply systems that are in open circuit with the sea. According to Knoepffler (1994), no marine aquarium in France treats 100% of the waste water from its tanks that is subsequently deposited in the sea. Treating this water would in fact be very costly. These establishments work on the principle that an exotic species, especially one that comes from warm waters, has little chance of developing in a totally different environment. Under these conditions, the risk of species escaping from an aquarium is high. In the North-Western Mediterranean, the green tropical alga *C. taxifolia* was probably introduced in this way (Meinesz and Hesse 1991). In addition, certain aquariologists may deliberately pour

Fig. 5: Worldwide distribution of *Sargassum muticum* (from Belsher 1989, modified). (1) Japan, native region (Yendo 1907). (2) From Alaska to Baja California; first observations on the American Pacific coast in British Columbia (Canada) in 1944 (Scagel 1956). (3) Southern England; first observations at the Isle of Wight in 1971 (Farnham *et al.* 1973). (4) From Holland to Portugal; first observations in France at St Vaast la Hougue in 1975 (Cosson *et al.* 1977); (5) Mediterranean; first observation at Thau lagoon (France) in 1980 (Belsher *et al.* 1984); (6) West coast of Sweden in 1987 (Karlsson 1988).

the contents of their aquaria into the sea, either to get rid of them, or thinking that they are doing something useful. A case involving *C. taxifolia* is quoted by Laborel (in Boudouresque and Ribera 1994).In terrestrial waters, there are large numbers of species that have escaped from aquaria; in particular, this is the case for 78 introduced fish species (Welkomme 1992).

4.7 *Lessepsian migrations*

In the Mediterranean, there is one unique route for the introduction of species: the Suez Canal. The canal was opened in 1869, and linked two biogeographical provinces that had been separated for several million years, the Mediterranean and the Red Sea. For a long time, the existence of highly saline lakes (the Bitter Lakes) along the course of the canal represented an obstacle to migrations of species. Today, desalination of the lakes has made possible exchanges between the two seas. Migrations of species from the Red Sea to the Mediterranean through the Suez Canal (Lessepsian immigrants) is the most spectacular biological invasion that has occurred anywhere in the world. Between 200 and 300 species are involved (Por 1978, 1990; Zibrowius 1991; Galil 1994), including about twenty algae (Table IV). In the Mediterranean, the Lessepsian immigrants represent by far the strongest contingent of introduced species. However, virtually all of them have remained localised in the Eastern Mediterranean, referred to as the Lessepsian province (Por 1990). Migrations in the other direction (from the Mediterranean to the Red Sea), that Por (1978) referred to as "anti-Lessepsian", have been much less common: only fifty or so species, which include no algae. This may be explained by the fact that the sea level in the Eastern Mediterranean is a little lower than in the Red Sea, a phenomenon that has been accentuated by the construction of the Aswan Dam (Egypt) and the reduction of the flow rate of the Nile. Accordingly, the water in the canal generally circulates in the Red Sea – Mediterranean direction. In addition, the Eastern Mediterranean, whose flora and fauna were impoverished after the quaternary glaciation period, is a competitive vacuum; according to Por (1978), this is in fact the main reason for migration through the Suez Canal as mainly a one-way traffic.

Unlike the Suez Canal, the opening of the Panama Canal, which links the Pacific to the Atlantic across Central America, has only resulted in the passage of a very limited number of euryhaline species. There is no positive evidence that any plant species is involved (Por 1978; Hay and Gaines 1984). According to Hay and Gaines (1984), it is not the lock system that segments the canal, nor the fresh water lakes along its course that explain the difficulty of exchanges of flora and fauna between the two oceans: many Caribbean species can attach themselves to the hulls of ships and withstand a 6 to 12 hour passage (the transit time for most ships) through fresh water. The primary barrier to succesful transport and establishment of these Caribbean species appears to be herbivore activity and lack of reef generated refuge areas on the Pacific coast.

5. FACTORS FOR SUCCESSFUL INTRODUCTIONS OF SPECIES AND MODES OF EXPANSION

There are four successive phases in the introduction of a species: arrival, settlement, expansion and persistence (Mollison 1986). It is during the first two phases that the success (or failure) of the introduction will be decided; the settlement phase may conclude with the naturalization of the species.

5.1 *Arrival*

The arrival of a few specimens of an exotic species (see Section 4) does not automatically imply its establishment, much less its naturalization, that is to say its definitive integration (at least on the human time-scale) among the flora or fauna of a region. The converse is almost certainly true: the successful introductions only represent a small percentage of the potential introductions. Most of the Japanese species observed by Gruet *et al.* (1976) on oyster spat of *Crassostrea gigas* imported from Japan and immersed at Croisic and at Bourgneuf (Nantes, France) have apparently not naturalized. Farnham (1994) mentions the case of a foliaceous red alga that was observed at Falmouth (Great Britain) in 1977 and has never been seen again since.

5.2 *Settlement phase*

Settlement by a species means the constitution of populations of individuals born *in situ*, in their new station; there may be a succession of several generations. The settlement phase may result in the naturalization of the species. The species is considered to be naturalized when it has survived the habitual variations of the physical, chemical or biotic (competition) factors prevailing in the region. It would be logical here to suggest a minimum duration for the settlement phase, after which the species might be considered to be naturalized. This is however difficult; the time required for the new population to experience the full range of physical, chemical and biotic variations varies from one region to another. In addition, the probability that the population will undergo conditions that are even further from the mean than those that it has already undergone, can never be totally excluded. This means that one can hardly ever be completely sure that a species has really been naturalized. Several of the species that we present as introduced (see Section 2) are perhaps still in the settlement phase. This is the case in the Netherlands, where the maintenance of some of the introduced species is apparently linked directly to human activities (presence of hard artificial substrates, aquaculture), so that their occurrence remains precarious according to Hartog and Van der Velde (1987). In all, according to Di Castri (1989), only 5% of the species that arrive succeed in becoming naturalized.

According to Williamson and Brown (1986), the biological characteristics of a species that are likely to ensure its successful introduction are: (i) the absence of natural enemies; this is the case, for example, for the green alga *Caulerpa taxifolia*, that is strongly avoided (in summer) in the North-Western Mediterranean by the herbivorous sea urchin *Paracentrotus lividus* (Boudouresque *et al.* 1992; Lemée *et al.* 1994a, 1994b); (ii) a strong capacity for dispersal and (iii) a r-selection type strategy. Crisp (1958) added the size of the inoculum, and thus the genetic variability of the introduced species; this is indeed a major factor in determining the success of the introduction. Williamson and Brown (1986), however, point out that none of the above conditions is in itself either essential or sufficient to explain the success of the introductions that have been observed. For example, in the Thau lagoon, *Undaria pinnatifida* became naturalized even though it is a species that is highly appreciated by the sea urchin *Paracentrotus lividus* (San Martin 1986).

Over-introduction (repeated input of an exotic species at the same site) is also worth considering. It is possible that momentary failures or precarious successes finally meet with success, as soon as the variability of the environment to genetic diversity ratio reaches a favourable level: the successive arrivals of new individuals in fact extends the gene pool of the colonising nucleus, and provides it with adaptive potential that a single arrival would not have been able to provide (Occhipinti Ambrogi 1994).

In fact, the success of an introduction resides as much in the biological characteristics of the species as in those of the host environment. An essential factor for success would thus appear to be the availability of a vacant ecological niche (Williamson and Brown 1986), and more generally, the low biodiversity of the host community (or region) (Boudouresque 1994; Ribera 1994). The low biodiversity of the Levantine Basin (South-Eastern Mediterranean), that has resulted from its history – the closing of the Isthmus of Suez and the quaternary glaciations – no doubt explains the exceptional success that the Lessepsian immigrants have enjoyed (Spanier and Galil 1991). The same is true of the Baltic Sea, where a certain number of ecological niches appeared to be vacant (Leppakoski 1994). In the south of England, the Solent, where numerous species have been introduced, is considered by Farnham (1980) to be an area that is relatively favourable for introductions because of the occurrence there of "open" communities, and the relative rarity of "closed" communities involving Fucales and Laminariales. In seas or basins with high biodiversity, such as the Mediterranean (with the exception of the Levantine basin), it is the biotopes with low biodiversity (naturally or as the result of human pressure) that have been host to the majority of the successfully introduced species: lagoons (Table V), harbours and polluted areas (only for the fauna; Boudouresque 1994). The case is similar in the estuaries of North-Western Europe, where introduced species only represent 3 to 5% of the species in the freshwater sector (upstream) and in the marine sector (downstream), whereas they may represent 20–28% of species in the brackish sector, where biodiversity is low and the available niches are numerous (Wolff 1973; Vaas 1975). In the Baltic Sea, too, Leppakoski (1994) noted that eutrophic areas, coastal lagoons and fouling on hulls were the environments that had been most strongly altered by introduced species. Farnham (1980) suggests that fouling has been over-estimated as a cause of species introduction, in that environments that are as severely polluted as harbours appear to him to be unfavourable environments for successful introductions. Our feeling is the contrary, i.e. the low biodiversity of harbours makes them highly favourable environments for introductions. The fact that in the Mediterranean, the lagoons and polluted environments (in the latter case, for the fauna in particular) are the biotope into which the majority of the non-Lessepsian species are introduced (Table V) might be considered not as a consequence of their low biodiversity, but as an artefact. It is indeed logical that introductions caused by man should first affect environments that are subject to human pressure, whatever their biodiversity. Aquaculture, that is generally the main source of introductions, is mainly practised in lagoons. However, in the case of lagoons, the possibility that it is a matter of artefact may be rejected, since there are aquaculture farms in the open sea, such as those in the roadsteads of Toulon, the Gulf of Fos and Sète (on the French coast), and they do not appear to have given rise to introductions (Ribera 1994). Communities with high bio-diversity probably offer the greatest resistance to introductions; it is perhaps no accident that in the Mediterranean, the meadow of *Posidonia oceanica* (Spermatophyta, Najadales) and the "coralligène" community are rarely cited as biotopes of introduced species (Table V). Similarly, in the Baltic, the open coasts and open sea are relatively little affected (Leppakoski 1994).

Table V. Number of species of marine algae, Lessepsian and non-Lessepsian, introduced in the Mediterranean, according to the biotope or environment initially colonised.

