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Review

Biological invasions as a component of global change in stressed marine ecosystems

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Abstract

Biological invasions in marine environment are the lesser known aspect of global change. However, recent events which occurred in the Mediterranean Sea demonstrate that they represent a serious ecological and economical menace leading to biodiversity loss, ecosystem unbalancing, fishery and tourism impairment. In this paper we review marine bioinvasions using examples taken from the Mediterranean/Black Sea region. Particular attention is given to the environmental status of the receiving area as a fundamental prerequisite for the colonisation success of alien species. The spread of the tropical algae belonging to the genus *Caulerpa* in the northwestern basin of the Mediterranean Sea has been facilitated by pre-existing conditions of instability of the *Posidonia oceanica* endemic ecosystem in relation to stress of both natural and anthropogenic origin. Human interventions caused long-term modification in the Black Sea environment, preparing a fertile ground for mass bioinvasion of aquatic nuisance species which, in some cases, altered the original equilibrium of the entire basin. Finally, the Venice lagoon is presented as the third example of an environment subjected to high propagule pressure and anthropogenic forcing and bearing the higher "diversity" of non-indigenous species compared to the other Mediterranean lagoons. Stressed environments are easily colonised by alien species; understanding the links between human and natural disturbance and massive development of non-indigenous species will help prevent marine bioinvasions, that are already favoured by global oceanic trade.

Keywords: Non-indigenous species; Disturbed ecosystems; Mediterranean Sea; Black Sea; Venice Lagoon; *Caulerpa* spp.

1. Foreword

Since the Rio Convention, global change and biodiversity are two central concerns in both political and scientific debates. In addition to climatic changes, the global environment is undergoing modifications brought about by human's increasing use of the environment, and biodiversity issues are at stake, not only because of the extinction of endangered species, but because of new equilibria in the communities resulting from human-induced changes.

Bioinvasions, that is the colonisation of species native to other areas of the planet in new locations, have been recognised as an expression of global change (Vitousek et al., 1996; Bright, 1999) as they are altering the biodiversity of nearly all the environments (Robinson and Dickerson, 1987; Soulé, 1990; Hobbs and Mooney, 1998; Levine, 2000) and are often related to climatic and other changes in the globe (Bianchi and Morri, 1993; Bianchi, 1997; Dukes and Mooney, 1999; Duarte et al., 1999).

In recent years many reviews have been published (Carlton, 1989; Eno, 1996; Carlton, 1999; Ruiz et al., 2000a; Occhipinti Ambrogi, 2001), highlighting the ongoing modifications in the marine environment in many regions of the world. Our focus here will be the analysis of the relationship between invasions by alien species and the degree of overall stress experienced by invaded marine systems, often caused by human intervention.

Examples will be taken from the Mediterranean Sea, owing both to the authors' direct involvement in marine biological research in this region and to the relative scarcity of published information on bioinvasions in the area.

2. Introduction

In marine environments, biological invasions mediated by humans through navigation are known, or at

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least supposed, since ancient times, but the rate of dispersal has been raising dramatically since the introduction of modern ships and due to the use of large volumes of sea water for ballasting (Carlton, 1985; Williams et al., 1988; Carlton and Geller, 1993; Gollasch et al., 1999; Harvey et al., 1999; Gollasch et al., 2000; Ruiz et al., 2000b). The second cause of transfer of marine species from different areas of the world is considered to be aquaculture, through which far-reaching exchanges have also increased (Hiram and Li, 1981; Cesari and Pellizzato, 1985; Zibrowius and Thorp, 1989; Grizel and Héral, 1991; Sauriau, 1991; Mazzola, 1992). The lack of information concerning the putative transfers that might have occurred in the past without being demonstrated have lead to the definition of cryptogenic species, whose importance has been stressed by Carlton (1996) and in many cases is also imputable to lack of taxonomic expertise (Boero et al., 1997).

The notion of increasing transfer of species from other biogeographic areas into a given sea or ocean can be expressed as increased propagule pressure (Ruiz et al., 2000a) and can be considered true also for the Mediterranean Sea, even if circumstantial evidence is lacking from a quantitative point of view.

The discussion of possible effects of invasions on the native biota and on the equilibria of the communities is not the primary scope of this paper. It has to be pointed out, however, that at least in some areas, exotic species have been additions rather than displacements or even extinctions of native species (Reise et al., 1999).

