Advances in Oceanography and Limnology
Vol. 1, No. 1, June 2010, 199–218

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Marine alien species as an aspect of global change

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(*Received 6 December 2009; final version received 22 February 2010*)

The transport of organisms across oceans is an anthropogenic agent of global change that has profoundly affected the natural distribution of littoral biota and altered the makeup of biogeographic regions. The homogenization of marine biotas is a phenomenon especially affecting coastal regions and is spearheaded by a suite of opportunistic species at the expense of native species. Climate change may exacerbate the trend: sea surface temperatures, hydrodynamics, pH and carbonate cycles, already show marked fluctuations compared to the past. Alien invasive species are impacted by the change of marine climate in a variety of ways, which are we have just begun to notice, observe and interpret. A conceptual framework has yet to be conceived that links theories on biological introductions and invasions with the physical aspects of global change. Therefore predicting the scale of invasions or their impact on biodiversity is a daunting task. Integration of biological and environmental information systems, niche models, and climate projections would improve management of aquatic ecosystems under the dual threats of biotic invasions and climate change. The recorded spread of alien species and analysis of patterns of invasions may serve as the starting point for searching connections with climate change descriptors. The Mediterranean Sea is home to an exceptionally large number of alien species, resulting from its exceptional history and multiple vectors. For much of the twentieth century alien thermophilic species, which had entered the Mediterranean through the Suez Canal, have been confined to the Levantine Basin. In recent years climate driven hydrographic changes have coincided with a pronounced expansion of alien thermophilic biota to the central and western basins of the Mediterranean. We discuss some changes in emergent functions and services in Mediterranean ecosystems under the combined effect of invasive species and climate changes.

Keywords: bioinvasions; alien species; climate change; Mediterranean Sea

1. Introduction

Biological invasions in world's oceans are not only an academic subject for marine biology specialists, but a growing concern for both nature conservation and economic activities; while the awareness of the general public is being raised by national governments and international agencies. Alien taxa (synonyms: exotic, non-native, non-indigenous, allochthonous) are species, subspecies or lower taxa introduced outside of their natural range (past or present) and outside of their natural dispersal potential. Their presence in the given region is due to intentional or unintentional introduction or care by humans, or they have arrived there without the help of people from an area in which they are alien.

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ISSN 1947–5721 print/ISSN 1947–573X online

DOI: 10.1080/19475721003743876
http://www.informaworld.com

This includes any part, gamete or propagule of such species that might survive and subsequently reproduce [1–4]. Invasive species are those alien taxa that have established large populations, significantly expanding their range, and/or exert substantial negative impact on native biota, economic values, or human health [5]. This paper encompasses different scientific approaches that have been proposed to deal with changes caused by alien species introductions and issues of 'global change'. This latter is mainly perceived as change in the earth's climate, but in fact it is closely interlinked with the evolution of biodiversity of our planet [6,7]. The interactions between the global change in distribution of biota and the global change of habitat conditions, mainly caused by climate warming, are highly complex and will be outlined in the next section of the paper. Bio-invasions processes are very dynamic and their outcome depends not only on human mediated transport, but also on the physical chemical and biological conditions of the receiving environment and hence (in a global perspective) on climate change and its related consequences. Ecological equilibria will evolve and predictions are still rather rough. In Section 3 some approaches are outlined and some of the changes that are already beginning to emerge are quoted. The Mediterranean Sea, for historical, physical and biological reasons, is an area where signals of early alert are visible, and examples from the literature in Section 4 will be used to further document the changes that are rapidly taking place under the combined pressure of alien species and climate change.

2. Climate change and alien species: a framework of possible interactions

Climatic variables are primary drivers of distributions and dynamics of marine communities ([8–10] and References therein). Climate change is affecting the marine systems through warmer temperatures, hydrographical changes, carbon cycle and acidiphication. In the same time human activities, such as shipping, aquaculture, and canal construction, are affecting species distribution worldwide. These changes are expected to have a profound effect on the structure and productivity of marine ecosystems. Though often considered independent of each other, there is a strong likelihood that these two primary drivers of global environmental change interact. Climate change may enhance the ability of certain alien species to invade new regions, while simultaneously eroding the resistance to invasion of native communities by disturbing the dynamic equilibrium maintaining them. Climate change facilitates overcoming historic geographic barriers (e.g. through the opening of new polar routes for navigation due to ice melting). Eventually this will increase the societal and environmental impacts of alien species [11,12].