Biotope and environment	Non-Lessepsian sp.	Lessepsian sp.
Brackish lagoons	17 to 18	0 to 1
Polluted biotopes (incl. harbours)	2 to 23	5 to 6
Photophilous sublittoral biotopes	5 to 11	11 to 14
Sciaphilous biotopes (incl. "coralligène")	3 to 5	–
Posidonia oceanica meadow	0 to 1	–
Intertidal	1	–
Unknown	1	8

In the terrestrial domain, Baltz and Moyle (1993) have shown the remarkable ability of communities of native stream fishes to resist invasion by introduced fishes as long as the streams are relatively undisturbed by human activity. According to these authors, the communities resist invasion through both environmental and biotic factors.

In the terrestrial as in the marine environment, the environments that are disturbed by human activity are particularly vulnerable to introductions of species (Rapport *et al.* 1985; Mooney and Drake 1987).

Finally, genetic reworking (hybridization, polyploidization) may play a much more important role in the success of species introductions than the rarity of the available data might suggest. The best known case is that of the grass *Spartina* which colonises the coastal marshes in the intertidal zone in Britain. *Spartina alterniflora* (Spermatophyta, Poales), which colonises the North American coast from Canada to Texas, was introduced at Southampton (south coast of England) at the beginning of the 19th century (Thompson 1991). It still occurs there, but it has never spread beyond the Southampton area. In about 1870, a hybrid appeared between *S. alterniflora* and the native species *S. maritima*: *S.* x *townsendii* (Stapf 1908); this hybrid is sterile, and it too has remained restricted to the Southampton area (Thompson 1991). Some twenty years later, in about 1890, a spartine resembling *S.* x *townsendii*, but fertile, appeared; this plant was very vigorous, and spread along the whole of the coast of Great Britain. It is an allopolyploid from *S.* x *townsendii*; a new species was born, referred to under the name of *Spartina anglica*. What had happened? In the hybrid *S.* x *townsendii*, the maternal and paternal chromosomes from *S. maritima* ($2n = 60$) and *S. alterniflora* ($2n = 62$) were juxtaposed. But during meiosis, the maternal and paternal chromosomes were too unalike to pair: meiosis therefore did not occur, and the hybrid was sterile. Its perenial growth therefore depended either on vegetative multiplication, or on new hybridizations between related species. The doubling of the chromosomes offered a way out: each chromosome, derived from the paternal or maternal stock, would now have a copy; if each pair with its copy, meiosis becomes possible. *Spartina anglica* is indeed a polyploid: $2n = 120$ to 124 (Marchant 1968; Gray *et al.* 1990; Thompson 1991). The low genetic variability of *S. anglica* would appear to indicate that allopolyploidization only occurred once, or only a limited number of times (Thompson 1991). The vigour of hybrids is a well-documented phenomenon, the causes of which are varied and still under debate (Stebbins 1971; Tal 1980).

5.3 *Expansion phase*

Once naturalized, the introduced species starts the expansion phase: it will try to occupy the whole of the biotope or biotopes to which it may have access (ecological expansion) and the whole of the geographical range to which it may have access (geographical expansion).

The ecological expansion will depend upon the same parameters than the settlement phase (see Section 5.2). During this phase of expansion, development may be exuberant. This is the case at present in the Mediterranean for *Caulerpa taxifolia* (Meinesz and Hesse 1991).

The geographical expansion of the introduced species may occur either naturally (natural progression) or with human assistance (Ribera 1994). The simplest case of natural progression, in the marine environment, is expansion in the direction of the prevailing current. It was thus that *Halophila stipulacea* (Spermatophyta, Hydrocharitales), in the Eastern Mediterranean, reached the Levantine, Turkish, Greek, Albanian, Maltese and Italian coasts (Hartog 1972; Biliotti and Abdelahad 1990; Hartog and Van der Velde 1993; Zibrowius 1993), spreading in the direction of the current (anticlockwise), while in the other direction, it reached no further than Marsa-Matruh in western Egypt (Aleem 1962). Similarly, the red alga *Acrothamnion preisii* mainly extended its range in the Mediterranean in the direction of the prevailing current (Boillot *et al.* 1982; Cinelli *et al.* 1984; Thelin 1984). First observed at Leghorn (Italy) (Cinelli and Sartoni 1969), it spread towards Nice (Boillot *et al.* 1982), then on to the coast of the Var (France) (Thelin 1984); it was common at Menton in 1992 (Verlaque 1994), and now occurs on the island of Mallorca in the Balearics (Ferrer *et al.* 1995). It has thus spread for more than 1,000 km. In the opposite direction, southwards, it has spread no further than the island of Elba, which represents a progression of only 100 km (Cinelli *et al.* 1984) (Fig. 6). Similarly, and still in the Mediterranean, *Undaria pinnatifida* (Boudouresque *et al.* 1985) and *Sargassum muticum* (Knoepffler-Péguy *et al.* 1985; Belsher and Pommelec 1988), starting from the Thau lagoon (France), have extended their range towards Spain (which they have not yet reached) (Fig. 6).

Another type of natural progression is diffusion: from its point of introduction, the species spreads in all directions, without any one direction appearing to be particularly favoured (Ribera 1994). An example of this is *Stypopodium shimperi* (Fucophyceae, Dictyotales), which, starting at the Suez Canal, spread as far in one direction (Israel, Syria, Cyprus and Turkey) as in the other (Egypt, Libya) (Verlaque and Boudouresque 1991) (Fig. 7). The local spread of *Caulerpa taxifolia* (in the Alpes-maritimes, France) has followed a similar pattern (Meinesz and Hesse 1991; Meinesz *et al.* 1994).

Finally, the spread of *Codium fragile* in the Mediterranean would appear to have been fairly irregular. It was reported for the first time in the Pyrenées-Orientales (France) (Feldmann 1956), and subsequently appeared at both near and distant sites, with no apparent link with either the direction of the currents or the distance (Fig. 8).

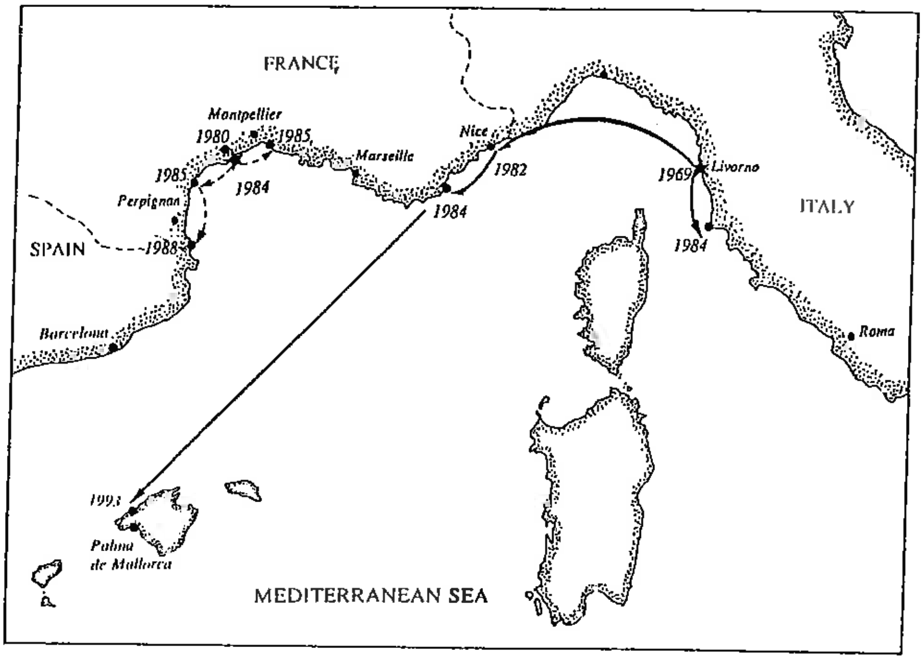

Fig. 6: Chronology of the expansion of *Acrothamnion preisii* (solid line) and *Sargassum muticum* (broken line) in the Western Mediterranean (from Ribera 1994, modified).

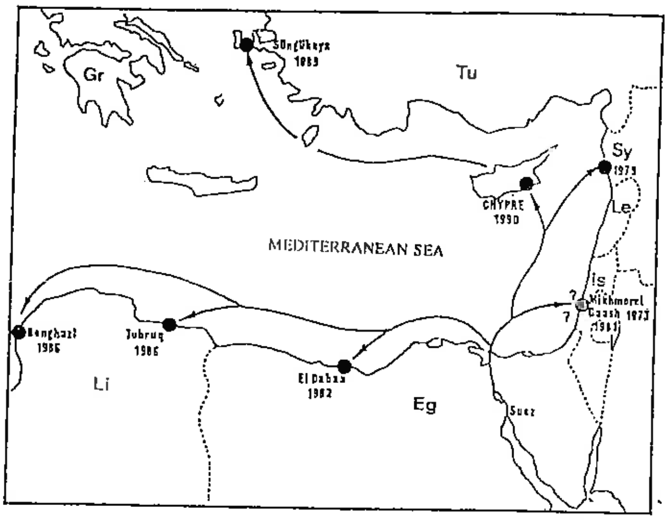

Fig. 7: Chronology of the expansion of *Stypopodium schimperi* in the Eastern Mediterranean (from Verlaque and Boudouresque 1991).

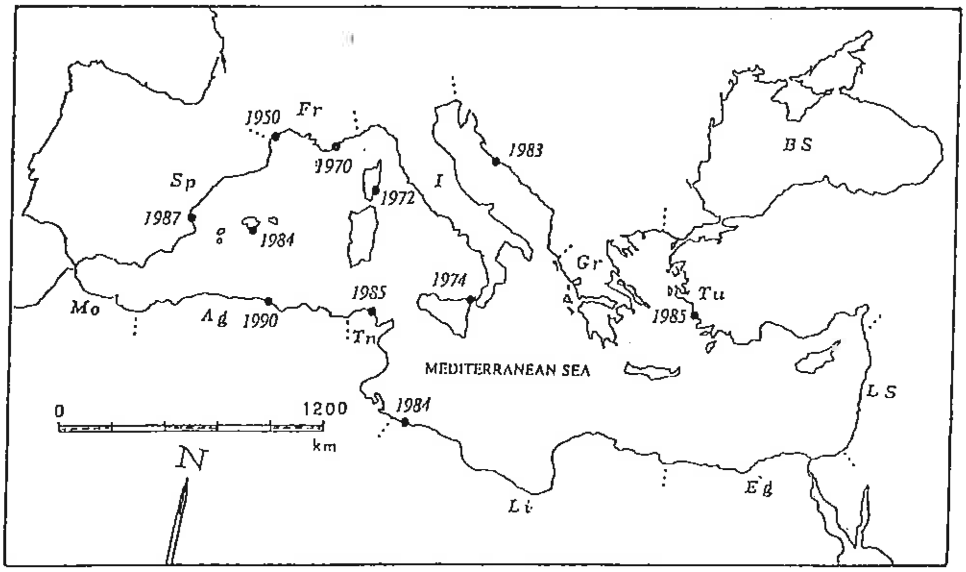

Fig. 8: Chronology of the expansion of *Codium fragile* in the Mediterranean (from Ribera 1994).