Bioinvasion studies are mostly focussed on properties of the species that have successfully established in non-native environments (see Kolar and Lodge, 2001). The common properties of ecosystems affected by such species have been investigated in fewer studies, although invasibility of stressed ecosystems has been advocated in many papers, since Elton's classicbook (Elton, 1958).

Under this assumption, we will concentrate on the influence of human-induced environmental stress over the probability of success in establishing populations of alien species.

The ancient historical navigation in the Mediterranean Sea and the relative scarcity of detailed information on the flora and fauna for some areas of this sea makes it impossible to establish lists of cryptogenic species that might be revealled to be too large and uncertain to help in the analysis. Nor will very ancient records of introductions be used in this review, instead we will concentrate on the reports of invasions which have occurred in the last 40 years, following the same criteria used by the International Commission for the Scientific Exploration of the Mediterranean-CIESM (http://www.ciesm.org) for the preparation of the Atlas of exotic species in the Mediterranean. Some reviews of introduced species in the Mediterranean have been published (Zibrowius, 1991; Boudouresque, 1994; Galil, 2000) and the current effort in the community of marine biologists is directed towards the establishment of lists of non-indigenous species for selected groups of animals and plants (Galil and Zenetos, 2002; Gomoiu et al., 2002; Occhipinti Ambrogi, 2002; CIESM: atlas of exotic species: http://www.ciesm.org; ERNAIS: European network on aquatic invasive species http://www.zin.ru/projects/invasions/).

Selected environments have been studied in detail, among them the Israeli coast in connection with the so-called Lessepsian migration (Por, 1978; Galil et al., 1990; Tom and Galil, 1991), the lagoon complexes in southern France (Verlaque, 2001) in connection with oyster culture, and the Northern Adriatic lagoons (Occhipinti Ambrogi, 2000a), subjected both to large ship traffic and to extensive mariculture. The Black Sea has experienced faunistic "revolutions" with deep consequences on the ecosystem (Shiganova et al., 2001).

The notion of stress (or disturbance) of the environment, and particularly for marine ecosystems, has been used extensively in the literature (Lewin, 1983; Suchanek, 1994; Leppäkoski and Mihnea, 1996; Bianchi et al., 1998) and will be used in this review in a broad sense, assuming various types of disturbance both natural and man-induced.

Humans influence marine ecosystems in many ways: through organic enrichment, pollution, physical habitat alterations, and selective harm to plant and animal populations (McIntyre, 1999; Bianchi and Morri, 2000).

Natural stress has been advocated for estuarine environments and for other habitats with variable salinity that most commonly exhibit lower diversity and abrupt changes in dominant species (Marques et al., 1993; Cognetti and Maltagliati, 2000). This review will take into account the general situation of the Mediterranean Sea with respect to known invasions and will describe three examples of successful invasions in connection with environmental stress of varying type and intensity. The first case is concerned with the spread of two species of algae (*Caulerpa taxifolia* and *C. racemosa*) along the Western Mediterranean coasts, where the native angiosperm *Posidonia oceanica* undergoes a rapid decline. The second case study involves the impressive series of records of massive development of recently introduced species in the fauna of the Black Sea, an enclosed basin, with peculiar physiographic features. The third example is the recent history of introductions in the Lagoon of Venice which offers the opportunity of long-term comparisons of community changes.

3. The Mediterranean fauna and flora and the incidence of invasive species in recent years

The Mediterranean and the Black Sea are ecologically diverse, representing about 6% of the total world marine species, even though the surface of the Mediterranean is only 0.8% of the total surface of the oceans. An estimate of 8500 species of macroscopic marine organisms has been made for the Mediterranean (7200 metazoans and 1300 macrophytes). This faunal richness is also accompanied by a high level of endemic species (more than 25% in total). Areas of lower diversity are located in the Eastern Basin, in the Black Sea and in the Northern Adriatic (Fredj et al., 1992; Bianchi and Morri, 2000).

The list of invasive species established by Zibrowius (1991) comprises of more than 160 species and many others have been added since then owing to occasional observations, even though a systematic survey has not yet been planned.