2.1. *Global warming and shift in distribution of species*

To the extent that dispersal and resource availability allow, species are expected to track the warming climate and shift their distributions towards higher latitudes. Polewards range shifts have been observed in many regions and across different taxa [13]. Records show significant shifts of phytoplankton and zooplankton communities in concert with regional oceanic climate regime shifts [14]. Shifts in marine fish and invertebrate communities have been well documented off western North America and the United Kingdom [10,15]. The distributions of 90 demersal species of exploited and non-exploited North Sea fishes responded to recent increases in sea temperature (+1.05°C), with two-thirds of the species shifting in mean latitude, depth, or both, over 25 years. The shift was marked in particular in short-lived and small sized species [16]. Such shifts augur profound impacts on commercial fisheries. These observations of climate driven range shifts may lead, over time, to alteration of latitudinal distribution and when these are checked by impassable barriers, to species extinctions. The consequences on local species richness are often foreseen as negative, but some recent observations are at variance with this paradigm: so far temperature increase has not led to biodiversity loss in North Sea fish fauna and even has a positive effect on species richness, with the advent of southern species [17]. The introduction of alien species by human-mediated transport is concomitant with range expansion caused by climate change; both agents result on the introduction of species in new habitats and regions, however some important differences have been underlined by Lonhart [18]: vectors and rates of movement are very different, so that man-mediated introductions are local and frequent while climate related expansions occur at large scale and slow rate; alien species often come from geographically disjoint areas, whereas range expansion implies contiguous areas; matching of habitat conditions and ecological characters of species in the latter is by far more difficult and coevolution is less probable. In spite of differences, the response of established invasive species to recent global warming mirrors native species: on the Pacific coast of North America, all nine of the invasive species that have apparently responded to recent global warming moved poleward [19]. The benthic fauna of the Antarctic region has been influenced by the effects of warming climate and ship-mediated introductions on species composition [20]. In particular, the Antarctic fauna is characterised, since late Eocene, by the absence of skeleton-crushing (durophagous) predators. This absence has been interpreted as a consequence of physiological barriers due to cold temperatures established in geological time following studies on palaeontology, biogeography, oceanography, physiology, molecular ecology, and community ecology [21]. Some alien species of predators, such as *Hyas araneus* (L.), and large king crabs, are now re-invading the Antarctica, owing to a warmer climate [19]. They have been probably introduced to Antarctica via the transport of adults on ships' hulls or larvae in ballast water [22,23].

2.2. *Climatic conditions and the success of alien species in their new environment*

Climate change may impact the process of invasion by affecting the sources of alien species, pathways of dispersal, and their establishment in host ecosystems. Of these the last is the most important and relevant constraint, since the influence of climate change can be considered less decisive in generating additional propagule pressure, or to modify patterns and pathways of dispersal as they are defined primarily by human economic and trade activity [24]. After the introduction a given species may remain geographically confined for a period ranging from years to a century, followed by a phase of active population growth and expansion, or it may pass an asymptotic growth phase and disperse very quickly over a large geographic region. Numerous factors may trigger the rapid growth phase, notably natural or human-induced disturbances. Climate change, creating disturbance events, may favour previously quiescent alien species providing more chances to survive, reproduce and compete with native species [25]. Occhipinti-Ambrogi [26], on the basis of the model by Colautti et al. [27], has discussed climate change impact on the transition between different temporal stages of an alien species invasion, pointing out that modified climatic conditions affect the environmental filters between successive stages. In the following points we list five potential consequences of climate change on invasive species development and summarise the relevant key hypotheses, as reviewed by Hellmann et al. [12].

(1) Altered mechanisms of transport and introduction: propagule pressure may be altered by climate-dependent changes in maritime transportation routes [28,29], and in intentional introductions for mariculture, recreation or conservation objectives.
(2) Altered climatic constraints on invasive species: warm stenothermal alien species will be able to spread further if conditions become more similar to their native range, and they will be able to establish persistent populations [30].
(3) Altered distribution of existing alien species: cold-temperature constraints on alien species will be reduced at their higher-latitude or depth range limits. Warm-temperature constraints on alien species will increase at their lower-latitude or depth range limits. Hydrologic constraints on alien species will be altered by changing current patterns and termohaline gradients [31,32]. Many invasive species are fast-growing and responsive to resources and will be favoured by environmental changes that increase disturbance and/or resource availability, which will facilitate their spread.
(4) Altered impact of alien invasive species: the population densities of some invasive species already present in a given area, and thus their impact on native species, will be altered. Per capita or per biomass impacts of some invasive species will be altered through effects on their competitive interactions with native species [33]. Relative impact of some invasive species will increase when the abundance of native species or resources decrease in response to the invader [34].
(5) Altered effectiveness of management strategies for invasive species: since management practices such as eradication and biocontrol are seldom used at sea [35], potential alterations at his stage are less likely to occur than in inland waters.

2.3. *Driving forces act synergetically*

Distribution shifts and range expansion of alien species can be favoured by climate change, but very often rely on continuous or even increasing propagule pressure by human transportation.

