Limnol. Oceanogr., 55(4), 2010, 1478–1484

doi:10.4319/lo.2010.55.4.1478

Global climate change amplifies the entry of tropical species into the Eastern Mediterranean Sea

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Abstract

Using long-term data of 149 warm alien species since 1924, we show that the introduction of warm and tropical alien species has been exacerbated by the observed warming of the eastern Mediterranean Sea. The phenomenon has accelerated after an abrupt shift in both regional and global temperatures that we detect around 1998, leading to a 150% increase in the annual mean rate of species entry after this date. Abrupt rising temperature since the end of the 1990s has modified the potential thermal habitat available for warm-water species, facilitating their settlement at an unexpectedly rapid rate. The speed of alien species spreading and response to global warming is apparently much faster than temperature increase itself, presenting an important warning for the future of Mediterranean Sea biodiversity. In addition to the sea warming, other factors that enable and enhance biological invasions, such as salinity increase and oceanographic forcing, are also discussed.

Increased tropical influx through the Gibraltar Strait and the Suez Canal has resulted in the so called "tropicalization" of the Mediterranean Sea (Bianchi and Morri 2003), a process poorly understood to date. Scenarios proposed by the Intergovernmental Panel on Climate Change that project further warming make the biological tropicalization of the Mediterranean Sea inevitable. Although only a small fraction of the many marine species introduced outside of their native range are able to thrive and invade new habitats, their effect can be dramatic. Marine invasive species are responsible for local population loss (local metapopulation extinctions) worldwide, a phenomenon so severe that it is regarded as the second biggest cause of biodiversity loss after habitat destruction (Breithaupt 2003). If tropical alien species continue to increase, this will have substantial consequences on marine biodiversity, implicating environmental and economic, as well as health, issues.

Warming of the planet is now unequivocal, and its current effect on the biosphere has been documented in both terrestrial and marine ecosystems (IPCC 2007; Beaugrand et al. 2008). Many reviews have been published (Carlton 1999; Ruiz et al. 2000; Occhipinti-Ambrogi 2007) highlighting the ongoing modifications in the marine environment worldwide, while ocean temperatures are predicted to increase as climate change continues (Dukes and Mooney 1999). Climate change and habitat disturbance by human activities can affect species distribution and resource dynamics in ecosystems and consequently can interact with biological invasions (Vitousek et al. 1997; Dukes and Mooney 1999).

In the Mediterranean Sea, where biodiversity changes occur at an unprecedented rate (Zibrowius 1992; Zenetos et al. 2008; Zenetos in press), the importance of investigating the causes for these alterations is a matter of urgency. In fact, owing to its unique location at the crossroads between the Atlantic and Indo-Pacific biogeographic domains, the magnification of climatic signals makes the Mediterranean Sea a remarkable case to investigate the influence of climate change on biodiversity. Current research focusing on the link between climate variability and marine alien species has been limited so far to individual species or taxonomic groups (i.e., fish) assessing mainly the effect of water warming on their dispersal within the Mediterranean Sea (Ben Rais Lasram et al. 2008; Ben Rais Lasram and Mouillot 2008), rather than identifying a direct link between their introduction (including all available taxonomic groups and species) and global warming. Alien species enter the Mediterranean Sea mainly via the Suez Canal (actively or passively), but also via Gibraltar and Dardanelles through shipping (ballast water, fouling) and aquaculture (EEA 2006). Until the mid 20th century the alien species introduction, establishment, and expansion rates were low (Zenetos et al. 2008), mainly as a result of the water temperature and salinity barriers between the Red Sea and the Mediterranean Sea (Galil 2006). The effects of climate change and invasive species have been implicated in the decline and even collapse of several marine ecosystems (Harris and Tyrrell 2001; Stachowicz et al. 2002; Frank et al. 2005). The tropicalization of the Mediterranean has been attributed to the combination of four factors, namely, the Atlantic flux, Lessepsian migration, human action (aquaculture), and present climate warming (Bianchi and Morri 2003; Bianchi 2007). When many stressors act in synergy, they may eventually have unexpected and irreversible consequences for native communities and economically valuable human activities such as fisheries (Occhipinti-Ambrogi and Savini 2003; Whitfield