Ribera and Boudouresque (1995) have reviewed the introductions of macrophytes. Boudouresque and Verlaque (2002) list 85 species meeting the criteria of being declared 'introduced'. They discuss the proportion of introduced macrophyte species that become invasive and conclude that nine species out of 85 are considered invasive, i.e. they play a conspicuous role in the recipient ecosystem, becoming the dominant species or taking the place of keystone species. In some cases they are economically harmful.

A peculiarity of the Mediterranean marine fauna is its colonisation by Indian Ocean species, the so-called Lessepsian migrants (Por, 1978), which have been entering through the Suez canal since its completion in 1869. It has been calculated that these species (over 300) now constitute nearly 5% of the global Mediterranean fauna and 13% of the species found in the southeastern Mediterranean, and this invasion is continuing (Galil, 2000).

The reduced biodiversity in the Oriental basin and the Aegean Sea has been explained by the climatic crises that have repeatedly occurred in geological times (Por and Dimentman, 1985), and have caused many niches to empty, leaving a place for the invasion of opportunistic allochtonous species (Giaccone and Di Martino, 1997).

Besides Lessepsian invasions, the main vectors for invasions in the Mediterranean are aquaculture (especially developed in the lagoons along the French coastline and the Italian Adriatic) and unintended transport (e.g. via ballast water). The oyster transfer is considered the number one vector of macroalgae introduction in the Mediterranean Sea (Verlaque, 2001); this is probably also true for many animals. It is not easy to discriminate among different vectors, since specific investigations have not always been performed even in the case of the most remarkable invasions. In the case of *C. taxifolia* (discussed below) the introduction was most likely started by the discharge from aquarium tanks used for decorative purposes. *Rapana venosa* was first introduced in the Black Sea (the vector remains uncertain) and was secondarily transferred to the Adriatic and eventually to other seas, probably via ship traffic (for detailed information on *R. venosa* see Mann et al., 2002).

4. The occurrence of *Caulerpa* spp. is taking advantage from the decline of *P. oceanica*

Two species of tropical algae are currently colonising the coasts of the Mediterranean: *C. racemosa*, an immigrant from the Red Sea, and *C. taxifolia*, accidentally introduced by aquariologists in 1984 (Jousson et al., 1998). The ecological and economic threats posed by these species (especially *C. taxifolia*) encouraged scientists to organise international campaigns of public awareness, research and prevention in Monaco, France, Italy, Spain, Croatia and Tunisia, the most colonised countries by these NIS (see: www.com.univ-mrs.fr/gis-posi/ and www.caulerpa.org).

The same invasive strain of *C. taxifolia* (different from the tropical populations in its original area) has also been found on the Californian coast, raising considerable alarm (Jousson et al., 2000).

Caulerpa taxifolia and *C. racemosa* are outcompeting the endemic Mediterranean seagrass *P. oceanica* (de Villele and Verlaque, 1995; Ceccherelli and Cinelli, 1998) and are threatening macroalgal diversity (Ferrer et al., 1997; Piazzi et al., 2001). It must be underlined that *P. oceanica* supports a highly productive and very diverse community, considered as the climax for soft substrata of the Mediterranean infralittoral zone (Pérès and Picard, 1964), and that its conservation is of primary importance to the ecosystem's stability (Moreno et al., 2001).

In this section of the paper we review some features of the invasion, suggesting that the success of these two *Caulerpa* species is favoured not only by the high ecological fitness of the invaders (Meinesz and Hesse, 1991; Meinesz et al., 1993; Gacia et al., 1996; Delgado et al., 1996) but also by the characteristics of the receiving environment.

By the end of 2000, *C. taxifolia* has colonised 131 km^2 of bottom areas in 103 localities along 191 km of coastline in six countries and is actively expanding (Meinesz et al., 2001). *Caulerpa racemosa* has expanded in more countries (Verlaque et al., 2000) but has not been surveyed in a coordinated fashion.

Caulerpa invasion appears to be successful when seagrass meadows are already experiencing a decline. Ceccherelli and Cinelli (1999a) and Ceccherelli et al. (2000) found that very dense *P. oceanica* meadows are able to confine *C. taxifolia* and *C. racemosa* to their margins, therefore, healthy *P. oceanica* could be considered as a natural barrier to colonisation, being able to contrast the invaders by a shading effect. Therefore, the causes of tropical seaweeds invasion of the Mediterranean Sea should be researched also in the conservation status of *P. oceanica* meadows.