Interactions among species introductions, global warming, storm frequency and sea level rise, combining with regional factors such as declining nutrient have been described as the main determinants of drastic changes in the ecosystem of the Wadden Sea. *Spartina anglica* C.E. Hubbard, introduced in 1920 is now expanding after a long time lag, due to earlier warming springs. *Crassostrea gigas* (Thunberg, 1793) was introduced for aquaculture in the belief that it will not reproduce in the wild due to low temperature but is now building extensive reefs. *Crepidula fornicata* (Linnaeus, 1758) had been previously limited by severe winters but is now thriving, as are some ascidians and *Ensis (directus) americanus* (Conrad, 1843). Consequences are seen in food web interactions (less pelagic food web, more macrophytes and algae, more filtration, less predators) and habitat modifications: oysters have replaced mussels as reef builders, *Spartina* has trapped sediments and reinforced banks [36,37].

A notable example from the US regards the European green crab (*Carcinus maenas*) (L., 1758), which was introduced to the mid-Atlantic coast in the early 1800s, and has subsequently spread 1000 km upstream, where the invasion seemingly stalled in the 1960s around Halifax, Nova Scotia, presumably owing to the increased time needed for larval development as water temperature decreases. However, in the 1990s, *C. maenas* populations suddenly expanded farther north into the Canadian Maritimes. Roman [38] demonstrated that the new expansion was driven by a new introduction of *C. maenas* to northern Canada from Europe that possessed distinct haplotypes from the older established population in North America. The actual poleward range extension observed is attributable to numerous factors, among which global warming, increased propagule pressure, and, according to Byers and Pringle [32], the presence of upstream retention zones in tidal environments. The latter authors contend that, once inoculated farther north of Halifax by humans, *C. maenas* could be retained and even expand because of the presence of upstream retention zones throughout the Canadian Maritimes, e.g. the Straight of Canso and the Bras d'Or Lakes. Moreover, once anchored there, these upstream *C. maenas* populations should then flood downstream areas with their propagules and have a great competitive advantage over downstream populations, which they will eventually displace.

3. Are predictions possible?

We face the possibilities that biological invasions will be favoured by climate change and that local assemblages will be altered by global change (bioinvasions + climate). Even without the complexity introduced by changing climatic conditions, forecasting the dynamics of invasions has been considered a daunting task [39]. The high level of uncertainty concerning determinants of invasiveness of species and invasibility of habitats engendered different approaches, including assessment of the biological characters of the most 'invasive' species, the probability of transport (if vectors are known) [40], and the susceptibility of habitats to invasions [41].

Predictions as to how climate change will influence aquatic invasive species are hampered by uncertainty in climate-change scenarios and by inadequate knowledge of how factors, such as temperature and hydrography, influence the distribution and abundance of aquatic organisms. Even if one considers temperature models, that are used for broad-scale predictions of species invasions, predictions for local scale, in which multiple factors likely interact, are scarcely useful [42].

3.1. *Niche theory and predictions*

While invasion has been regarded as an enormously complex process, some phases of the process are considered predictable; for example, modelling the ecological niche characteristics of a species can predict its potential geographic distribution at a level sufficient for management [40,43].

The conditions for a successful invasion involve the intersection of a species, its vector, and an appropriate receiving environment. This climate matching approach relies on the assumption that invasive species conserve their climatic niche in the invaded ranges. Climate matching is thus a useful approach to identify areas at risk of introduction and establishment of newly or not-yet-introduced neophytes, but may not predict the full extent of invasions [44].

Locke [45] developed a screening tool for potential tunicate invaders of Atlantic Canada by using species distribution (biogeography) and vector traffic patterns.

He derived a ‘watch list’ for early detection of species to be monitored examining Tunicates with a known history of introductions and comparing donor regions and maritime routes. Should the climatic conditions be perturbed significantly, the differences of temperature regimes between Canada and some potential donor regions could not justify the exclusion of some species from the list of candidates.

Many modelling exercises can be quoted, even if a common drawback is the lack of detailed information on the actual occurrence of species over large areas. For instance, Reusser and Lee [46] used a new modelling technique (Non-Parametric Multiplicative Regression – NPMR) to predict species distribution over different spatial scales for estuaries and their habitats over the entire west coast of the United States, where they could make use of a large data set of species with associated landscape and watershed characteristics. Lee et al. [47] suggest that combining the outputs from biological information systems with environmental data would allow the development of ecological niche models that predict the potential distribution or abundance of native and non-native species. Environmental projections from climate models can be used in these niche models to project changes in species distributions or abundances under altered climatic conditions and to identify potential high-risk invaders.

3.2. *The special case of pest prediction*

An interesting case of possible interactions between climate change and effects of the altered distribution of organisms is that of pathogens. Pathogens have been seen as the main cause for the loss of biodiversity in some areas, their spread having caused unprecedented declines in host populations due to changes in their mutual relations. This is a particular case of concern for predictions, due to the health and economic consequences, besides those concerning biodiversity, and also a subject where traditionally climate linked predictions are used in order to forecast epidemic outbreaks. However, given the paucity of baseline disease data, the multivariate nature of climate change, and nonlinear thresholds in both disease and climate processes only a few attempts have been made.