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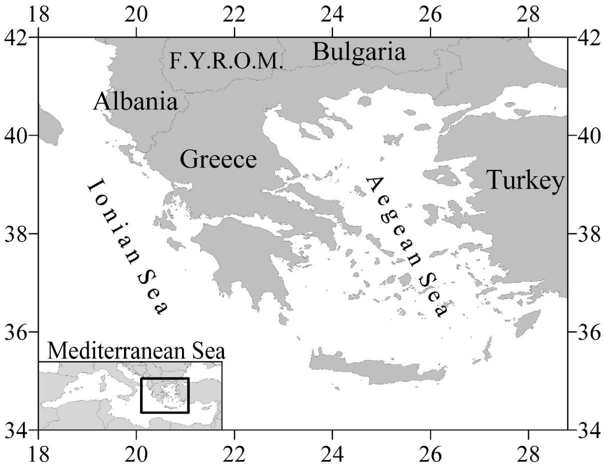

Fig. 1. Study area of the eastern Mediterranean Sea, where the long-term alien species data were collected.

et al. 2007). The most evident effects of the invasion of species can be detected at three different levels, namely, biodiversity, economy, and human health.

Biodiversity changes in the Mediterranean Sea occur at an exceptional rate, bringing the rate of introductions to 1 species every 1.5 weeks (Zenetos in press). The relative importance of biotic processes (e.g., competition and facilitation) of the native–invader relationship and of the abundance of resources in the invaded habitat is not to be neglected. Biotic factors can at times also play a major role in the success and expansion of invasions, particularly competition with and predation by either native species or, indeed, previous invaders. It has been argued that a high resident diversity may be linked to reduced success in the establishment of alien species (Kennedy et al. 2002).

The dispersal success and expansion of an invasive species depends upon the suitability of the new abiotic environment, and thus climate match is a key element for assessing species success (Ben Rais Lasram et al. 2008). In this study we aim to explore long-term (1924–2007) alterations in new alien species arrivals in the eastern Mediterranean (Fig. 1) in relation to local and global climate trends.

Methods

Alien species data—Our definition of alien species in this study follows that of the Convention on Biological Diversity: "A species, subspecies or lower taxon, introduced outside its natural past or present distribution; includes any part, gametes, seeds, eggs, or propagules of such species that might survive and subsequently reproduce." The marine alien species data were extracted from the Ellenic Network on Aquatic Invasive Species (ELNAIS) website, which contains comprehensive information for each species and is archived in the Hellenic Centre for Marine Research (HCMR). The list is updated with every new record and regularly reported (Zenetos et al. 2009). Only the warm and tropical species were extracted (149) from 1924 to 2007, while the temperate and cold species were removed (*see* Web Appendix, www.aslo.org/lo/toc/vol_55/issue_4/1478a.html). Data used in this study describe fish, reptiles, parasites, phytobenthos, phytoplankton, zooplankton, and zoobenthos, covering a large spectrum of the ecosystem. Many marine taxa in Greece are inadequately and unequally monitored, and thus many groups go uninvestigated. Absent from our analyses, for example, are sponges, hydroids, flatworms, nemerteans, rotifers, kamptozoans, oligochaetes, isopods, tanaids, mysids, cumaceans, ostracods, ascidians, and many groups of protists. It is a safe assumption that the number of newly introduced tropical species is higher than reported.

In addition, a possible and documented (Galil 2006) source of bias is associated with the date of alien species introduction. Since research efforts vary greatly along the coasts of Greece, even the better studied localities suffer from temporal gaps. Moreover, the known occurrence of the species greatly reflects the availability of the relevant specialists (Bianchi and Morri 1994). Finally, it is impossible to know exactly the year of first collection of certain species, because authors of systematic or natural history works do not always provide the collection date. Thus, we use here only the species with well-established first dates of collection, whereas the rest were excluded from the analysis. This exclusion had a slightly negative effect on the correlations (owing to the smaller number of species).