Posidonia oceanica regression in the Mediterranean is a known problem, faced by the scientific community well before the introduction of *Caulerpa* spp. (Pérès and

Picard, 1975). There are various causes leading to the decline of this important ecosystem endemic of the Mediterranean Sea, directly or indirectly related with the increasing anthropogenic pressure that the coastal zone of the Mediterranean has been experiencing. Direct human impact on the *P. oceanica* ecosystem are represented by wastewater discharges. Pergent et al. (1999) observed a strongly localised impact of aquaculture facilities on *Posidonia* beds: meadows are absent beneath fish farms and bear evident signals of stress (reduced shoot density) in the surrounding areas. Wastewater discharge alters the water column increasing turbidity and enriches the substratum with organic matter and nutrients. Chisholm et al. (1995) found that areas of the sea bed where *P. oceanica* has been substituted by *C. taxifolia* are characterised by sediment with high esoenzyme activities, NH_4^+ concentrations and production rates, but with a very low ability to transform organic nitrogen into NH_4^+ relative to the quantity of organic matter available. This unbalanced nitrogen recycling, together with high phosphate concentration (typical of sediment polluted by urban wastewater), appears as a key factor advantaging *C. taxifolia* when in competition with *P. oceanica*. Moreover, the authors suggest that *C. taxifolia* success may be due to its ability to produce subterranean rhizoids able to extract organic and inorganic nutrients from sediments and bearing endocellular bacterial that facilitate removal of hydrogen sulphide from polluted sediments. Competition for nutrients between *C. taxifolia* and the seagrass *Cymodocea nodosa* has been investigated by Ceccherelli and Cinelli (1997): nutrients addition experiments demonstrated that the alga is favoured by high nutrients loads in the sediment, while the seagrass is not.

Natural seagrass cover of the Mediterranean sea bottom has also been depleted by bottom trawling and anchoring (Sanchez-Jerez and Ramos Espla, 1996). Eradication by fishing nets and anchors had a dual role in the fast spreading of *Caulerpa* species into the Mediterranean; they ploughed the sea-bottom depleting the native seagrass meadows and prepared the ground for an easier spreading of *Caulerpa*, while simultaneously helping dissemination of the exotic algae by fragmentation of the thallus (Ceccherelli and Cinelli, 1999b; Relini et al., 2000).

Taking the above, eutrophic polluted waters and general human impact on the coastal zone played a leading role in lowering competitive ability of native seagrasses, permitting the invader to dominate in the environment. This could explain the massive, but patchy, distribution of *Caulerpa* spp. along the Mediterranean coasts that frequently occurs in areas containing dead or dying *P. oceanica* beds (Chisholm et al., 1997). Experimental results on the two *Caulerpa* species confirm that their growth increases with density augmentation, suggesting an increase of the invasion; moreover where the two species co-occur, *C. racemosa* would be favoured with regards to the outcome of the competition over *C. taxifolia* (Piazzi and Ceccherelli, 2002).

An indirect cause of regression of *P. oceanica* beds may be the anthropogenic forcing of the marine climate (Duarte et al., 1999): the Mediterranean is experiencing sustained long-term trends of warming in the waters, sea level rise and a clear monotonic decreasing trend in water transparency. Decreasing water transparency in the NW Mediterranean caused a reduction of the deep edges of seagrass meadows, Duarte et al. (1999) estimated its extent in 4 m regression of the meadows deep boundaries in a 20 year period. The decreasing trend in water transparency is the result of centuries of overexploitation of the coastal area. Deforestation for implementing agriculture and urbanisation, has been leading to an increased water run-off with a high load of fine suspended sediment reducing light penetration and photosynthetic efficiency of benthic primary producers. Peirano and Bianchi (1995) quantified the decline of *P. oceanica* in the Ligurian Sea (NW Mediterranean) using curves of disturbance and comparing seagrass cover of defined physiographic units and different types of natural and anthropogenic stress such as: river flow, harbour surface, coastal length of towns, and terrestrial links (roads and railways).