The hypothesis that climate warming will affect host-pathogen interactions was made by Harvell et al. [48] through the following processes:

(i) increasing pathogen development rates, transmission, and number of generations per year;
(ii) relaxing overwintering restrictions on pathogen life cycles; and
(iii) modifying host susceptibility to infection.

Changes in these mechanisms could cause pathogen range expansions and host declines, or could release hosts from disease control by interfering with the precise conditions required by many parasites. Links between pathogens and changing ocean temperatures have been observed for human diseases, such as cholera and emerging coral pathogens associated with coral bleaching [49].

For instance, in the temperate north-western Mediterranean Sea, large-scale disease outbreaks in benthic invertebrate species have recently occurred during climatic anomalies characterized by elevated seawater temperatures; in 1999, gorgonians, scleractinian corals, zoanthids, and sponges in the Ligurian Sea were affected by a temperature-linked epizootic, where mortality likely resulted from the effects of environmental stress and an unidentified opportunistic pathogen [50,51]. From experimental inoculations of four bacterial isolates onto healthy *Paramuricea clava* (Risso, 1826,) a *Vibrio coralliilyticus* strain (a thermodependent pathogen of a tropical coral species), was recognized as the probable causative agent [52].

The recent increase of oyster disease outbreaks may be related to climate change. Parasites have been introduced into new areas through increased shipment of host oysters for fisheries and aquaculture, and changing environmental conditions may have triggered host-pathogen dynamics [53]. A notable example is the mid-1980s northward expansion of oyster diseases. The agent of Eastern oyster disease (*Perkinsus marinus*) extended its range from Long Island to Maine during a winter warming trend. El Niño events are known to influence *Perkinsus marinus* infection intensity and prevalence in the Gulf of Mexico, where it is endemic [54]. Although there is evidence for temperature and climate-related links in some marine diseases, lack of reliable baselines and incomplete disease time series complicate the partitioning of climate effects and other anthropogenic disturbances, such as the high densities under which animals are grown and the high temperatures sustained in hatcheries favour the proliferation and transmission of opportunistic pathogens.

3.3. *Observation of what is happening is a good start*

Climate change is no more a fancy prediction derived from complicate models of the ocean-atmospheric coupling: observational evidences accumulate on the rapid, albeit not uniform, rate of temperature increase and related phenomena (see for instance [55]). Plants and animals can survive only within certain climatic zones, so with the warming of recent decades many of them are seen to migrate poleward. The study of Parmesan and Yohe [9] found that 1700 plant, animal and insect species moved poleward at an average rate of 6 km (about 4 miles) per decade in the last half of the twentieth century. The invasion success of Ponto-Caspian crustacean onychopods (cladocerans) in inland and coastal waters outside their native range has been attributed to increased temperatures in receiving water bodies, where these euryhaline species have found optimal conditions. For instance *Cercopages pengoi* (Ostroumov 1891) has been introduced to the Baltic Sea and North American Great Lakes, by resting eggs accumulated in the sediments of ballast tanks [56]. There are many examples of geographic range shifts or phenological shifts consistent with climate change predictions for terrestrial, inland and marine species [9,10,16,57,58]. It is commonly assumed that more northerly species will contract their ranges in response to climate warming [59], but just the opposite has been seen during recent decades in at least one part of the northwest Atlantic. In shelf ecosystems upstream of the tail of the Grand Banks, the predominantly positive NAO conditions since the 1970s have led to colder bottom waters that are physiologically favourable for boreal species like the northern shrimp *Pandalus borealis* Krøyer, 1838 [60].

4. The Mediterranean Sea as a miner's Canary

The recent evolution of biodiversity in the Mediterranean Sea serves us with an example of changes occurring under the pressure of both climate forcing and species introductions. The present Mediterranean biota contains an exceptionally large number of alien species, resulting from a long history of introductions and presence of exceptional pathways of introduction. The recent warming trend in sea surface temperatures [61] and other hydrological changes, enumerated below, may have facilitated the spread of thermophilic species [62]. The consequences of these changes, and the concomitant effects of pollution, coastal eutrophication, habitat destruction, fisheries overexploitation etc., are raising a growing concern [63].