Temperature data—The advanced very high resolution radiometer (AVHRR) sea surface temperature (SST) product was ordered from the National Aeronautics and Space Administration, Physical Oceanography Distributed Active Archive Center. The AVHRR *Pathfinder 5* monthly mean products, characterized by a spatial resolution of 4 × 4 km^2, were used (1985–2007). The SST data were spatially averaged for the area of study (Aegean and eastern Ionian Seas; Fig. 1). In order to avoid potential bias related to solar radiation (the diurnal fluctuation in SST) that can occur during the daytime from surface heating (Raitsos et al. 2006), the nighttime SST products were used.

Northern hemisphere temperature (NHT) anomalies were obtained from the Climatic Research Unit and Hadley Centre (Jones et al. 2008). The data used were from 1850 to 2007 and were expressed as anomalies relative to the 1961–1990 reference period means (Brohan et al. 2006; Jones et al. 2008).

The regional air temperature data were collected and provided from the meteorological stations of the Hellenic National Meteorological Service (HNMS) at 15 stations (north, middle, and south Aegean and eastern Ionian Seas). Monthly means were produced from the 10-d mean data, for the period 1980–2003 (latest data availability).

Correlation analysis—The statistical comparison between the temperature data was performed by using a linear correlation analysis. The probability of significance of the coefficient of correlation was adjusted to correct for temporal autocorrelation (p_{ACF}). Probabilities were calculated with consideration of temporal autocorrelation (Pyper and Peterman 1998).