In conclusion, three basic factors acted synergically to promote the invasion of *C. taxifolia* and *C. racemosa* in the Mediterranean: (1) easy dissemination, (2) high environmental fitness and tolerance to pollution, (3) a strongly disturbed receiving environment, which is too fragile to contrast propagule pressure.

5. The Black Sea, an enclosed sea subject to mass development of non-indigenous species

Immigrants that have penetrated the Black Sea in this century include, among others, the hydroids *Blackfordia virginica* and *Bougainvillia megas*, the polychaete *Ficopomatus* (= *Mercierella*) *enigmaticus* and the crab *Rhithropanopeus harrisii* (Zolotarev, 1996). Although the total number of introduced species is not high, some of them have developed mass populations, causing very large changes in the sea's communities. The Black Sea is a semi-enclosed sea, connected to the Mediterranean through the narrow Bosphorous channel and receiving the inflow of large rivers such as the Danube, the Dniper and the Don. Its conditions are naturally very demanding on the biota (the large part of the deep waters are anoxic) and has recently experienced huge changes in water quality caused by human interventions both on the hydraulic regime of the rivers and on the nutrient and pollutant discharge. Long-term modifications to the Black Sea marine environment resulting from human activity have induced significant changes on phytoplankton, zooplankton, zoobenthos and fisheries (Bakan and Buyukgungor, 2000).

The gastropod mollusc *R. thomasiana* (= *venosa*) a native of the Sea of Japan, was first discovered in 1947 in Novorossiysky Bay (Drapkin, 1953) and has settled along the entire coast of the Black Sea and the south rim of the Sea of Azov. It has reached high biomass and has had serious consequences on oyster and mussel beds where it feeds upon bivalves (Zolotarev, 1996). The present distribution of the whelk includes some areas of the Aegean Sea and of the Italian coast.

Mya arenaria, native of the Northern Atlantic, was first detected in 1966 and became very abundant in a short time in the northwestern and western part of the Black Sea and in the Sea of Azov, reaching a peak in 1972. Later, it was affected by a dystrophic crisis that destroyed the entire benthos and it has not fully recovered except in areas near the estuaries. Its relations with the native fauna are not fully understood; it has coexisted with the native *Lentidium* (= *Corbula*) *mediterraneum* in the area of the Danube delta, but was favoured, as was the crab *R. harrisii*, by some pre-existing modification in the native communities (Manoleli, 1979).

Another bivalve of Indo-Pacific fauna, *Scapharca* (= *Anadara*) *inaequivalvis*, was found in the Black Sea in 1968, almost at the same time as in the Adriatic Sea, and has spread to the whole basin, often becoming the dominant species, especially along the Bulgarian sector (Zolotarev, 1996).

The most striking example of an invasion which has had a large influence on the ecosystem functioning of large areas of the Black Sea is that of the planktonic *Mnemiopsis*.

The ctenophore, *Mnemiopsis leidyi*, was accidentally introduced into the Black Sea in the early 1980s, probably with ballast water from NW Atlantic (Vinogradov et al., 1989). It spread north to the Sea of Azov, south to the Sea of Marmara and the Aegean Sea. In 1999 it reached the Caspian where it is currently expanding (Shiganova et al., 2001). In the Black Sea and the Sea of Azov, the mass development of this species, unprecedented in its native areas, lead to a catastrophic decline of zooplankton and of the once flourishing pelagic fisheries (Kideys, 1994). The success of *M. leidyi* has been explained (Shiganova et al., 2001) by the lack of predators, the ability in the competition with pre-existing gelatinous consumers of zooplankton, such as *Aurelia aurita*, and the predation on eggs and larvae of zooplankton-eating fish. The success of this species, and the spectacular consequences on the environment, have been registered so far only within the Black Sea and the Sea of Azov and not in the other areas where it has established. The changes caused by the environmental changes in the organisation of biological communities have favoured the development of *M. leidyi* in the Black Sea, while in the Aegean Sea the introduction of the species has been equally demonstrated in many places. Nowhere have large blooms with negative consequences on zooplankton been observed. Paradoxically, the appearance of yet another invasive species, *Beroe ovata*, a predator of the ctenophore, has led to a recovery of the previous planktonic food chain (Shiganova et al., 2001).