Expansion by diffusion is achieved by species with a relatively wide ecological niche, in such a way that the spread occurs progressively into neighbouring areas, and does not depend on chance encounters with favourable biotopes. Conversely, irregular progression, and to a lesser extent, progression in the direction of the prevailing current, is generally found in species with a narrow ecological niche (Ribera 1994).

Human-aided dissemination adds to the list of causes of species introduction: aquaculture, aquariology, boat anchoring, etc. Here it is a matter of multiple introductions. The result is progression by "leaps" to geographically distant sites without intermediary stations. The pattern of settlement is thus irregular, as noted above for certain natural progressions. An example is *Undaria pinnatifida*, which was introduced into the Mediterranean in the Thau lagoon with the spat of the Japanese oyster *Crassostrea gigas* in the early 1970s (Boudouresque *et al.* 1985), and which has recently been reported in the lagoon at Venice (Italy), where this oyster is also farmed (Curiel *et al.* 1994). Observations by Hay (1990) show that *Undaria pinnatifida* sporophytes, and even the mature plants, are transported on ships' hulls for hundreds of kilometers between New Zealand ports. This is also the case for *Caulerpa taxifolia*, which was introduced in France from outfalls from two separate aquaria, in the Monaco area (Meinesz and Hesse 1991) and at Saint-Cyr (Jacques Laborel, pers. com.). In addition to spreading locally through diffusion (see above), the dissemination of *C. taxifolia* has also occurred from anchorage to anchorage, often over long distances, transported with the anchor and chain in the anchor locker of pleasure craft (Meinesz 1992; Meinesz *et al.* 1994), from the French Côte d'Azur towards Mallorca (Balearics, Spain), Imperia (Liguria, Italy), the island of Elba (Italy) and Messina (Sicily). Finally, this may also be the case for certain stations of *Codium fragile* (see above and Fig. 8).

The modes of dissemination specific to each species play an important role with regard both to the mode of introduction and the mode of expansion after introduction (Ribera 1994). Species such as *Sargassum muticum* drift on the surface and may thus "leapfrog" considerable distances. Drifting *S. muticum* has been sighted in Belgium, whereas the species has not yet been reported there in fixed form (Coppejans *et al.* 1980; Wallentinus, in press), and flotsam has reached the coasts of the Balearics in the Mediterranean (Rull Lluch *et al.* 1994). Species such as *Caulerpa taxifolia*, the cuttings of which do not float, jump shorter distances (except when aided by man). The longevity and weight of the spores and zygotes influence the distances of dissemination. The occurrence in the cycle of a rampant and microscopic generation (gametophyte) or vegetative stage are factors that strongly favour dispersion. They easily pass unnoticed when they are fixed on aquacultural species (e.g. Molluscs), and they may be transported long distances on the hulls of ships (fouling).

The speed of expansion of an introduced species is highly variable. The spread of *Caulerpa taxifolia* in the Mediterranean has been very rapid. In 1984, it covered 1 m^2, in 1990 3 ha, in 1991 30 ha, in 1992 427 ha (including 73 ha of total cover) (Meinesz *et al.* 1993), in 1993 1,300 ha (Meinesz *et al.* 1994). On average, the area covered increased by a factor of 6.1 every year from 1984 to 1991 (Boudouresque *et al.* 1992). Ten years after its introduction, the most distant stations are more than 1,000 km apart. In 20 years, *Sargassum muticum* has colonised several thousand km of the Atlantic coast of Europe, from Norway to Portugal. The most distant stations are 2,500 km apart as the crow flies (Fig. 1). It took this species 45 years to spread roughly the same distance from Alaska to Baja California (Pacific coast of North America). In the Mediterranean, it took more than a century for *Halophila stipulacea* to occupy a range stretching 2,000 km from Syria to Malta and Sicily (Biliotti and Abdelahad 1990). Finally, nearly two centuries after its introduction in the south of Great Britain, the North-American grass *Spartina alterniflora* has remained restricted to the immediate vicinity of its point of introduction.

The duration of the geographical expansion phase is also highly variable. Expansion has probably stopped for *Sargassum muticum* both on the Pacific coast of North America (45 years after introduction) and on the Atlantic coast of Europe (20 years after introduction). On the other hand, the spread of *Caulerpa taxifolia* in the Mediterranean continues (10 years after introduction), as does that of *Codium fragile* (45 years after introduction). On land, the barbary fig *Opuntia ficus-indica* (Spermatophyta, Caryophyllales), introduced deliberately in Australia in the late 19th century, spread continuously for 80 years. In the early 1970s, it occupied 18 million hectares, and it continued to spread at a rate of 400,000 ha/year. Its spread was halted by biological techniques (see Section 9).

5.4 *Persistence phase*

The persistence phase, which follows the expansion phase, may take one of two forms: (i) decline followed by stabilisation at a lower level than the maximum attained during the expansion phase; (ii) a plateau close to the maximum attained.

At the end of the expansion phase, it is not unusual for the proliferation of an introduced species to decline, although this is not the general rule. At the beginning of the century, in Brittany (France), *Colpomenia peregrina* enjoyed a spectacular initial development, achieving virtually total cover of the oyster beds (Sauvageau 1906); a few years later, *C. peregrina* had stepped back into the ranks, and was unobtrusive in the coastal communities (Sauvageau 1908). In the Thau lagoon, *Sargassum muticum* declined in the late 1980s following the expansion of the sea urchin *Paracentrotus lividus*, which grazes on the germlings (Lauret *in* Belsher 1991). In the Mediterranean, *Codium fragile* went through a phase of proliferation in the Marseilles area in the early 1960s; it was washed up onto the beaches in large quantities during storms, and formed heaps of "wrack" that were sufficiently sizable for the municipal authorities to have them removed with mechanical diggers; it has since regressed (Boudouresque 1994). A similar situation occurred in Great Britain with the planktonic diatoms *Coscinodiscus wailesii* (Centrales), *Pleurosigma planctonicum* (Pennales) and *Thalassiosira angstii* (Centrales) (Boalch 1987, 1994). In terrestrial fresh waters, *Elodea canadensis* (Spermatophyta, Hydrocharitales), introduced in Europe during the First World War, developed to the point that in Great Britain it clogged rivers and canals; it has since regressed and is no longer a nuisance (Simpson 1984).

Ecological decline (decrease in abundance, and consequently in impact on the ecosystems), when it occurs, generally starts while the geographical expansion phase is in progress. The ecological expansion phase and the geographical expansion phase are thus two non-synchronous phenomena. In addition, it should be pointed out that the decline of an introduced species is almost always ecological and not geographical: it is extremely rare for the range of an introduced species to shrink once the geographical expansion phase is completed.

The causes of the decline of certain introduced species, after their ecological expansion phase, are poorly known. Among the possible causes, one might mention: (i) indigenous predators becoming accustomed to its consumption; (ii) the proliferation of potential predators or parasites, that are indigenous, and therefore present at the time of introduction, but in insufficient numbers to control the invasion; (iii) low genetic variability (due to the inadequate size of the inoculum), which makes adaptation to environmental change or fluctuations difficult; (iv) decline in genetic vigour due to consanguinity (consanguinity depression) and/or the elimination of certain alleles (Boudouresque 1994).

For other introduced species, a plateau follows the expansion phase, but no decline occurs (or has yet occurred). This is the case in Great Britain for *Spartina anglica*, which today occupies 10,000 ha (Charman 1991). The possibility of a decline of *S. anglica* in Great Britain because of its low genetic variability and the appearance of parasitic fungi has been mentioned by Thompson (1991). In the North European Atlantic, the *Gyrodinium aureolum* (Dinophyta, Gymnodinales) continues to produce blooms 25 years after its introduction (Hansen and Sarma 1969), with mortality of fishes and invertebrates (Boalch 1987, 1994).

As for the expansion phase (ecological and geographical), it is impossible to predict the duration of the plateau of the persistence phase (on the hypothesis that it must have an end): each introduced species is in fact a special case. The expansion of *Eichhornia crassipes* (water hyacinth; Spermatophyta, Liliales), which originated in Amazonia, ceased when it had colonised all the intertropical fresh waters of the planet, that is to say the whole of the domain to which it could have access. There is no apparent sign of decline in either abundance or the extent of its geographical range more than a century after the beginning of its introduction and expansion, and several dozen years (almost a century in some areas) after it reached the plateau phases (Barrett 1989).

6. ECOLOGICAL IMPACT OF BIOLOGICAL INVASIONS

Many introduced species, that have proliferated and caused serious environmental imbalance or nuisance, have been responsible for no such problems in their native region. Sometimes, they play a discrete role there and pass unnoticed. Examples of this are *Sargassum muticum* which is unobtrusive in Japan (Boalch 1994), and *Caulerpa taxifolia*, which is very uncommon and does not play a major role in the formation of dense meadows in tropical waters. The dinoflagellate *Gyrodinium aureolum* does not cause toxic blooms on the east coast of the United States, where it originates (Boalch 1994). The reason is that in their native regions these species, after a very long period of co-evolution between predator and prey, parasite and host, pathogenic agent and target species, exist in a complex equilibrium state.

A great deal of work has been devoted to the impact of biological invasions on terrestrial environments and fresh waters: there has been a wealth of publications, conferences and surveys. It is known in particular that the impact of species introductions on insular environments (Hawaii, New Zealand, etc.) has been very heavy, with the disappearance of several hundred indigenous species (impact on biodiversity) and certain ecosystems (impact on ecodiversity). By contrast, the impact on the marine environment is very poorly known (Posey 1988), even when it concerns dominant species of large size. *Asparagopsis armata* sometimes covers as much as 100% of the substratum in winter in the North-Western Mediterranean growing to a height of 20 or 30 cm. Associated with *Codium fragile*, it is the dominant species in certain infralittoral communities in the Marseilles area. *Womersleyella setacea* (Rhodophyta, Ceramiales), first discovered in the Var (Verlaque 1989), covers the "coralligène" communities of the Scandola reserve (Corsica) with a virtually monospecific layer 5 cm thick: it would be interesting to determine its impact on the calcareous algae that build the "coralligène" banks.