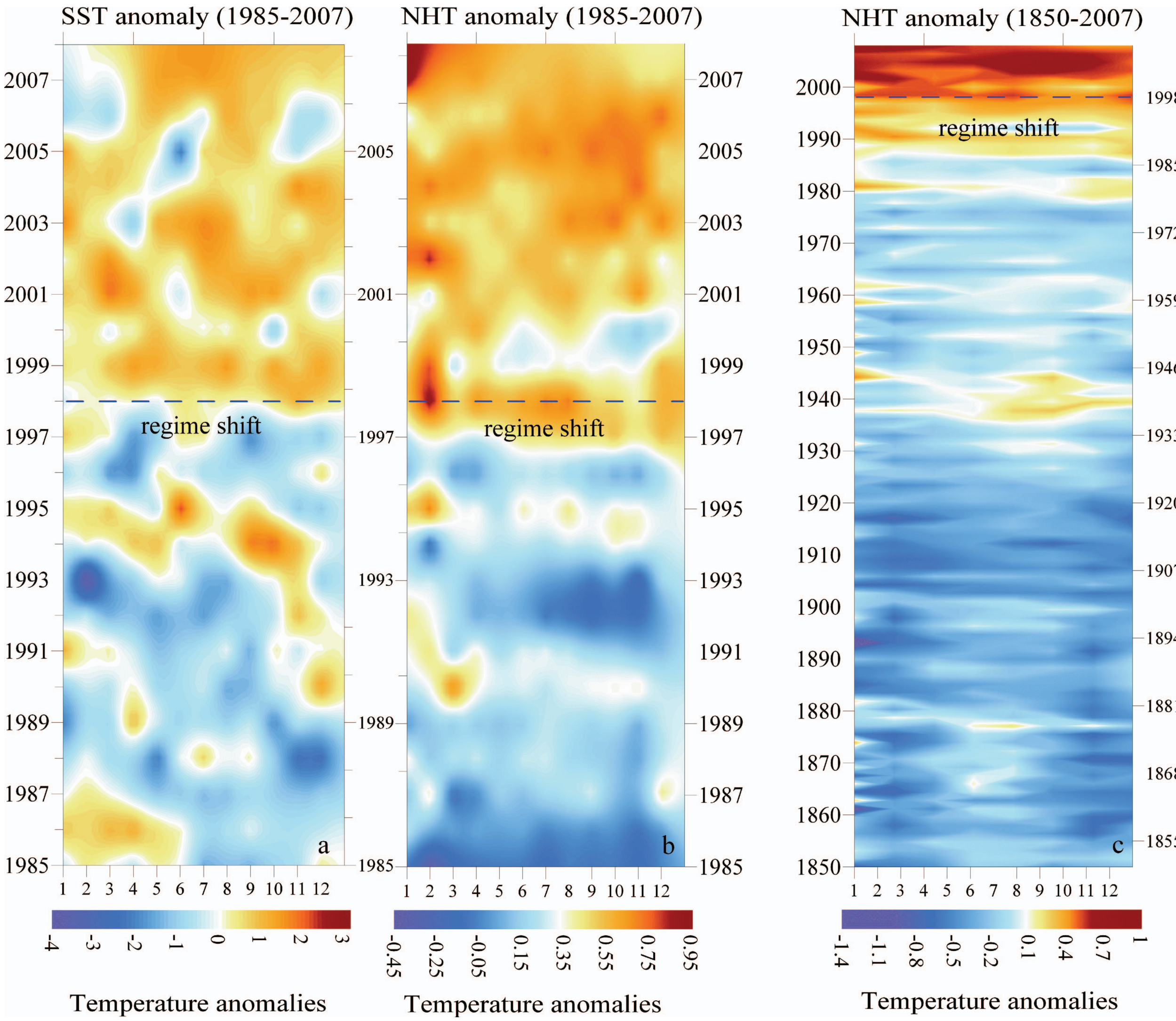

Fig. 2. Long-term or year-to-year changes in both regional and global monthly temperature; on the x-axis the months (1–12) can be seen. (a) Satellite-derived SST (1985–2007) for the Aegean and eastern Ionian Seas. (b) NHT anomalies (1985–2007). (c) NHT anomalies for the period 1850–2007. The blue line in 1998 shows the temperature regime shift, which appeared to be the most abrupt change occurring in the last 158 yr. All the data are expressed as anomalies in order to be comparable; note the different scale in each plot.

Results

We first examined whether there was evidence of warming in the eastern part of the Mediterranean Sea and how it was linked to large-scale change in temperature using NHT anomalies. The 23-yr time series of regional SST for the Aegean and eastern Ionian Seas revealed a pronounced change in temperature around 1998 (Fig. 2a). The increase in regional temperature paralleled changes observed in NHT anomalies (Fig. 2b). Both large-scale and regional temperature changes were significantly positively correlated at an annual ($r = 0.68$, $p_{ACF} = 0.0101$) and at a monthly scale ($r = 0.38$, $p_{ACF} = 0.0146$). The mean annual SST of the preshift (1985–1997) was 18.5°C, whereas the mean of the postshift period (> 1998) was 19.3°C (0.8°C increase). The most prominent alterations in the temperature regime occurred during the summer months (0.93°C of warming after the shift) and particularly in August (1.27°C increase). Long-term changes in monthly NHT anomalies revealed that the temperature shift located at the end of the 1990s was the most intense change that occurred in the last 158 yr (Fig. 2c).

To examine whether this observed warming facilitated the introduction of new alien species, their relationships with water, air (local), and global temperatures were investigated (Fig. 3). A unique long-term dataset of warm-tropical alien species in Greek waters (ELNAIS) was used, containing a total of 149 species and covering many taxonomic groups belonging to benthic and pelagic communities including both primary producers and consumers. Year-to-year changes in the entry of alien species paralleled the increase in water temperature (Fig. 3a). A cross-correlation analysis indicated a positive correlation with satellite-derived SST 2 yr later (2-yr alien response, $r = 0.6$, $p_{ACF} = 0.01$; original time series: $r = 0.37$, $p_{ACF} = 0.13$ [not significant]). Marine alien species were also