Unlike the cases presented above, the introduction of fish species has most often been deliberate and has apparently not caused large consequences. The recent case of the mullet, *Mugil soiuy*, native to the Amur river estuary and the Sea of Japan, demonstrate that numerous attempts were necessary before the establishment of a successful reproducing population in the Sea of Azov in the early 1980s. A small stock has been exploited along the Turkish coast since the 1990s. The environmental conditions are good to this species whose growth rate exceeds that of the native mullets (Okumus and Bascinar, 1997).

In conclusion, the Black Sea is subject to mass invasion of non-indigenous species that have caused important consequences in the food chain and in the overall ecological properties of the system. This in turn can be linked to the extreme hydrologic and environmental conditions of this enclosed sea.

6. The Lagoon of Venice, conservation and innovation

The Lagoon of Venice has been preserved from filling in historical times by fluvial sediments or by becoming a coastal bay by the continuous intervention of humans. It is therefore little wonder that its biological communities are also the result of man-mediated influences. In particular, the introduction of alien species of animals and plants has been operated by naval traffic (a large petrochemical industry is located on the mainland and is served by an harbour visited by oil tankers) and by aquaculture, both actively performed in enclosed shallow areas of the lagoon and in inland-based facilities.

The stress on the environment is very intense and the hydraulic regime has been changed by the digging of the deep canals necessary for large ships and has in turn influenced the dispersal of pollutants and nutrients inside the lagoon. The industrial, urban and agricultural discharges that are eventually disposed into the lagoon have been increasing and the sediment load and turbidity are influenced by tidal resuspension, digging and erosion of the sand bars.

In comparison with other Mediterranean coastal lagoons, Venice has a large number of species and rather complex biotic interactions, and has long been the subject of many investigations. At least 30 introduced species have been recorded in the Lagoon, many of which have built up large populations and have supplanted native species (Occhipinti Ambrogi, 2000a).

The algae *Undaria pinnatifida*, *Sargassum muticum* and *Antithamnion pectinatum*, whose introduction is likely to be related to the importation of bivalve spats and transplants of cultured oysters, have changed the submerged landscape along many of the lagoon canals. These large algae have been recorded for the first time in the last decade and are now dominating the native species, which are all of a smaller size (Curiel et al., 1999).

The oyster *Crassostrea gigas* and the clam *Tapes philippinarum* have been imported in the lagoon in order to replace two species of bivalves that had undergone severe reductions in population. They are fully acclimated and exploited by fishermen (Cesari and Pellizzato, 1985; Breber, 1992). *Dyspanopeus sayi* had become the most widespread decapod crustacean in the lagoon before the end of the century (Mizzan, 1995), but it is currently declining.

The invasion by the exotic bryozoan *Tricellaria inopinata* has had a profound influence on the community of small sessile invertebrates that colonise all the hard substrata which frequently occur in the Lagoon of Venice: canal banks, piers, piles used for navigation, aquaculture facilities, including overgrowth of mussels and other calcareous organisms. *T. inopinata* has been described as a new species from the Lagoon of Venice (d'Hondt and Occhipinti Ambrogi, 1985), but has most probably been introduced from Japan, where the species complex is originating. From the Adriatic Sea, it has continued to expand to the coasts of the North Sea (Dyrynda et al., 2000; De Blauwe and Faasse, 2001). After its introduction, *T. inopinata* expansion in the entire Lagoon has been very rapid and it has become the dominant species over the many bryozoans already present. After a general decline that has affected all the bryozoan species, *T. inopinata* is still the main species in all the areas of the Lagoon. The differences in species composition between areas with different environmental characteristics, such as freshwater or marine influx, hydrodynamics, organic content, were marked in the years before the arrival of *T. inopinata* (Occhipinti Ambrogi, 1991). They have now reduced and, except in very low salinity, the communities are not distinguishable (Occhipinti Ambrogi, 2000b), revealing a loss of biodiversity.

7. Discussion

The first and most common cause of "natural stress" is to be found in variable salinity environments. Therefore, with consideration to two of the examples chosen for this review (the Black Sea and the Lagoon of Venice) which show substantially lower salinities than the rest of the Mediterranean, we will first discuss the relationship between invasion success and variable salinity.

Wolff (1999) has shown that the percentage of exotic species in waters of low salinity in the Netherlands is larger than in salinity higher than 20 psu. He states that it is likely that brackish waters are poor in species and empty niches can be exploited by immigrants.