Generally speaking, 80% of introduced species have no effect on the indigenous communities (Simberloff 1981). For the European coastal waters, this is, for example, the case for *Bonnemaisonia hamifera* (Rhodophyta, Bonnemaisoniales), for *Undaria pinnatifida* (Castric-Fey *et al.* 1993) and (currently) for *Colpomenia peregrina* (Farnham 1980). In the Thau lagoon where there are a dozen or so introduced species, their biomass only represents 4.4% of the total biomass of the macrophytes in the lagoon (Dubois and Lauret 1991).

On the other hand, other introduced species do have an impact on the indigenous species or communities: this is referred to as biological pollution (Sindermann *et al.* 1992). When the introduced species is in competition with indigenous species, the latter can be seen to be in regression. This phenomenon may result in the total elimination of one or several species, or their restriction to redoubts or less favourable ecological niches. This shift of ecological niche is more easily observable for the marine fauna; in the Mediterranean, the introduction of certain fish species has resulted in some indigenous species being confined to deeper waters (Spanier and Galil 1991; Por 1978). In Boundary Bay (British Columbia), the exotic seagrass *Zostera japonica* has extensively colonised formerly unvegetated tidal flats and dramatically altered the habitat structure (Baldwin and Lovvorn 1994). In certain regions (southern coasts of England and Ireland), the introduced green alga *Codium fragile* is in competition with the indigenous species *C. vermilara* and *C. tomentosum*, and the abundance of the latter, which has a similar morphological habit and close ecological niche, has declined (Parkes 1975; Farnham 1980). In Hawaii, the introduced Rhodophyta *Hypnea musciformis* (Gigartinales) and *Acanthophora spicifera* (Ceramiales) occupy the same ecological niche as the indigenous species *Laurencia nidifica* (Ceramiales) and *Hypnea cervicornis* (Gigartinales); only the latter species has seen its abundance decline (by half) as a result of the competition (Russell 1992). In the Sydney Harbour area (Australia) the introduced species *Caulerpa filiformis*, recorded as a rarity in the 1930s and 1940s, is now becoming a local dominant; it seems established that this species is fast replacing a number of other species in this area (May 1976). In the Alpes-Maritimes, the green alga *Caulerpa taxifolia* forms dense meadows that have replaced the beds of photophilous algae on rock as well as the *Posidonia oceanica* meadow (Meinesz and Hesse 1991; Boudouresque 1992; Boudouresque and Gómez 1992); the number of species of algae is four times lower, the biomass of indigenous algae is 9 times lower and indigenous algal coverage is almost 500 times lower than in the photophilous algal communities that they replace (Boudouresque *et al.* 1992). More than 15 to 25 years after its settlement (the exact date is open to debate), *Sargassum muticum* has caused a decline in the abundance of certain indigenous species, but there is no evidence that it has eliminated indigenous species, at least the large sized species such as the *Laminaria* or the *Fucus* (Rueness 1989). Nevertheless, in the English Channel (Atlantic), *Sargassum muticum* is in competition with various species, in particular *Laminaria* spp., *Cystoseira* spp., *Scytosiphon lomentaria*, *Gracilaria verrucosa* (Rhodophyta, Gigartinales) and *Chondrus crispus* (Rhodophyta, Gigartinales); when the *S. muticum* stand is particularly dense, there occurs total elimination of rival species locally and seasonally (Fletcher and Fletcher 1975; Critchley 1983).

The elimination of native species may give rise to alterations in the functioning of the ecosystem. Large-sized algae, such as the Laminariales and the Fucales, which are often key-stone species, have a strong potential impact. In California, settlement by *Sargassum muticum* in 1976, favoured by a temporary temperature increase (El Niño), ultimately prevented the recruitment of the giant alga *Macrocystis pyrifera*, by drastically reducing the light available on the substratum (Ambrose and Nelson 1982). In British Colombia (Canada), *Sargassum muticum* reduced the coverage of *Rhodomela larix* (Rhodophyta, Ceramiales); nonetheless, in the event of experimental or natural (storms) elimination of *S. muticum*, the *R. larix* is capable of recolonising its former station, and then preventing subsequent recolonisation by *S. muticum* (De Wredde 1983). In the Thau lagoon, *S. muticum* eliminated the indigenous species *Cystoseira barbata* (Fucophyceae, Fucales) in certain stations; by forming a very dense canopy, preventing the light from filtering through at the time when *C. barbata* is fertile (February to April), *S. muticum* blocks its recruitment. In addition, the Shannon Diversity (0.3 to 0.8) and the Evenness (0.1 to 0.2) are exceptionally low in the *S. muticum* communities (Gerbal *et al.* 1985).

Apart from the regression or elimination of species, other factors linked to species introduction have an impact on the functioning of the ecosystem. The possible diffusion into the water of toxins from *Caulerpa taxifolia* in the Mediterranean may result in alterations. For example, a certain number of ciliates are highly sensitive to the toxic terpenoids produced by *C. taxifolia*, at doses of 0.5–1.0 μg/ml (Dini *et al.* 1992; Guerriero *et al.* 1992); since the ciliates play an important, though often little known, rôle in the food chain, a direct impact on the metazoans might be expected. In the Thau lagoon, the accumulation and decomposition of large quantities of *Laminaria japonica* results in the phenomenon of anoxia in summer (Anon. 1982). In the terrestrial domain, the water hyacinth, *Eichhornia crassipes*, that is slightly or not at all consumed by herbivores, putrifies at depth, and thus reduces the oxygen content of the water and drives away the fish fauna (Barrett 1989).

Nevertheless, the impact of the introduced species can only become apparent in the long term. The biological invasions must be examined on broad spatial and temporal scales: short-term or narrowly focused studies can lead to incorrect conclusions (Berman *et al.* 1992). Rueness (1989) noted that the 15–20 years during which *Sargassum muticum* has been present in Europe represent a relatively short period of time in this field; in addition, the continuous arrival of new introduced species (*Undaria pinnatifida*, *Laminaria japonica*, etc.) may generate a cumulative effect or synergy that goes far beyond the impact of each species considered on its own.

In certain cases, when the introduced species are keystone species or strong interactors, new ecosystems may be formed based on the original food chains; this has been the case in the Black Sea and in the Baltic (Leppakoski 1994). In the Mediterranean, the *Caulerpa taxifolia* meadow may be another example.

Introduced species sometimes occupy a wider niche than in their native region; furthermore, their morphological characteristics may be different. In Japan, for example, *Sargassum muticum* is one rather unobtrusive species among thirty or so species of the genus *Sargassum*, restricted to the infralittoral fringe, and measuring no more than 1.0–1.5 m in length (Rueness 1989); in Europe, its ecological niche is wider; it is found from mid-littoral pools to 20 m depth (Norton 1977) and may exceed 10 m in length (Belsher and Boyen 1983). *Undaria pinnatifida* grows better in Brittany, where it may reach 2 to 3 m in length, than in its native region, Japan, where it does not exceed 1.5 m in length (Perez *et al.* 1988). Similarly, New Zealand populations of *U. pinnatifida* exhibit a more vigorous cycle than those in Asia, since thay have no autumnal hiatus between sporophyte generations: sporophytes are always present (Hay and Villouta 1993). The same is true for *Caulerpa taxifolia*, which in the Mediterranean forms extremely dense meadows (more than 8,000 leaves/m^2) with leaves that may exceed 60 cm in length (Meinesz and Hesse 1991), whereas in warm seas, these meadows are generally patchy or very patchy, and the leaves range from 2 to 15 cm and rarely exceed 25 cm. Gray (1986) explains these differences between original populations and introduced populations by genetic reorganisation that affects the gene pool of the pioneering individuals that were at the origin of the introduced population.

Apart from real introductions of species as such, introductions of genes probably occur, even though this phenomenon is very poorly documented. In Corsica (France), strains of *Hypnea musciformis* from Senegal have been cultivated (Mollion 1984); the species occurs in Corsica, but gives poor results in culture, in contrast to the Senegalese strains, which suggests genetic differences; these genes may perhaps have been introduced. The introduction of *Chorda filum* (Laminariales) and *Sphaerotrichia divaricata* (Chordariales) (Riouall 1985) into the Thau lagoon, may just as likely have come from the North Atlantic as from Japan (with oyster spat of *Crassostrea gigas*), since the species occurs in both regions. In the case of *S. divaricata*, Peters *et al.* (1992) have offered evidence of a barrier of sterility between the plants in the Thau lagoon and those in the North Atlantic, and conclude that the introduction originated in Japan. An intraspecies sterility barrier of this kind probably does not affect all the species that are widespread on a global scale; if Japanese strains of *S. divaricata* and (possibly) *C. filum* arrived in the Thau lagoon, they may just as likely have reached the Atlantic coast of Europe, although it would be more difficult to spot them there, with the consequent genetic contamination of the native species (when they are not protected by a sterility barrier). *Laminaria japonica*, introduced into the Thau lagoon, could hybridize with a North Atlantic species, *Laminaria saccharina* (Bolton *et al.* 1983); for the time being, these two species are not in contact, but the mixing of their genome is altogether probable should contact occur (Rueness 1989). In fresh water, hybridization of introduced species with neighbouring indigenous species, and the resulting genetic drift, have been well documented (Mazzola 1992). Finally, it is particularly important to remember that by bypassing geographical barriers on a massive scale, the transportation of ballast waters is responsible for intensive genetic mixing on a global scale, the consequences of which are unknown (Carlton and Geller 1993).

7. NUISANCES RESULTING FROM BIOLOGICAL INVASIONS

Nuisances here means a negative impact on the utilisation of the sea by man. The nuisances caused by introduced species are much better documented than their impact on the natural environment. All sectors of activity may be affected: fishing, aquaculture, tourism, shipping and coastal industries.

7.1 *Fishing*

The proliferation of algae may cause difficulties with regard to the use of fishing equipment. In the Gulf of Giens (France, Mediterranean), *Womersleyella setacea* (=*Polysiphonia setacea*) interferes with fishing by clogging up the nets (Verlaque 1989). The same is true of *Acrothamnion preisii*, that Italian fishermen refer to as "pelo", in the Leghorn area (Italy) (Cinelli *et al.* 1984). Between Menton and Monaco (Mediterranean), fishermen complain that when the sea is rough, strips of *Caulerpa taxifolia* stick to their nets, making them visible to the fish, which can then avoid them (Meinesz, pers. com.). In 1988, *Polysiphonia breviarticulata* caused a planktonic bloom along 200 km of the coasts of North and South Carolina (USA), causing problems for the local fishery (Kapraun and Searles 1990). In Great Britain in the late 1970s, the mucilage produced by the Bacillariophyceae (Centrales) *Coscinodiscus wailesii* clogged up trawl nets; one trawl was even lost because of the excess weight (Boalch and Harbour 1977b; Boalch 1987).