The recognition that marine organisms had been introduced into the Mediterranean from other parts of the world came gradually. Naturalists noted the many fouling species on vessels reporting from distant regions of the world: 'it should not be overlooked, that those species, as *Balanus tintinnabulum*, *amphitrite, improvisus*, and, in a lesser degree, *B. trigonus* and *Tetraclita radiata*, which seem to range over nearly the whole world (excepting the colder seas), are species which are habitually attached to ships, and which could hardly fail to be widely transported' ([64], p. 163). In 1873 the tri-masted *Karikal* arrived at the port of Marseille from India carrying on its flanks a '...petite forêt d'êtres vivants était peuplée de Crustacés' ([65], p. 4) including *Planes minutus*, *Pachygrapsus transversus* (reported as *P. advena*) and *Plagusia squamosa*, the latter numbering in the hundreds of specimens. But it was the opening of the Suez Canal that focused scientific attention on the movement of marine species. Even before the Suez Canal was fully excavated it was argued that 'Le percement de l'isthme de Suez... offrira... une occasion précieuse de constater les phénomènes que doivent amener l'émigration des espèces et le mélange des faunes' ([66], p. 97). Indeed, Keller, who traveled to Egypt in 1882 and 1886 to seek evidence for the presence of Red Sea and Mediterranean species in the Canal, considered it '... auch als Karawanenstrasse für die thierischen Bewohner beider Meere benutzt' ([67], p. 3).

While Erythrean aliens were pouring through the Suez Canal into the Levantine Basin, along the European coast of the Mediterranean alien shellfish and their 'associates' were introduced via shipping and mariculture. Though records of alien species introduced into the Western Mediterranean kept appearing in the scientific literature, their number and impact were considered negligible and thus they '... have not been the subject of inventories as representative as those of lessepsian migrants' ([68], p. 45). The rapid spread and conspicuous impacts of a pair of invasive chlorophytes [69,70], have helped raise awareness of the raging problem of alien species in the Mediterranean. The European Commission Environmental Programme and the Commission Internationale pour l'Exploration Scientifique de la Mer Méditerranée (CIESM) have organized a workshop on 'Introduced species in European coastal waters' [71], that was followed by CIESM research workshops on 'Ship-transported alien species in the Mediterranean and Black Sea' [72] and on the 'Impact of mariculture on Mediterranean coastal ecosystems' [73] (www.ciesm.org). The first comprehensive inventory of alien decapod and stomatopod crustaceans in the Mediterranean was published in 2002 (www.ciesm.org/atlas), followed by a project funded by the European Commission under the Sixth Framework Programme, that created an inventory of alien species in the European marine environment, including a Mediterranean-wide dataset and collated data on invasive and potentially invasive species in particular habitats (DAISIE European Invasive Alien Species Gateway, http://www.europe-aliens.org/). Drawing on the latter database, another EU project, IMPASSE (http://ec.europa.eu/research/fp6/ssp/impasse_en.htm), has studied aquaculture related introductions in European waters, including the Mediterranean Sea.

Over 620 metazoan species have been listed as alien in the Mediterranean Sea (compared with 10,000–11,000 native metzoan species) (Galil, in preparation). All are littoral and sublittoral and most are benthic or demersal species (or their parasites). Since the shallow coastal zone, and especially the benthos, has been extensively studied, and is more accessible, the chances that new arrivals will be encountered and identified are higher. Also, the species most likely to be introduced by the predominant means of introduction (Suez Canal, vessels, mariculture) are shallow water species.

There is no doubt that the location of the opening of the Suez Canal at the southeastern Levantine Sea directly influenced the outcome of the Erythrean Invasion. The higher sea surface temperature (SST) [61], the prevailing counter clockwise coast-hugging currents and the wide shallow shelf influenced establishment success. Already in the 1950s it was suggested that the establishment of Erythrean aliens was related to a rise in SST: the sudden escalation in the populations of certain Erythrean aliens had been attributed to a rise of 1–1.5°C during the winter of 1955 [74–76]. Ben Tuvia ([77], p. 254) contended that the thermophilic aliens require 'temperatures high enough for the reproductive processes and development of eggs, and minimum winter temperatures above their lethal limits' to establish populations in the Mediterranean.

4.1. *The speeding spread of alien species*

For much of the twentieth century Erythrean aliens were confined within the Levantine Sea, but the 1990s saw the breaching of the barrier. The sudden spread of Erythrean species westwards and northwards coincided with significant hydrographic changes which include a shift in the source of the Eastern Mediterranean Deep Water from the Adriatic to the southern Aegean Sea [78]. The increased outflow of the newly formed, denser water through the Cretan Arc Straits into the eastern Mediterranean has been compensated by inflowing Levantine surface and intermediate water [79,80]. The more extensive inflow of the warm-water Asia Minor Current along the Anatolian coastline, carrying westwards warm, salty water from the Levant, was positively correlated with the initiation of a significant increase in the number of Erythrean aliens along the southwestern Anatolian and the southern Aegean coasts: only one of the 13 Erythrean decapod and stomatopod species now known in the Aegean Sea, the swimming crab *Thalamita poissonii* (Audouin, 1826), was collected before 1991 [81].