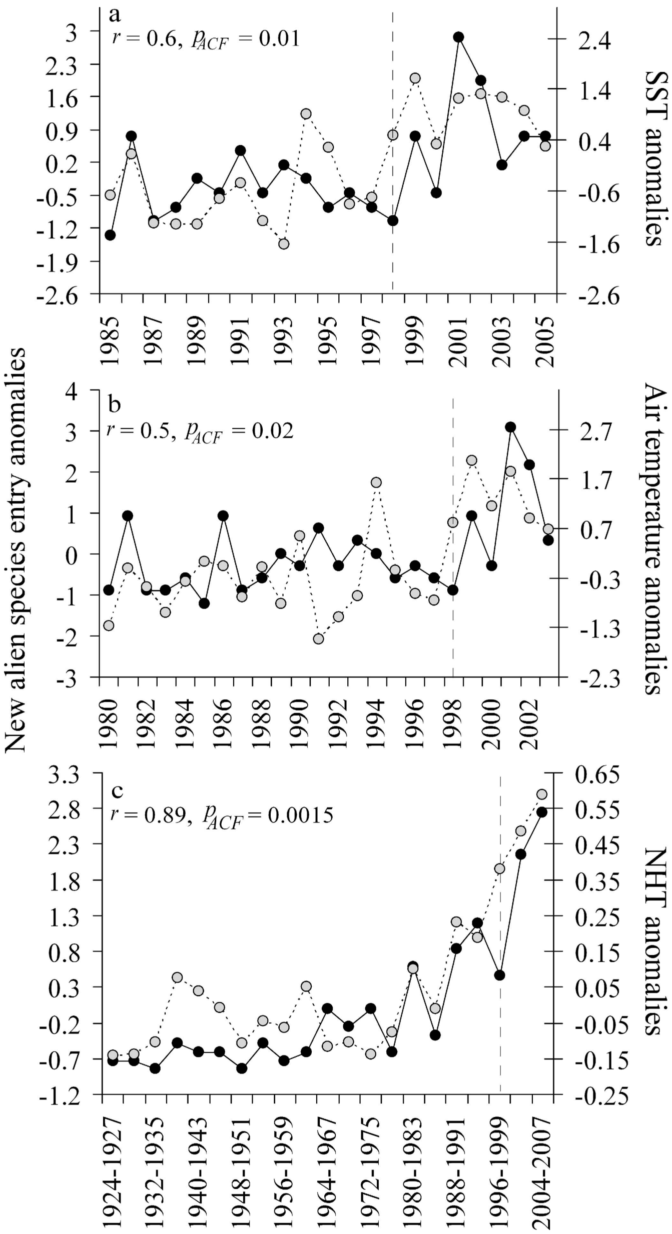

Fig. 3. Year-to-year and long-term changes in new alien species arrivals vs. marine and air temperatures (expressed as anomalies). (a) Alien species against regional satellite-derived SST (annual mean). (b) Alien species vs. regional air temperatures (annual mean). (c) Long-term 4-yr averaged alien species against NHT anomalies (1924–2007). (a, b) Presented with a lag of 2 yr for alien species, since cross-correlation analysis revealed that their number covaried positively with changes in temperature 2 yr later (air and marine temperatures). The solid black line represents alien species and the dashed gray line temperature data. The vertical line shows the 1998 temperature shift. The coefficient of linear correlation (r) and its associated probability (p_{ACF}) are indicated.

significantly positively correlated to air temperature with a lag of 2 yr (Fig. 3b; $r = 0.5$, $p_{\mathrm{ACF}} = 0.02$; original, $r = 0.11$, $p_{\mathrm{ACF}} = 0.62$ [not significant]). The lag of 2 yr found between temperature change and the arrival of new alien species may be related to the time needed for a species to settle, reproduce, and expand enough to be detected. However, this is not always the case, since the relationship failed in some particular years, such as the cold periods in 1989 and 1993 associated with a relatively high number of alien species entry (Fig. 3a).

The relationship between the entry of new species and NHT anomalies was investigated at a decadal scale (1924–2007). A 4-yr mean was used instead of annual, as a result of the gaps in alien species data. The choice of a 4-yr mean was the best compromise between a minimum amount of gaps and an overaveraging or smoothing of the data. The relationship between alien species and NHT anomalies was apparent (Fig. 3c; $r = 0.89$, $p_{\mathrm{ACF}} = 0.0015$). Both temperature and alien species remained nearly stable (small fluctuations) between 1924 and 1979, and no significant correlation was found for this period. After the end of the 1970s, rapid concomitant changes in both time series were observed. The year 1980 was the first instance of intense warming, since 1850, that was particularly pronounced during the winter months (Fig. 2c), a critical condition for alien species survival (Ben-Tuvia 1966). From 1924 to 1997, the mean rate of alien arrivals was on average 2.4 species per year, whereas after 1998, this rate accelerated to on average six species per year, representing an increase of 150%.