Sometimes the impact of introduced species may result, directly of indirectly, in a decrease in stocks of populations of commercially-valuable species. In New Zealand, the development of *Codium fragile* subsp. *tomentosoides* constitutes a threat to shellfish beds, according to Adams (1994). Nevertheless, this phenomenon mainly concerns the fauna, because of the introduction either of species that compete with the commercially exploited indigenous populations (Travis 1993), or of pathogenic organisms that have a negative impact on them (Buslé, in press).

7.2 *Aquaculture*

The negative impact on aquaculture (fish and shellfish farming) takes a similar form to that affecting fishing: (i) decline of stocks of commercially valuable species, (ii) introduction of pathogenic organisms, (iii) problems for the functioning and operation of aquaculture farms.

(i) In the years following its introduction in Brittany, *Colpomenia peregrina* developed in abundance on the oysters. At low tide, the water in the thallus, which is hollow, is drained off; when the tide comes in, it only refills with water slowly, and thus constitutes a kind of buoyancy tank for the oyster, which floats for some time and drifts out of the oyster park. Sauvageau (1906) wrote: "*One can imagine the great harm that may be done to oyster farming by the invasion of this new commensal*" that the oyster farmers called the "oyster thief". The financial losses were sufficiently high for the matter to be referred to parliament (Knoepffler 1994). This species had caused similar damage in Great Britain (Cotton 1908). *Sargassum muticum*, when it is attached to oysters, may also cause them to drift away because of its "floats". Similarly, large-sized specimens of *S. muticum* and *Undaria pinnatifida* spread out on the surface in shellfish farms and help to reduce the light available, thus inhibiting the development of the populations below (Verlaque 1994). The development of *S. muticum* has been alleged to be responsible for the loss of 30% of the profits from aquaculture farms on the Atlantic coast (Belsher 1991).

(ii) Periodically, "unknown" diseases of bacterial or parasitic viral origin strike cultures in many parts of the world. For example, in Martinique (French Antilles), production of bass was wiped out by a disease known as "the staggers", resulting from a hitherto unknown virus that affected the nervous system of fish. Similarly, in Norway, the salmon were hit by an infectious anemia caused by another unknown virus. Naturally, since the pathology of the marine species is a relatively recent discipline, it is not inconceivable that the agents of these diseases may be indigenous. Nevertheless, the irresponsible practices of many fish and shellfish farmers (see below), added to the lack or inadequacy of quarantine measures, supports the hypothesis that these diseases or these parasites may have been imported accidentally. In 1981, algae thought to belong to *Eucheuma spinosum* (Rhodophyta, Gigartinales) from the Philippines were immersed in open sea in the French Antilles (Guadaloupe), 48 h after being collected and without any quarantine measures, in order to compare their growth rate with that of the indigenous *E. spinosum*. Within two months, they were dead, victims of necroses that the authors of the experiment (Barbaroux *et al.* 1984) attributed to the disease "ice-ice", that is known in South-East Asia. The authors noted that this disease had not been passed on to the indigenous *Eucheuma*, and therefore assumed that they must therefore have become immunized. It would thus appear that Barbaroux *et al.* (1984) knowingly took the risk of introducing a disease into a region where it did not hitherto occur! In fresh water too, many diseases have made their appearance with fishes that were introduced without quarantine measures (Mazzola 1992).

The current development of unicellular algae that produce paralytic, diarrhoeic or neurotoxic toxins, and represent a very serious nuisance to both fish and shellfish farming, can probably be explained by several factors: (i) more intensive observation; (ii) alterations in the chemical composition of coastal waters (pollution); (iii) introduction of exotic species or genes. In the latter case, the cause may be the mixing on a global scale of waters because of the unloading of ballast water from ships. This may have resulted in the introduction of species of toxic Dinophyta in regions where they did not occur, or the introduction of races of species that already occurred, but were genetically different from the local race with which they may have hybridized. The vigour of hybrids is known, and they may present ecological and physiological characteristics that are very different from those of the parent strains. These species of toxic dinoflagelates, which can affect fish and shellfish farms, pose a serious threat to public health and aquaculture; 6% of cargo vessels entering Australian ports carried the cysts of the toxic dinoflagellates *Alexandrium catenella* and *A. tamarense* (Hallegraeff and Bolch 1991). The example of Chile, the world's second biggest salmon producer, which lost half of its stock in a month, is an illustration of the potentially catastrophic impact of planktonic toxic algae on the economy. In South-East Australia, the introduction of the toxic *Gymnodium catenatum* (Gymnodinales) resulted in 1986 in a ban on the sale of cultured and wild shellfish, mussels, oysters and scallops (Pollard and Hutchings 1990; Grizel 1994). In the North Atlantic, the toxic *Gyrodinium aureolum* (Gymnodinales) cause mortalities in fish farms (Boalch 1987), and also in particular in the restocked scallop populations in the roadsteads of Brest.

(iii) In the Thau lagoon, the introduced algae *Sargassum muticum*, *Undaria pinatifida* and *Codium fragile* develop on the oyster ropes, adding considerably to the weight, and thus making them more difficult for the oyster farmers to handle (Boudouresque 1994) – the additional load may be as much as 14 kg of *S. muticum* per rope (Lauret *et al.* 1985). In Great Britain, the proliferation of *Sargassum muticum* in the shellfish beds, or in the immediate surroundings, represents a considerable nuisance and has made it necessary for the beds to be cleared (Belsher 1991).

7.3 *Shipping*

Sargassum muticum represents a hazard for shipping, for example in the Gulf of Morbihan (France, Atlantic) (Belsher 1991). An accident was reported in Jersey (Great Britain), where a ferry whose propellers were jammed by *S. muticum* collided violently with the quay. The introduction of *Macrocystis pyrifera* in Europe, had it been carried out, would have constituted a hazard for coastal shipping (Boalch 1981). This giant alga forms real underwater forests, and its stipes with attached leaves, fixed on the bottom at depths of 20 m, spread out on the surface. Rumour has it that it was the French navy that was behind the ban on the species' introduction in France because of anxieties about the safety of nuclear submarines passing through the Brest Channel.

7.4 *Public health and tourism*

The introduction of toxic species may have a direct or indirect impact on public health through the ingestion of herbivorous organisms or filter feeders. In Europe, we have no need to be reminded of the frequent bans on sales of shellfish following the proliferation of toxic unicellular algae. *Fibrocapsa japonica* (Raphidophyceae, Rhaphidomonadales), which has recently been reported on the French coast, was associated in Japan with red tides and the death of marine animals (Iwasaki 1971; Hara and Chihara 1985; Billard 1992). Cholera has long been associated with the seasonality of algal blooms off Bangladesh (Epstein 1993); microbiologists have now identified a viable form of *Vibrio cholerae* in a wide range of marine life, including Cyanophyta and Phaeophyceae; in the abundant coastal sea life along the Latin American Pacific coast, nourished by the Humboldt current, it has found a reservoir for surviving; a heavy inoculum of carriers infected with *V. cholerae* (algae and the organisms that consume them) was generated and transported into multiple communities (Epstein 1993). An indirect consequence of introductions of species may be pollution induced by anti-fouling products used to try to prevent them from settling in conduits. In the United States, for example, the legislators are under pressure to make the measures governing the use of biocides more flexible (Durnil *et al.* 1990).

Because of the economic impact, nuisances affecting tourism are worth emphasising. In Cyprus, an introduced *Cladophora* (perhaps *Cladophora patentiramosa*, Verlaque, pers. comm.) proliferated off the beaches, and its flotsam accumulated on the beaches themselves, thus hindering bathing (Demetropoulos and Hadjichristophorou, pers. comm.). The development of populations of *Codium fragile* may favour the accumulation of stones on sand beaches (Ben Avraham 1971). The planktonic bloom of *Polysiphonia breviarticulata* along the North and South Carolina coasts (USA) caused problems for recreation in 1988 (Kapraun and Searles 1990).

Scuba diving is a leisure activity that is developing rapidly. In the Mediterranean, which is a major tourism region, this sport is currently one of the driving forces that is contributing to the maintenance or development of tourism. The new uniformity of the underwater landscape that has been observed between Nice and Menton (Alpes-Maritimes, France), in areas colonised by *Caulerpa taxifolia*, may have a strong negative impact on the development of scuba diving and tourism, should the alga continue to spread (Knoepffler 1994)

In the terrestrial domain, the water hyacinth *Eichhornia crassipes* is a good example. Its extraordinary capacity for proliferation enables it to cover water courses with a carpet that may be as much as 2 m thick, hindering shipping, blocking channels and causing flooding in the flatlands. The water hyacinth is in addition a microhabitat that is favourable for the agents of human diseases such as malaria, encephalitis and schistosomiasis (Barret 1989).

7.5 *Economic impact*

A commission of inquiry of the US Congress has estimated the economic damage caused by introduced species (terrestrial and marine) in America since the beginning of the century as at least $97 billion, including

$5 billion for the zebra mussel *Dreissena polymorpha* alone (Windle *in* Kiernan 1993). This is a minimum estimate, since only 79 of the 4,500 species introduced into the United States have been taken into account. Yet Windle (*in* Kiernan 1993) has established that in the USA, 15% of introduced species have caused economic or environmental damage.

A similar inquiry in the various countries of the European Union would be welcome. It would certainly contribute to increasing awareness among political leaders and public administrators on the isssues and the stakes involved in the matter of species introduction.

The exotic species are practically impossible to eliminate once they have been introduced (see Section 9). Measures designed to limit their impact involve extremely high costs (Durnil *et al.* 1990), 10 to 100 times higher than the cost of the preventive measures that might have made it possible to avoid their introduction in the first place.

8. BENEFITS OF SPECIES INTRODUCTION

8.1 *Ecological benefits*

In some cases, introduced species may occupy vacant ecological niches. This has been the case for a certain number of Lessepsian immigrants in the Levantine Basin of the Eastern Mediterranean. Another example is *Spartina anglica* in the coastal marshes of Great Britain (Thompson 1991), where is plays an important role in fixing the substratum.

In Hawaii, the introduction of the Rhodophyta *Acanthophora spicifera* (Ceramiales) and *Hypnea musciformis* resulted in an increase in the algal biomass. These species are now being prominently used as a food source by the green turtle *Chelonia mydas*; this is the first known documentation of introduced algae being incorporated into the diet of the green turtle, a species considered endangered world-wide (Russell and Balazs 1994). A similar example is the introduced seagrass *Zostera japonica* which in British Columbia provides an important feeding habitat for many migratory waterfowl, which graze on it more intensively than they do on the indigenous species *Z. marina* (Baldwin and Lovvorn 1994).