But Erythrean aliens are found much further westwards – among the marine alien species recorded from the coast of Italy are 46 Erythrean species. The bivalves, *Brachidontes pharaonis* (Fischer P., 1870), *Pinctada radiata* (Leach, 1814), *Fulvia fragilis* (Forsskål in Niehbur, 1775), and the gastropod *Cerithium scabridum* (Philippi, 1848), are likely to have been vessel transported, either from established Levantine populations or from their native range. Both *B. pharaonis*, *P. radiata* and *C. scabridum* were initially recorded in the late 1960s and early 1970s, but spread only in the past decade, whereas *F. fragilis* was first sighted as recently as 2003 in Livorno, but has since been recorded from the Gulf of Pozzuoli (Naples), Castellaneta Marina (Taranto), Calabria, Messina Strait (Reggio Calabria Airport) and Syracuse, Sicily [82]. Indeed, in past decade witnessed a rapid expansion of alien species: the bluespotted cornetfish, *Fistularia commersonii* Rüppell, 1835, was first recorded in Italy in 2002 from the straits of Sicily [83,84]. In the following year it was recorded from the Gulf of Castellammare in the southern Tyrrhenian Sea [85], and seems to have established populations along the central Tyrrhenian coasts soon after [86–88]. In 2005, a specimen was collected off the east coast of Sardinia [89]. In 2007 a single adult fish was caught near Sanremo [90] and in 2008 a school was sighted near Laigueglia, Savona [91], both localities on the northwestern Tyrrhenian coast of Italy. In 2007 a specimen was collected in Montenegro, on the east coast of the Adriatic Sea [92].

The fact that a fish described as 'tropical, reef-associated' (www.fishbase.org) thrives in the Mediterranean is cause for alert.

The last decades of the twentieth century saw pronounced thermal fluctuations and a significant increase in the average SST in the Mediterranean, and a growing concern over the 'tropicalization' of its biota by the marked rise in the number, abundance and geographic expansion of thermophilic alien species, with the Levantine Sea acting as a reservoir [81,93]. Persistence of the warming trend would likely have a significant influence on the establishment and distribution of thermophilic species and, consequently, on the biodiversity of the Mediterranean [94,95]. Rising seawater temperature may change the pool of species which could establish themselves in the Mediterranean, enable the warm stenothermal species (native and alien) to expand beyond their present distributions, and may impact on a suite of population characteristics (reproduction, survival) that determines interspecific interactions, and, therefore, the dominance and prevalence patterns of both native and alien species, and provide the thermophilic aliens with a distinct advantage over the native Mediterranean biota. To date, aquaculture- introduced warm water species have not been recorded as invasive in the Mediterranean, with the exception of *Penaeus japonicus* (Bate, 1888), an Erythrean species that has turned invasive in the eastern basin, at variance with inland water bodies that have been invaded by *Tilapia* spp. introduced through aquaculture facilities. Nevertheless, the concern for species associated with aquaculture transfer of stocks is high, bearing in mind the spread of alien algae in western Mediterranean lagoons [96].

Though no extinction of a native species is known, sudden decline in abundance concurrent with proliferation of aliens had been recorded. Examination of the profound ecological impacts of some of the most conspicuous invasive alien species underscores their role, among multiple anthropogenic stressors, in altering the infralittoral communities [97]. Local population losses and niche contraction of native species may not induce immediate extirpation, but they augur reduction of genetic diversity, loss of functions, processes, and habitat structure, increase the risk of decline and extinction, and lead to biotic homogenization. A handful of Mediterranean invasive aliens have drawn the attention of scientists, management, and media, for the conspicuous impacts on the native biota attributed to them. Perhaps the most notorious and the best studied invasive species in the Mediterranean are a pair of coenocytic chlorophytes: *Caulerpa taxifolia* [69] and *Caulerpa racemosa* var. *cylindracea* [70]. Other studies traced the impacts of invasive aliens that entered the Mediterranean through the Suez Canal and displaced native species [98].

The Mediterranean Sea is highly susceptible to ship-transported bioinvasions: one-fifth of the alien species recorded in the Mediterranean have been primarily introduced by vessels [97]. And no wonder – in 2006, 13,000 merchant vessels made 252,000 calls at Mediterranean ports and an additional 10,000 vessels transited through the sea [99]. The increase in shipping-related invasions was noted in recent publications, and may be attributed to the increase in shipping volume throughout the region, changing trade patterns that result in new shipping routes, improved water quality in port environments, augmented opportunities for overlap with other introduction vectors, and rising awareness and research effort [72,100]. The swarms of the vessel-transported American comb jelly, *Mnemiopsis leidyi*, that have spread across the Mediterranean, from Israel to Spain, in 2009, raise great concern because its notorious impacts on the ecosystem and the fisheries (*www.ansamed.info*).

