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Mechanisms impeding natural Mediterranization process of Black Sea fauna

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Abstract

The inherent low species biodiversity of the Black Sea (roughly one-third of the Eastern Mediterranean Sea) is a sign of ineffective bio-invasion process of Mediterranean species. This phenomenon is explained on the basis of a hypothesis that strong physical gradients and some accompanying physiological limitations along the colonization route of Turkish Straits System (TSS) make Mediterranean pelagic and benthic plankton species and fish larvae vulnerable to long-distance natural expansions. The physical barriers include strong inter-basin temperature and salinity contrasts, two-layer counter-flow and stratification along the TSS, very strong local vertical mixing and hydraulic adjustment processes along the Canakkale and Istanbul Straits. The physiological barriers are related to stresses induced by strong and abrupt temperature, salinity, and oxygen changes that affect the growth, mortality and reproduction characteristics within the two layer water column structure of the TSS. Long-term behavioral, ecological, and evolutionary acclimatization processes in the Marmara Sea environment to overcome these barriers constitute an essential first stage of species expansions to the Black Sea. Among the new physiologically adapted 'source' populations, only those which manage to arrive at the southwestern Black Sea shelf region may have a chance to acclimatize Black Sea conditions and ultimately establish self-sustaining populations. These physical and physiological stresses are so strong and robust that inter-annual and decadal climate- and eutrophication-induced perturbations can hardly alter this persistent structure. Starting by the second half of the previous century, the TSS has also been serving as an ideal invasion corridor for intentional or non-intentional alien species introductions via intensifying ship traffic.

Keywords: Black Sea, bioinvasion, colonization, mediterranization, physical controls, physiological stresses

Introduction

The study of invasions in coastal marine systems is now a rapidly growing multidisciplinary topic due to serious ecological and socio-economical consequences. Bioinvasion research today covers biogeography (patterns of invasions, alien species inventories, vectors, invasive corridors), ecophysiology (salinity/oxygen tolerance, life strategies, reproduction mode), functional ecology (benthic-pelagic interaction, trophodynamics of invaded ecosystems, habitat changes), molecular genetics (origin of invasive species and pathways, hybridisation process, implications for micro- and macro-evolutions), ecological economics (estimation of costs related to bioinvasions), and technical aspects (ship ballast water treatment options, invasion risk assessment schemes). In the present work we use the term of invasive species for all types of species introduction, although it is often used to refer to those of ecologically and/or economically harmful.

Introduction of nonindigenous species and the likelihood of self-sustained, established populations in new environments depend greatly on the delivery pattern of organisms (propagules) through natural colonization routes or human activities (Rahel 2002). Invasions and species biogeographic expansions have always been a part of nature. They have been either facilitated or impeded by environmental conditions and human-mediated activities. For example, one of the consequences of 1-2^{o}C increase in annual-mean sea surface temperature of the Northern Hemisphere due to the anthropogenic climate warming over the last several decades was to promote northward migration of warm water species and domination of thermophilic alien species at higher latitudes as reported for the North Atlantic Ocean (Beaugrand *et al*. 2002; Parmesan and Yohe 2003), the North Sea (Nehring 1996; Perry *et al*. 2005). Climate-driven northward range expansion of marine species can even be observed at a top predator level as recently reported for the critically endangered Balearic shearwater *Puffinus mauretanicus* in northeast Atlantic (Wynn *et al*. 2007). Some new warm-water species of tropical origin were also registered recently in the Mediterranean Sea (Bianchi 2007; Gambaiani *et al*. 2009). Other means of biogeographic species expansion that is becoming very important especially for stressed ecosystems but beyond the scope of the present study include human-induced intentional or unintentional introductions via ship ballast waters, aquaculture, the opening of navigation channels (Ruiz *et al*. 1997; Occhipinti-Ambrogi 2007).