In certain, very particular areas of the world where biodiversity is very low as the result of relatively recent climatic events (quaternary glaciation), such as the Baltic Sea and the Levantine Basin of the Eastern Mediterranean, the increase in biodiversity resulting from species introduction may be considered as having a positive impact. Detailed investigations are however required to provide positive confirmation of this.

In most regions of the world, in the absence of sequential inventories, we do not know whether the flux of introduced species has resulted in the disappearance or rarification of indigenous species, or whether the introduced species have simply been added to the indigenous species. We refer of course to the marine environment, since for the terrestrial domain, the insular environments have proved beyond doubt the gravity of the impact of species introductions in terms of the disappearance of species (and therefore the decline in diodiversity) and ecosystems.

In any case, to consider that any increase in the number of species in a region (of whatever origin) is beneficial, is a rather primitive interpretation of the notion of biodiversity. It is important not to confuse the preservation of biodiversity worldwide (that is, the genetic patrimony) with a possible local increase in biodiversity under the impact of introduced species. In this case, the ecodiversity would in any case be altered. This simplistic interpretation (propagated by non-environmentalists and likely to appeal to some politicians, and whose logical result would be the worldwide standardization of all populations) is diametrically opposed both to the concept of biodiversity and to the ethics of the conservation of the environment. If this were in fact the case, zoos and botanical gardens would be the paradigm of biodiversity. And in the case of insular environments, where the flora and fauna is rich in endemic species but generally poor at the time of their discovery, and where many of these species have disappeared, to be replaced by a greater number of introduced species (including cattle, rats, mice, cats, cockroaches, Hydrangea, etc.), this would have to be seen as an enhancement of biodiversity.

8.2 *Economic benefits*

Setting aside their environmental impact, some exotic algae may be of commercial value (Verlaque 1994). Three edible species, *Porphyra yezoensis*, *Laminaria japonica* and *Undaria pinnatifida* that were accidentally introduced in the Thau lagoon, have been used for farming trials (Perez *et al.* 1984). Similarly, the deliberate introduction of certain species has made it possible to generate or to maintain commercial activities, in particular with regard to the fauna. *Undaria pinnatifida* was introduced for farming purposes on the Atlantic coast of France (Perez *et al.* 1991).

Nevertheless, for an introduced species to have any real economic benefit, it must be proved that the total volume of the catch or harvest (taking all species together) is greater than it was before its introduction: the commercially exploitable introduced species may simply have replaced an equally exploitable indigenous species (Boudouresque 1994).

It is as well to be very cautious with regard to the supposedly economic motives behind many cases of species introduction, or species introduction schemes. For many scientists, there is clearly a ludic aspect: introducing a species is a game and a challenge, often superficially disguised by an overlay of extremely naive economic considerations (Vasserot 1981a, 1981b, 1983, 1985a, 1985b, 1987). The fish and shellfish farmers often consider that the successful and profitable rearing of a species elsewhere in the world is a guarantee of high profits if the species is introduced in Europe. In fact, poor knowledge of the biological aspects of these organisms, i.e. of their biological cycle and ecological requirements, may result in the failure of any attempt to rear it in Europe. But even when the species are technically transposable, labour costs, the rental or purchase prices of coastal areas, the need for good quality coastal water and possible conflicts of interest with other users of coastal areas (e.g. for tourism) mean that aquaculture operations carried out successfully in developing countries, are not necessarily economically viable in Europe (Mazzola 1992). Finally, the economic benefits of the introduction of a species should not be assessed simply on the basis of strict profit and loss estimates (production costs, market and sale price), but on the basis of a wider view, taking into account losses from other business activities and the costs of any damage that may result. If *Macrocystis pyrifera* had been introduced in Europe, it would naturally have extended its range to many North Atlantic countries, with an ecological impact and commercial disadvantages that would probably have been very serious. In fact, a few years later, the price of alginates dropped, following the development of aquaculture in China, and it is far from certain that its exploitation would have continued to be as attractive a proposition as those who promoted its introduction had envisaged. More worryingly, one of the *Undaria pinnatifida* farms in Brittany went out of business in 1994: apparently, assessments of the dietary habits of the French (the seaweed was intended for human consumption) and the market studies (anticipated sales, price differentials with seaweed from the Far East) had not been carried out with sufficient thoroughness. In addition, experiments at sea with *Eucheuma spinosum* were carried out in the French West Indies (Guadeloupe) with a view to its possible cultivation (Barbaroux *et al.* 1984). The *Eucheuma* are one of the main sources of the phycocolloid carrageenin that is widely used in the food industry, (E 407); the Philippines and Indonesia are the main producers of *Eucheuma*, which is cultivated there on a large scale. This culture largely relies on child labour in countries where the standard of living is very low, so that the price per ton of *Eucheuma* is relatively low. A proper economic feasibility study would certainly have shown that it was utterly unrealistic to imagine that *Eucheuma* could be competitively farmed in a French department such as Guadeloupe.

Occasionally, the alterations that exotic species introduce into the ecosystem also bring economic benefits. E.g. *Spartina anglica* accelerates the fixation and consolidation of the soil in the coastal marshes, protects them against the sea, and thus facilitates their eventual use by man (Thompson 1991). In Great Britain, according to fishermen, catches of eels are greater within the *Sargassum muticum* communities (Critchley 1983).

Research has been undertaken with a view to putting a value on accidentally introduced species. One of the most intensively studied species is *Sargassum muticum*. While the species turns out to be a potential source of alginate, the alginate content is low and of poor quality. However, a pharmacological assessment has revealed a positive action against platelet aggregation and high blood-pressure, among other benefits. Finally, in horticulture, extracts of *S. muticum* have a positive impact on the germination of cultured plants and the successful growth of cuttings (Belsher 1991). Nevertheless, these studies do not appear to have yielded conclusive results, and none of these possibilities has given rise to exploitation on an industrial scale (Belsher and Pommelec 1988; Belsher 1991).

9. ATTEMPTS TO ERADICATE OR CONTROL INTRODUCED SPECIES

The complete or partial eradication of an introduced marine species that is a source of nuisances is certainly very difficult, if not impossible, given the present state of our knowledge and techniques (Dorchada *et al.* 1990). In addition, there has been little research in this field. The work that has been done mainly concerns the *Sargassum muticum*. Manual eradication was attempted in Great Britain, but without success (Gray and Jones 1977; Farnham 1980). In the intertidal zone, a tractor-drawn harrow was used to clear the mussel beds at Cotentin (France), but this technique involves considerable disturbance to the substratum. In the sublittoral zone, a dredger has been used to clear the channels of the Gulf of Morbihan (France) and to reopen them to boat traffic. The shellfish beds at the l'île de Ré (France) have been cleared by means of a chain dragged by two amphibious vehicles; but this system resulted in the fragmentation and dispersal of most of the algae (1,000 t), for only 250 tonnes landed.

Chemical techniques involving the use of herbicides, copper sulphate, sodium hydrochlorite and phytohormones, have been tried out in Great Britain and France. While certain products, such as copper sulphate, have proved effective, their low specificity and persistence in the medium make them unsuitable for use except in exceptional circumstances (Jupin 1989; Belsher 1991).

Biological techniques appear to be an attractive alternative. These techniques are however slow to put into operation. In the terrestrial environment, experience has shown that it requires on average 10 years of research to develop a biological tool. In marine environment, examples of biological techniques of this type are rare, and for the algae, non-existant. But on the basis of our experience of their use on land, where there have been far more failures than successes, we should consider them with caution. In Australia, it was a biological solution (the introduction of a Diptera), after a dozen unsuccessful attempts, that finally put an end to 70 years of uninterrupted spread of the Barbary fig *Opuntia ficus-indica*. It was also a biological weapon, the introduction of the beatle *Cyrtobagous salviniae*, which feeds exclusively on the floating fern *Salvinia molesta*, which finally got the better of this plant in the lakes of Australia, New Guinea, India and Namibia (Barrett 1989). Nevertheless, the fact that a species is the parasite or predator of another species, in a given context, does not necessarily mean that the latter is its exclusive, or even preferred, target. In a different context, it might well attack other species, and even neglect its usual target (the introduced species that we wish to eliminate) in favour of indigenous species. "*Introducing one exotic marine species to control another could open a Pandora's box*" (Travis 1993).

Finally, analysis of the genetic structure of introduced populations and original populations is likely to provide not only very important data that will be helpful for designing chemical and biological techniques, but also genetic tools (Occhipinti Ambrogi 1994).

10. INADEQUACY OF EXISTING LEGISLATION

De Klemm (1994) distinguishes between three types of species introduction: (i) deliberate; (ii) accidental introduction through the escape of species (aquaculture farms, laboratories, etc.), including deliberate release into the wild by do-gooders; and (iii) purely accidental introductions (commensals or parasites of other organisms, ballast water, fouling, etc.). While a few international texts of law (incidentally rather vague) and the national legislation of certain countries deal with the first two types of introduction, the third has been generally ignored. The same applies to the principle of precaution adopted during the 1992 Rio summit: "*When there is a danger of appreciable reduction or loss of biological diversity, the absence of absolute scientific certainty should not be invoked as a reason for deferring measures that might prevent the danger or attenuate its effects*".

10.1 *International conventions*

There are few international texts dealing with the prevention of introduction of non-indigenous marine and fresh water organisms (Carlton 1989). Article 196 of the Law of the Sea Convention and resolutions I to IV (Third United Nations Conference on the Law of the Sea, eleventh session, 1982, Montego Bay) stipulate that "*States shall take all measures necessary to prevent, reduce and control ... the intentional or accidental introduction of species, alien or new*[2], *to a particular part of the marine environment, which*

[2] The term new species refers here to the GMOs (genetically modified organisms)

may cause significant and harmful changes thereto". Unfortunately, this convention is still not in force (De Klemm 1994; Knoepffler 1994). The Biodiversity Convention (1992 Rio Convention) requires the contracting parties "*to prevent the introduction of, control or eradicate those alien species which threaten ecosystems, habitats and species*"; but it adds "*as far as possible and appropriate*", which considerably limits its scope. Other texts might be cited: (i) the Convention on the Conservation of Migratory Species of Wild Animals (1979 Bonn Convention); (ii) the Revised Code of Practice to reduce the risks of adverse effects arising from introductions and transfer of marine species , adopted in 1990 by the ICES (International Council for the Exploration of the Sea[3]; Wallentinus, 1994); (iii) recommendation no. R(84)14 of the Council of Ministers of the member states concerning the introduction of non-indigenous species, adopted by the Council of Ministers of the Council of Europe (1984); (iv) the EIFAC Code of Practice of the European Inland Fisheries Advisory Commission (1984); (v) the IUCN position statement on translocation of living organisms, adopted by the International Union for the Conservation of Nature and its Resources (1987). In 1969, the IUCN was in fact already concerned at the introduction of exotic plants and animals, and published in its Bulletin a series of Recommendations for respective governments.