4.2. *Changes in emergent functions and services in Mediterranean ecosystems*

In-depth *in-situ* or experimental studies of changes in ecosystem functions and services in the Mediterranean Sea due to the introduction of alien invasive species are rare. The aliens' impacts have been inferred on the basis of observations, rather than rigorous experimentation. The combined effect of invasive species, some of which are ecosystem engineers, and climate change has profoundly modified the functioning of Mediterranean ecosystems.

The extremely invasive *Caulerpa racemosa* var. *cylindracea* (Sonder) Verlaque, Huisman and Boudouresque, 2003, endemic to southwestern Australia, was discovered in the Mediterranean in 1990, and has since spread from Cyprus to Spain and even unto the Canary Islands [70,101]. The species is considered an habitat modifier and ecosystem engineer [102]. Its compact multilayered mats forming 'web-like green meadow' contribute to large-scale landscape modification, even in highly diverse, native macroalagal assemblages with dense coverage [103,104]. Invaded assemblages have been characterized by lower alpha diversity, but the difference between assemblages at 5 and 25 m depth were smaller than in non-invaded assemblages, due to proliferation of few opportunistic species [105]. Its invasion may modify water movement, sediment deposition, substrate characteristics and landscape, as well as benthic assemblages.

An invasive strain of a tropical green alga, *Caulerpa taxifolia* (Vahl) C. Agardh, widely available through the aquarium trade, was unintentionally introduced into the Mediterranean in 1984 [106]. The species' rapid spread, high growth rate, and its ability to form dense meadows (up to 14,000 blades per m^2) on various infralittoral bottom types, especially in areas plagued by higher nutrient loads, led to formation of homogenized microhabitats and replacement of native algal species [107–109]. *Caulerpa taxifolia* is associated with reduction of species richness of native hard substrate algae [107] and, under certain conditions, outcompetes *Cymodocea nodosa* (Ucria) Ascherson and *Posidonia oceanica* L. Delile [110,111]. Moreover, the most potent of its repellent endotoxins caulerpenyne, is toxic for molluscs, sea urchins, herbivorous fish, at least during summer and autumn when metabolite-production peaks, and capable of decimating microscopic organisms [112–114]. The diminution in the structural complexity of the invaded habitat, together with the replacement of the rich native biota with the *C. taxifolia* species-poor community, result in a dramatic reduction in the richness and diversity of the affected littoral, and constitutes 'a real threat for the balance of the marine coastal biodiversity' [115].

The two species of siganid fish, *Siganus rivulatus* (Forsskål, 1775) and *S. luridus* (Rüppell, 1828), entered the Mediterranean from the Red Sea through the Suez Canal. Both species are found as far west as the southern Adriatic Sea, Sicily, Tunisia, and recently – west of Marseille, France [100,116]. The schooling, herbivorous fishes form thriving populations in the Levant Sea where they comprise 80% of the herbivorous fish in some shallow coastal sites and replaced native herbivorous *Sarpa* [117]. Prior to the arrival of the siganids in the Mediterranean, there were few herbivorous fish and invertebrates and their role in the food web off the Levantine rocky habitats had been negligible. The siganids increased the recycling of algal material accelerating the transfer of energy from the producer to the consumer levels, and by serving as major item of prey (up to 70%) for larger infralittoral predators such as groupers [118,119]. Their grazing pressure on intertidal rocky algae may have benefited the proliferation of an alien Erythrean mussel by providing suitable substrate for its settlement (see below). An analysis of the siganids' gut contents, in conjunction with the spatial and seasonal composition of the local algal community, showed that their diet has a significant impact on the structure of the local algal community: it seems that by feeding selectively they have nearly eradicated some of their favorite algae locally [120].

A small Erythrean mytilid mussel, *Brachidontes pharaonis* (Fischer P., 1870), spread as far west as Sicily, probably in ship fouling, where it is found in high-salinity, high temperature environments [121]. In the early 1970s *B. pharaonis* was many times rarer than the native mytilid *Mytilaster minimus* (Poli, 1795), along the Levantine intertidal rocky ledges [122]. A recent survey has shown a rapid shift in dominance [123]. The establishment of massive beds of *Brachidontes* has had significant effects on the biota of the hard substrate intertidal. The displacement of the native mussel by the larger, thicker-shelled Erythrean alien appears to have changed predation patterns so that the population of the native whelk, *Stramonita haemastoma* (Linnaeus, 1758), that was found to preferentially prey on *Brachidontes*, increased greatly [124].

The lack of publications is misleading and gravely understates the grievous state of the Mediterranean biota. Of the nearly 30,000 specimens collected by commercial benthic trawler off the central Israeli coast at depths between 15 and 30 m, on October 2008, only 9% were native Mediterranean species, the rest of the sample consisted of Erythrean aliens, such as the highly venomous striped catfish, *Plotosus lineatus* (Thunberg, 1787) (11,437 specimens), the blotchfin dragonet, *Callionymus filamentosus* Valenciennes, 1837 (5745), the silver sillago, *Sillago sihama* (Forsskål, 1775) (1423), the kuruma prawn, *Marsupenaeus japonicus* (Bate, 1888) (1154) and the velvet shrimp *Metapenaeopsis consobrina* (Nobili, 1904) (1138).