To investigate further the mechanism behind the water warming in the study area, in situ air temperature data (HNMS) were plotted against the SST (*see* Fig. 4). First the monthly means of both temperatures were illustrated as 24-month moving averages, to better visualize the trend (Fig. 4a). It is clear that both temperatures follow the same pattern, and a significant positive correlation was found in the monthly, as well as the annual, averaged data ($r = 0.92$, $p < 0.0001$ and $r = 0.82$, $p < 0.0001$, respectively). This figure confirms the observed global and local temperature climate patterns seen previously (Fig. 2). However, although the water and air temperatures exhibit very similar trends, in most of the cases, it is obvious that there is a time delay (SST shifts toward the right). Thus, a cross-correlation analysis was performed on the raw monthly data to indicate whether there is a statistical time lag. The highest correlation is at a 1-month lag ($r = 0.96$, $p < 0.0001$), whereas the correlation declines in the case of 2-months lag and thereafter ($r = 0.74$, $p < 0.0001$; Fig. 4b,c). These results show that air temperature is a key parameter influencing the water temperature, and that air temperature changes first, and this change is observable in the sea a month later.

Discussion

A large part of the eastern Mediterranean Sea, and particularly the Aegean and eastern Ionian Seas, is going through a substantial warming. This warming is significantly linked with global trends (and thus is not simply a regional phenomenon). Air temperature has an indirect effect on alien species (Fig. 3b), since air temperature changes a month before water temperature. The observed increase of 0.8°C SST in February during the last decade in

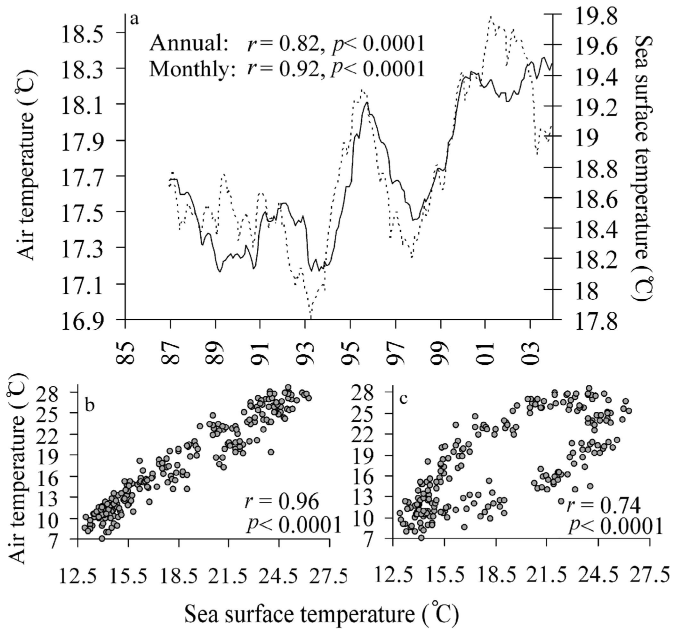

Fig. 4. Regional water temperature (solid line) against air temperature (dashed line) for the Aegean and eastern Ionian Seas. (a) Monthly averaged (1985–2003) sea surface temperature against air temperatures (°C), expressed as 24 months moving averages. (b, c) Monthly means of air and water temperatures at 1- and 2-month lags for water temperatures, respectively. The highest correlation is found at 1-month lag, indicating that the water is following the air temperature change, a month later. The coefficient of linear correlation (*r*) and its associated probability (*p*) are indicated.

the Aegean and eastern Ionian Seas is consistent with the results of a whole-Mediterranean scale analysis by Nykjaer (2009). In addition, a similar approach was adopted by Astraldi et al. (1995), who demonstrated that air and sea surface temperatures are significantly correlated in the Ligurian Sea (northwest Mediterranean Sea).