All these texts are in fact no more than recommmendations. In addition, only certain vectors or certain types of introduction are covered; the GMOs (genetically modified organisms) are for example not mentioned in the current version of the ICES Code of Practice. Finally, no authority is designated to assess the risks, which leaves the door wide open to whatever interpretation the country concerned considers (rightly or wrongly) to best suit its interests.

The International Plant Protection Convention of 1951, although in principle only dealing with domestic species and not targeting the introduction of species as such, could be used for this purpose. It in fact requires the contracting parties to deliver phytosanitary certificates for the exportation of plants, and authorizes governments to ban the entry of any plant into its territory for phytosanitary reasons. Marine algae are plants!!

Within the European Union, the legislation is equally imprecise. Council Directive 77/93 of 21 December 1976, amended by Council Directive 91/683 of 19 December 1991, concerns protection measures against the introduction into a member state of organisms harmful to plants or vegetal products. The aim is the protection of cultures against certain pests or parasites, rather than general protection of the flora; the list of harmful species, whose introduction is subject to controls, includes not a single

[3] The International Council for the Exploration of the Sea (ICES) groups the countries of the North Atlantic, north of a line from Gibraltar to Cap Hatteras (USA).

marine plant (Knoepffler 1994). Council Directive of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora (referred to as the Habitat Directive) is very unspecific on the issue (article 22b): "*Member states ensure that the deliberate introduction into the wild of any species which is not native to their territory is regulated so as not to prejudice natural habitats within their natural range or the wild native fauna and flora and, if they consider it necessary, prohibit such introduction*". Non-deliberate introductions, that are by far the most numerous (100% of marine macrophyte species in the Mediterranean; Table I), are not even mentioned; in addition, this directive appears to ignore the fact that a species, once introduced, is no respecter of the frontiers of the member states; assessment of the potential danger that an introduction represents cannot therefore be left to the one state that is contemplating deliberate introduction. European Directive 91/67 of 28 January 1991 on "*the conditions of health policing with regard to the sale of animals and products from aquaculture*" does not impose any constraints beyond those of pathology for the transfer of animals from one aquaculture area to another; (pathologically) healthy aquacultured products can therefore be transferred, without any decontamination or quarantine procedure, and therefore with the fauna and flora that accompany them, from the Canaries to Denmark or from Ireland to the Aegean, as long as the original area is free from disease; even then, the directive only concerns diseases that are likely to affect fish or shellfish farming species (Boudouresque and Ribera 1994). What is more, the agreement of the recipient country is not required; according to Wallentinus (1994), this Directive is in contradiction with the recommendations of the Code of Practice of the ICES. The two European directives quoted here should both be revised (Briand 1994). Only the introduction of genetically modified organisms (GMOs) is subject to strict rules (Nolan 1994).

10.2 *National legislation*

A few countries (Australia, New Zealand, USA, Canada, Germany, Great Britain and Switzerland) have adopted legislation of varying degrees of strictness and effectiveness to limit species introductions. Nevertheless, the risk of decision loops (where the applying authority is not really distinct from the permission-granting authority) is rarely excluded. In addition, virtually none of the legislative texts make provision for controls (once authorization has been granted) or for rapid remedial measures (while there is still time) in the event of escape.

In the USA, the Non indigenous Aquatic Nuisance Prevention and Control Act of 1990 deals in particular with ballast water. It is true that this law was introduced following economically disastrous species introductions (see Sections 3.2 and 8.5). A congressional commission of inquiry nonetheless concluded that: "*The laws and regulations designed to control* *the introduction of foreign species are inadequate and inconsistent. Federal and state governments sometimes have conflicting policies even for adjacent parcels of land*" (Windle *in* Kiernan 1993). The Federal government has, for example, no means of opposing the introduction of a species which does not appear on a list of reputedly "dangerous" species; the term is generally understood here to mean first degree danger (e.g. species that are venomous for man). With regard to environmental or economic danger, experience has proved that this cannot easily be inferred from a species' behaviour in its native region.

In Great Britain, the Wildlife and Countryside Act of 1981 forbids (without prior permission) the release of any animal that is non-resident or not a regular visitor (migratory species), including the species that have already been introduced. This law also applies to plants that are included in a pre-established list, which includes a few marine algae (De Klemm 1994).

In Germany, the Law for the Protection of Nature (1976) is more specific. It forbids (without prior authorization) the release or plantation in the wild of any non-native animal or plant. The principle of precaution is specifically mentioned in the text of this law: authorization is not granted if it is impossible to exclude the risk that the introduced species may alter the native species, endanger the survival or distribution of native species or populations of native species (De Klemm 1994).

In Switzerland, the introduction of non-native species, sub-species and races of animals and plants is subject to the authorization of the federal authorities (Law for the Protection of Nature of 1966). Authorization is also required for introduction into a canton where the species does not occur, even if it is native to one or several other Swiss cantons (De Klemm 1994).

In New Zealand and Australia, the legislation is much tighter, although it varies (in Australia) from state to state. In New Zealand, any importation of an exotic animal is forbidden. In Australia, even the quantity of holy water that can be brought back by pilgrims is restricted. This legislation generally goes further than the examples cited above, since it attempts to deal with the possibility of the escape (accidental release) or deliberate release of animals that were not intended for introduction. For the whole of Australia, the Australian National Parks and Wildlife Service controls the importation of all living organisms, under the terms of the Wildlife Protection (Regulation of Exports and Imports) Act of 1982 (Pollard and Hutchings 1990). In the Northern Territories, furthermore, the importation, sale and transportation of living exotic mammals, birds, amphibians and reptiles requires authorization; the release (accidental or deliberate) of an exotic animal is an offence. The Australian Quarantine Inspection Service imposes voluntary guidelines on ships entering Australian ports and deballasting (Hutchings 1992). Finally, in Western Australia, a whole range of imported goods are subject to inspection to ensure that they do not include any seeds of exotic species (De Klemm

1994). Despite this legislation, 20 to 30 species of plant continue to be naturalized each year in Australia (Groves 1993).

In France, the legislation and current practices are particularly lax. It is probably no coincidence that 51% of marine macrophytes introduced into Europe were first introduced in France (Fig. 9). Subsequently, most of them of course spread beyond French jurisdiction. A major example is *Sargassum muticum* that is today found from Portugal to Norway (Rueness 1989). The major role that France plays in species introductions can be attributed to the following reasons:

(i) the virtual absence of any specific legislation: nothing specific with regard to the authorization of culture in closed environment (scientific research, aquariology), quarantine and decontamination measures for avoiding accidental introductions, and above all controls to ensure respect of the norms. Even for deliberate introductions, there is total legislative confusion. The only legislative text that deals with the introduction of species is the Law for the Protection of Nature of 10 July 1976; Articles 3 and 4 of the section on the preservation of the biological patrimony stipulates that it is illegal to transport certain species; Article 5 specifies that authorization is required for the introduction of non-cultivated plants; but here again, it concerns plants that appear on a pre-established list that includes no marine plants (Knoepffler 1994).

(ii) Another reason for the high rate of introductions in France is the fact that mainland France is not separated by real frontiers from is overseas territories (Martinique, Guadeloupe, Réunion, Tahiti, etc), that are situated in biogeographical areas that are very different from those of the European seas; this facilitates the entry of exotic species into the country.

The spread of *Caulerpa taxifolia* in the Mediterranean has resulted in a ban on the possession, sale or transportation of the plant in France (Arreté of 4 March 1993) and in Spain (Catalonia, Decree 257/1992 of 26 October 1992; Valence, Decree 89/1994 of 10 May 1994). These measures have however been taken too late, since they were introduced after the species had escaped from aquariums, and do too little, since they do not solve the much more general problem of species introduction (Boudouresque and Ribera 1994). Furthermore, they do not appear to be fully enforced: Knoepffler (1994) cites tha case of an aquarium in Hérault (France) which continues to display *C. taxifolia*.

Paradoxically, although in France no text of law regulates the introduction of species in the marine environment, there are a few texts that could apply to the suppression of introductions that have a harmful impact. The decree of 9 January 1852 on marine pollution (article 6–13) punishes with a fine of up 159,000 francs anyone who "*throws, pours or allows to flow directly or indirectly into the sea ... substances or organisms that are* *harmful for the conservation or reproduction of marine mammals, crustaceans, shellfish, molluscs or plants, or are likely to render them unsuitable for human consumption*". This law was not repealed by the Law on Water (Law 92/3 of 3 January 1992), since article 22 of the Law on Water makes explicit reference to article 6 of the decree of 1852 (Knoepffler 1994).

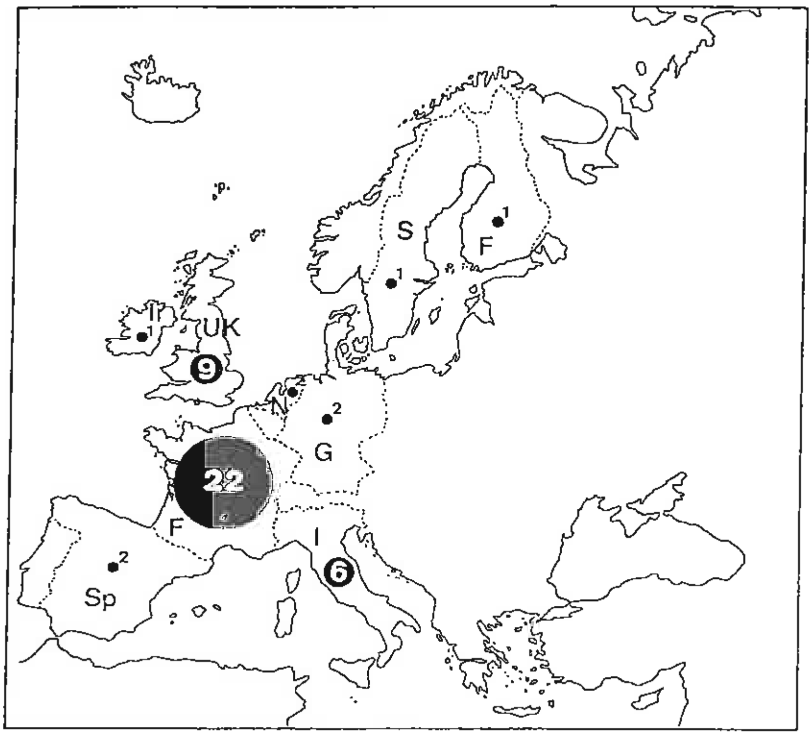

Fig. 9: Distribution by country of the number of first reports of introduced marine macroalgae in Northern and Western Europe (the appearance in a country of an introduced species previously reported in another European country is not included). The diameter of the black circles is in proportion to the number of introduced species.