The observation about the presence of empty niches leads us to consider other cases where general factors of disturbance had been related with invasion success.

The hypothesis of empty niches favouring the development of large populations of newcomers has been formulated, among others, by Beukema and Dekker (1995) studying *Ensis directus*, a North American razor shell whose extremely high secondary production was equal to that of the whole benthos in sandy exposed subtidal locations in the Dutch Wadden Sea. Also Vaas (1975) considered that the immigrant *Gobius niger*, while competing with *Pomatoschistus minutus*, occupied a different niche from *P. microps*, thus exploiting previously unaffected trophic resources.

Ruiz et al. (2000a) use the "invasion resistance hypothesis" to survey characteristics of recipient environments that prevent or facilitate survival and establishment of non-indigenous species and note a current lack of data to evaluate it, even when variation in invasion success among sites commonly occurs.

Nichols et al. (1990) and Van den Brink et al. (1993) also found that disturbance frequency and magnitude determined the success of invasions. The prediction that, in aquatic systems with high levels of human disturbance, a much wider range of species can invade than in systems with low levels of human disturbance was formulated by Moyle and Light (1996) for freshwater and estuarine fishes of California, together with the other predictions that successful invasions in aquatic systems are most likely to occur when native assemblages of organisms have been temporarily disrupted or depleted.

In the Mediterranean Sea similar observations have been reported by Galil (2000), quoting Chisholm et al. (1995) and Kokak et al. (1999).

According to Smith et al. (1999), the factors that can mediate biological invasions are invasion pressure (that is the number of propagules discharged per unit time and space), post-transport inoculant survival, and intra and interregional variation in susceptibility to invasion. In the case of the Mediterranean Sea, information on the first factor (propagule pressure) is vastly lacking, but the second factor (propagule survival) may also be thought of as the probability of the invader to find a suitable empty niche and the third (susceptibility to invasion) may be interpreted as the difference between stressed (disturbed) and non-stressed ecosystems. Thus, the old dispute about "invasibility" of ecosystems is no longer centred on their diversity or on the number of native species present against the capability of newcomers to cope with the new environment, but enlarges to the overall integrity of the ecosystem itself. The discussion is vast (Sakai et al., 2001), but in our opinion the basic fact is that invaders are favoured in places and times when stress is causing trouble to the existing biota and therefore vacant niches are open for colonisation.

The global change of climatic factors are also of importance when considering such stress on a wide scale. For the Mediterranean, it has been hypothesised that temperature rise could have been the cause of mass mortalities in many areas of France and Italy in the summer of 1999 (Laubier, 2001). Synergism between invaders, overfishing and climate change has been discussed by Harris and Tyrrell (2001).

Conversely, where and when anthropogenic stress is causing vast modifications in the habitat or environmental conditions, including trophic levels, the presence of non-indigenous species can offer the opportunity of increasing the adaptation of the whole biotic community to the new situation. This view has been supported by Leppäkoski et al. (1999) and Olenin and Leppäkoski (1999) describing the structural changes in the communities of the Baltic Sea following salinity and eutrophication changes and the spread of exotic species.

8. Conclusions

In the Mediterranean Sea stress on the marine environment favours the spreading of alien species. Invasions are facilitated either in environments strongly depauperated and subjected to strong pollution and anthropogenic forcing (the Black Sea basin) or by a weakening of a species of fundamental importance in structuring the native ecosystem (e.g. recession of *P. oceanica* meadows facilitating the spread of *Caulerpa* spp.) or in inherently unstable and variable environments subjected to multiple introductions (e.g. the lagoon of Venice). A healthy pristine community represents a natural impediment to bioinvasion; where and when this contrasting force is lacking, the alien species successfully outcompetes native ones; therefore environmental conservation plays a fundamental role in preventing further spreading of non-indigenous species. This would explain why not all areas subjected to same propagule pressure underwent similar invasion rates by non-indigenous species. Fortunately, a robust native ecosystem can successfully fight competing newcomers, thus in the Mediterranean Sea we can identify hot-spots for introductions. The identification and delimitation of these hot-spot areas of introduction represent the first objective to be achieved in order to control bioinvasions.

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