Temperature is a major factor influencing the settlement of tropical alien species (Ben-Tuvia 1966; Ben Rais Lasram et al. 2008). Warming of seawater influences the spatial and temporal distribution of many marine organisms, ranging from phytoplankton and zoobenthos to higher trophic levels (Beaugrand et al. 2008). This warming not only stresses the native dwellers, but also facilitates the arrival of alien ones, adding extra pressure on the ecosystem (Harris and Tyrell 2001). The survival, reproduction, and establishment of warm alien species in the new environment depends on the thermal regime, which has to match the thermal physiological requirement of the species. Winter temperatures are of great importance, since they must be above the lower lethal limit of these species (Ben-Tuvia 1966). In the Aegean and eastern Ionian Seas, the coldest month is February. This month experienced an increase in temperature of 0.8°C after the temperature shift in the late 1990s.

In addition to the abrupt warming, the arrival of new alien species reported in this study paralleled a pronounced increase in salinity in the eastern Mediterranean Sea, including the Aegean Sea (Theocharis et al. 1999). This rapid hypersalinity event was mainly caused by a substantial long-term decrease in precipitation over the entire eastern Mediterranean Sea and an intensification of winds over the Aegean (1988–1993), which resulted in an increased evaporation (Theocharis et al. 1999). An additional factor of the salinity rise in the Aegean Sea was the reinforced salt transport from 1987 to 1994 into the Aegean through the eastern Cretan Arc Straits (Theocharis et al. 1999). This effect of atmospheric and oceanographic forcing was also embedded in the long-term trend of salinity increase due to runoff control of major rivers (i.e., Nile, Black Sea Rivers) (Bethoux et al. 1990). This salinity increase may have also contributed to the arrival and settlement of new alien species. It should also be noted that human activities result in degradation of coastal marine ecosystems, and this pressure on native species may have left unused resources (Herbold and Moyle 1986), thus facilitating the establishment of new invaders. A clear example of such an event was reported by Daskalov et al. (2007), who showed that the outburst of an alien comb jelly species was triggered by the intense fishing (overfishing) that led to an ecosystem trophic cascade in the Black Sea. Relative to our study area, ecosystem degradation (including habitat modification and water quality changes) may exist in the Saronikos and Thermaikos Gulfs hosting the two major Greek ports (Pancucci-Papadopoulou et al. 2006).

Invasive alien species (IAS) are a major threat to global biodiversity (Bax et al. 2003). Our results show that the eastern Mediterranean Sea is facing a pronounced increase in aquatic invasions that have paralleled a substantial warming initiated at the beginning of the 1980s and accelerating at the end of the 1990s. The combination of both has led to the decline and even collapse of several marine ecosystems (Stachowicz and Byrnes 2006; Occhipinti-Ambrogi 2007). Mediterranean IAS may have an effect not only on ecosystems and human health (Streftaris and Zenetos 2006) but also on economically valuable activities such as fisheries (Occhipinti-Ambrogi and Savini 2003). Ocean temperatures are predicted to increase as climate change continues (IPCC 2007), a situation that will further alter marine ecosystems. This analysis suggests that the response of biological communities (in this case warm and tropical alien species) to abrupt temperature shifts can be substantial. The study identified a clear effect of global climate warming on marine ecosystems favoring and accelerating the settlement of new alien species at an unexpectedly rapid rate. The rate of entrance of the new invaders is greater than the temperature rate itself, presenting an important warning for the future of Mediterranean Sea biodiversity. This might have profound consequences for marine biodiversity, restructuring the whole ecosystem with potential consequences for ecosystem functioning and services.

Acknowledgments

We thank HNMS and Athanasios D. Sarantopoulos for processing and providing the air temperature data, and Abigail McQuatters-Gollop, Ioannis Raitsos, and Yaswant Pradhan for commenting on this manuscript. Thanks to James T. Carlton and one anonymous reviewer for their constructive comments. This research was supported by the Southern European Seas Assessing and Modelling (SESAME) project, European Commission Contract GOCE-036949, funded by the European Commission's Sixth Framework Programme under the priority "Sustainable Development, Global Change and Ecosystems."

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Associate editor: Everett Fee

Received: 28 July 2009
Accepted: 28 January 2010
Amended: 24 March 2010