In front of our very eyes the native macrobenthic biota of the soft sediments of the upper shelf in the southeastern Levantine Sea has been substituted by Erythrean aliens and constitute today an assemblage dominated by thermophilic invasive alien species.

5. Conclusions

Alien species introductions can lead to biological invasions concomitantly with climate change at a global scale in all planet's oceans. These two concurrent phenomena can interact between themselves and with others in a variety of ways. Man's role and responsibility is clearly involved in influencing the evolution of biological communities and ecosystem and the management and adaption strategies are clearly influenced by our understanding of how these changes occur. In our analysis we have tried to distinguish three interacting mechanisms influencing the distribution of species in marine environments: (i) the 'natural' range shift induced by climate change; (ii) the long distance transport of species by ships and aquaculture; and (iii) the secondary spread of species, after being introduced in a new location. The second one is characterized by being essentially discrete, i.e. man is bringing a species from a remote region of the sea to another region. The other two mechanisms involve the establishment of new climatic conditions, facilitating the spread in contiguous locations. The literature examples shown often describe how the local biodiversity is affected during the process of change, especially when native species are negatively impacted and alien species take their place: there is a strong correlation between the demise of native species and the success of alien species, but seldom a causation can be demonstrated. In other words, there is no evident answer to the following question: did the native ones became less abundant because of the aliens, or did the aliens become more abundant because the local species decreased in number for some other reason? In the Mediterranean Sea the physical conditions have probably enhanced the aliens, as in the case of Erythrean species, and maybe they have discouraged the natives, as in the case of Posidonia. So the changes in dominance between natives and aliens might be mediated by physical change. Evidently, the Mediterranean Sea is a warning example of the consequences of a very high propagule pressure of alien species (especially through the Suez Canal), coupled with the influence of changing climate and hydrographic conditions at a wider basin scale, leading to a revolution in much shorter times than the geological scale. We have limited knowledge concerning extinction of marine species caused by invasive aliens, though observations of extirpation and displacement of native species by aliens have been amply recorded. It is yet unresolved whether the deterioration of coastal habitats and their native assemblages permitted the establishment of opportunistic aliens, or the influx of aliens synergetically with the physical disturbance of the environment brought on the decimation of native communities. Still, the more common outcome at present is that species richness is locally increased when alien species are added to native ones. At some specific coastal regions, mostly heavily polluted or physically altered, like lagoons, estuaries, ports and marine farms, we witness the progressive homogenization of biotas, as only stress resistant opportunistic species, both native and 'cosmopolitan' invasive species dominate [125]. Homogenization is best documented for inland fish faunas, where a small set of species introduced for sport fishing, aquaculture, or ornamental purposes, has become widespread throughout the world [13], but it is known for marine faunas as well [126]. Studies on the ecology of alien species and changing climate should aim at disentangling cause/effect relationships, taking into account aspects, such as the influence of regime shifts on species interactions and phenology [127–129] microevolution and genetic aspects leading eventually to speciation [130]. Long-term data yield important insights on the impacts of anthropogenic disturbances and should be continued or resumed as in the case of the English Channel [30,131]. In the ongoing debates in the scientific community, priorities are shifting already. The sort of problems stakeholders increasingly face will be much less predictable than those associated with 'classic' pollution of the marine environment faced in the late twentieth century. Pressure from demography, economy and climate change builds up for a long time – and then triggers abrupt shifts – as the one we witness in the Mediterranean today. The current international system is ill-designed for such a world. The Copenhagen 2009 meeting demonstrated that the way governments deal with new threats is inappropriate to the task – it frequently takes decades just for them sign on already negotiated agreements, i.e. the International Convention for the Control and Management of Ships' Ballast Water and Sediments. Merely tinkering with reducing risk is insufficient. We call for a closer interlinking of regional (& international) scientific expertise to induce governments to recognize their mutual obligations and interests, and to consider the consequences of failure to act now on the biotic safety of the sea.

Acknowledgements

ICES (International Council for the Exploration of the Sea) sponsored the participation of one of us in the sixth International Conference on Marine Bioinvasions, held in Portland (Oregon) on August 24–27, 2009; most of the ideas developed in this paper were presented at the opening lecture by AOA. Research leading to the publication was funded by the E.U. Integrated Project SESAME [BG] and by the Porter School of Environmental Studies at Tel Aviv University with funding from the Italian Ministry of the Environment, Land and Sea [BG]. Two anonymous referees have raised constructive criticism on the manuscript.

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