In all, the current legislation is utterly inadequate in the face of contemporary practices in aquariology, scientific research and aquaculture, which are the main sources of species introduction in the marine environment (Ashton and Mitchell 1989; Briand 1994). Several examples offer good illustration of the irreponsibility that is shown in this field. The painful impression that emerges is that we are playing at sorcerer's apprentices: we introduce species first, see what happens and then think about it afterwards. In the circumstances, it is easy to appreciate the perplexity of the European Union, faced simultaneously with requests for financing for, on the one hand, the introduction of *Undaria pinnatifida* and on the other, for combating *Caulerpa taxifolia* (Nolan 1994). It is of course impossible to predict with certainty the impact of the introduction of a species into a new environment (Boalch 1994); nevertheless, there must be a happy medium between specious, interest-serving "scientific" studies (when there are any studies at all) and zero risk.

10.3 *A few recommendations*

Various international working groups have examined the question of the introduction of species, including the Working group on Introduction and Transfer of Marine Organisms of the ICES with regard to aquaculture (Grizel 1994; Wallentinus 1994). Their very realistic recommendations should serve as a basis for legislation. The example of the Japanese clam *Ruditapes philippinarum*, which was introduced into Europe in accordance with the requirements of the basic veterinary health rules (histological controls, quarantaine, production of a first F1 generation in the laboratory before proceeding to open sea culture), and which has not resulted in the introduction of commensal species or parasites, shows that introduction can be properly managed (Grizel 1994). The following general principles might serve as a basis for future legislation:

(i) The importation of living exotic species, originating in other countries, for the purposes of aquaculture experimentation, aquariology or scientific research, should be subject to authorization.

(ii) Deliberate introductions (aquaculture *in situ* or restocking) should be subject to authorization by a national authority, after consultation with a national Scientific Committee, then an international Scientific Committee (e.g. at European Union level). It should be the responsibility of the applicant to demonstrate the economic necessity of the proposed introduction, the absence of any alternative using the indigenous genetic patrimony, to assess any negative impact (economic, environmental and social) that may result and to provide cost and profit forecasts. Since the introduction of a species is irreversible, the time scale for estimation of the profit-cost forecasts should be at least twenty years. The scientific committees should have at their disposal the means to order expert second opinions, if required.

(iii) The entire coastline of the European Union covers a wide variety of biogeographical provinces. This is also the case within certain member countries: Spain (e.g. the Canaries and Balearics), France (Atlantic and Mediterranean), Italy (Sardinia and Northern Adriatic). Movements of living material between these provinces (aquaculture, aquariology, fishing bait) are therefore likely to involve the risk of introduction. Biogeographical provinces should be delimited, and transportation of biological material between them should be subject to authorization, control, decontamination and/or quarantine, and these should be defined (Ribera 1994).

(iv) It is imperative to establish specific methods of decontamination and/or quarantine for species that it has been decided to introduce and for aquacultural products that are introduced or transported from one region to another. These decontamination norms should be based on proper scientific research, and should not be carried out solely for health control purposes.

(v) Ballast water from ships coming into contact with the European Union should be properly treated (on board or in port facilities). Deballasting at sea, which has been authorized in the United States under the Non-indigenous Aquatic Nuisance Act, should only be envisaged on a temporary basis, since it would appear to be better suited to the specific case of the North American Great Lakes (fresh water) than to the European coast, and is only partly effective (Durnil *et al.* 1990). In general, the transportation of ballast water from one ocean to another should progressively be stopped, within the terms of international agreements.

(vi) The conditions under which exotic species are handled in aquariums (public or private) and scientific laboratories should be subject to strict regulations: closed circuit water supply systems, decontamination of waste water, etc.

(vii) Proper controls should be implemented in order to ensure that once authorizations are granted, the proper procedures are in fact respected.

In any case, legislation that is relatively flexible, but which is enforced intelligently by people who are properly informed of the issues is always preferable to legislation that is too rigid and poorly understood, and therefore not properly enforced. It is therefore an essential complement to any legislative measures that the public should be properly informed and made aware of the risks and of what is at stake in the matter of species introduction. Since 1992, visitors to Australia receive on arrival a brochure explaining the main Australian quarantine regulations, published in 49 languages. In the Mediterranean, since 1992, public awareness campaigns on the invasion of *Caulerpa taxifolia* have been carried out in Spain, Italy and France; posters and brochures have been distributed that explain the problem and ask the public to help with the early detection of new patches of *C. taxifolia*.

Finally, while the existing national and international legislation is at present too sketchy – when there is any – to hope to slow down the rate of introduction of species, the responsibility of states from which introductions to other states originated is clearly established in several international conventions that they have signed, and in general in international law. The Stockholm Declaration (1972) stipulates, for example, that it is the responsibility of states to ensure that the activities that come under their jurisdiction or their control do not cause damage to the environment of other states, or areas situated beyond their national jurisdiction (De Klemm 1994). It is not inconceivable, therefore, that should nuisances be caused in another country by introduced species, the case might be heard before an international court (tribunal or international court of justice) (Knoepffler 1994). This is another reason why the European countries should urgently draw up legislation to limit introductions of species, in particular accidental introductions, and to choose the species that they wish to introduce deliberately on the basis of proper understanding.

11. CONCLUSIONS

In the last century, the introduction of exotic species was systematically sought after. In France, for example, there was a national acclimatization company (Société Nationale d'Acclimatation) whose purpose was to acclimatize in Europe species of economic – but possibly also aesthetic – interest. Lamiral (1863) reported, for example, an (unsuccessful) attempt to acclimatize sponges from Syria in what was to become a hundred years later the Parc National de Port-Cros (Var, France). From the reports written at the time, it is clear that these activities were to some extent a game: the prize was the success of an operation of rearing or acclimatization. Worrying about the impact of these introductions on the native species and ecosystems, or the preservation of the natural environment, was clearly not among the cultural priorities of the age (Boudouresque 1994; Briand 1994).

Today, the increase in the rate of introduction of species, and the long-term danger of worldwide standardization of communities for a given latitude or biotope, represent a major problem for the scientific community (Sindermann 1991; Hedgpeth 1993). In addition, Vermeij (1993) considers that species extinctions (meaning here marine animal species) in the northwestern Atlantic may be partly responsible for the subsequent success of human-introduced species in subtidal and open-coast intertidal habitats.

The increasing rate of species introductions is linked, directly or indirectly, to economic interests. These may be in conflict with other economic interests (introduction of diseases or parasites, competition with commercially exploited indigenous species, nuisances, other uses of coastal areas), and also with ethical values that are difficult to evaluate in economic terms (Boudouresque 1994). The introduction of a species is a definitive act that we impose on succeeding generations for the centuries to come, whereas the motives that justified it may be based on the desire for very short-term and hypothetical benefits.

It is certainly not possible to put a complete halt to species introductions. We cannot, for example, clean the hull of every ship before allowing it to enter a port. In any case, it is perhaps not even desirable. Would we wish, for instance, to stop the flux of Indo-Pacific species through the Suez Canal? Economic imperatives sometimes even make introductions necessary. Furthermore, the current development of fish and shellfish farming will produce a dramatic increase in the range of species that are cultivated, and consequently in the number of introductions. Nevertheless, it would appear that the introductions that are deliberate and really necessary only represent a small proportion of the total, in comparison with accidental introductions. Most accidental introductions could have been avoided through relatively simple and inexpensive measures (certainly less costly than the nuisances generated by certain introduced species). Since the eradication of a species once it has been introduced is very difficult, if not impossible, and is in any case very expensive, it is obvious that a strategy of prevention should be the priority (Dorchada *et al.* 1990).

International law with regard to species introductions is generally restricted to declarations of intent, since governments hesitate to sign texts of law that are really binding. French law, which would appear to be one of the most indulgent among the industrialized countries, presents certain inexplicable loopholes (Knoepffler 1994). In addition, better knowledge of the biological aspects of the phenomenon is required if the legislation is to be given a proper scientific basis (quarantaine procedures, decontamination, etc.). Introductions of species raise the question of the responsibility of states and of the limits of that responsibility. Once a species has been introduced, whether deliberately or accidentally, it is no respecter of administrative or political frontiers.

Consequently, providing proper legislation (in most cases on a supranational scale) and ensuring its strict enforcement, would be a means by which the present rate of species introduction could be, if not halted completely, at least substantially slowed down. Similarly, general public awareness of the dangers of transfers of species, added to better scientific knowledge of the phenomenon, would make it possible, *a posteriori*, to control it (Ribera in press).

Studies on the impact in marine environment of introduced species on native species and communities are still sparse. Their conclusions differ: zero or slight impact (Simberloff 1981), displacement of native species occupying a close ecological niche (Spanier and Galil 1991), decrease in biodiversity (Cognetti and Curini-Galletti 1993), or, on the contrary, enhancement of biodiversity in the specific case of the Eastern Mediterranean and the Lessepsian immigrants (Por 1990), modification of the functioning of ecosystems or development of new ecosystems based on the introduced species, and finally alteration of landscapes. These studies (or forecasts) tell us little in fact about the impact that the current increase in the rate of introductions might have. It is in fact a change of scale that we are likely to have to face: what will happen if the introduced species become the majority and overwhelm the indigenous species, to build new communities whose composition, structure and functioning we are incapable of predicting? Carlton and Geller (1993) talk of ecological roulette !!

If nothing is done to reverse the trend that is at present taking shape, species introductions may turn out to be one of the major ecological problems of the twenty-first century. In contrast to other problems, such as pollution or forest fires, that we are beginning to learn how to control (with varying degrees of success) and which are reversible in the short or medium term, species introductions seem, in the present state of our knowledge and technical know-how, to be almost always irreversible (Windle *in* Kiernan 1993; Boudouresque 1994). Furthermore, even if we wished to, we could not simply call a halt and freeze the situation as it is now, as we could for coastal management. Finally, no sanctuary is safe from introductions of species: natural reserves, regional parks, national parks, natural monuments and the patrimony UNESCO may one day protect ecosystems that are dominated by introduced species whose characteristics are impossible to predict.

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