The eastern Mediterranean - Black Seas system (Figure 1a) is perhaps the largest nearly-isolated basin of Large Marine Ecosystems of the world with considerable differences in their oceanographic characteristics, plankton and fish faunas. The Turkish Straits System (TSS) formed by the Istanbul Strait (Bosphorus), the Marmara Sea and the Çanakkale Strait serves as a corridor for two-way translocation of species from their native habitats in the Black and Mediterranean Seas (Oztürk and Oztürk 1996; Kovalev *et al*. 2001). Limited species exchange and lack of adaptation capability of Mediterranean species to the Black Sea even occur today under the recent favorable conditions of climatic warming, habitat niche vacancy and eutrophication-induced resource availability. Thereby, both the Black and Marmara Seas have been maintaining intrinsic low plankton and fish species biodiversity since the beginning of post-glacial phase. Similar biogeographical peculiarities also apply to the Baltic Sea because of its intrinsic biogeographical barriers for species expansions due to a similar evolution pattern in the last 10,000 years of postglacial phase (Leppakoski and Olenin 2001).

The present study attempts to explain why species transfer from the Aegean Sea to the Black Sea has not been high enough as among other sub-basins of the Mediterranean Sea. It asserts that peculiarities of the colonisation route from the Aegean Sea to the Black Sea have been continually imposing severe constraints on the migration and settlement of Mediterranean species into the Black Sea. This paper first provides background information on the biodiversity changes of the Mediterranean and Black Seas and then an understanding of how Mediterranean species perceive specific physical and physiological gradients on their way to the Black Sea. We then move on the specific examples of acclimatization in the Marmara and Black Seas, and touch briefly up on human-induced invasions through the TSS invasion corridor. We finally discuss the major findings and possible future research directions.

Historical and present status of biodiversity in the Aegean, Marmara, and Black Seas

The species richness of the Mediterranean proper declines eastward toward both the Levantine basin of the eastern Mediterranean and the Black Sea. For example, Table 1 compiled from recent observations demonstrates the decreasing trend of some benthic species number from the Aegean Sea to the Black Sea. A total of 828 non-indigenous marine species have been introduced into European coastal waters by natural and man-made changes during the 20th century (Streftaris *et al*. 2005). While the Mediterranean basin was the primary recipient with 615 species, the Black Sea came second from the last with a total of 41 species after the Arctic basin (15 species). This number will be even less if those introduced accidentally are excluded from the list.

The analysis provided by Garibaldi and Caddy (1998) classified the Aegean, Marmara and Black Seas in the form of three different faunal provinces. The plankton community structure shifts from a warm-temperate and subtropical, hypersaline character in the Eastern Mediterranean and the southern Aegean to an arcto-boreal (relatively cold water) tendency in the northern Aegean transitional zone and a brackish-water tendency dominated by eurytherm and/or euryhaline species in the Black Sea (Siokou-Frangou *et al*. 2004). The Black Sea and the Mediterranean proper also show a clear distinction in terms of their fish stock sizes and species of importance, although several pelagic migratory fish species undergo seasonal exchanges between them. A rich variety of commercial fish species in the Black Sea, comparable to the Aegean Sea, is due to some endemic Pontian relics from the ancient fresh water lake period.

Historically, the Black Sea biodiversity may be put into two categories as before and after its connection to the Mediterranean Sea (Zaitsev and Mamaev 1997). In the early times of being a fresh water lake it has been inhabited by brackish water type plants and animals (called today as Pontian relics) as well as some cold-water species (arcto-boreal relics). Today they constituted not more than 20% of the total Black Sea fauna. The rest is formed by the Mediterranean species that have been settled and ultimately adapted to local environmental conditions after the connection of Mediterranean and the Black Seas. The number of the Mediterranean- originated thermophilic species is in fact not very high; the sum of major taxa (Spongia, Polychaeta, Mollusca, Bryozoa, Echinodermata, Pisces) amounts to 550 as compared to 1757 in the Mediterranean (Zaitsev and Mamaev 1997). This ratio is 808 to 2637 for benthic invertebrates. These numbers imply that only about one-third of the Mediterranean benthic and pelagic taxa were able to migrate and settle successfully into the Black Sea. Some zooplankton groups of stenohaline, warm-temperate and subtropical origin (e.g. doliolids, salps, pteropods, siphonophors, euphausiids) have been totally unable to adapt to low water temperature and/or low salinity conditions and/or due to the lack of suitable habitats. Mesopelagic and 132 deep sea species are absent as well due to oxygen depletion below ~100 m depth.

Table 1. The number of species of some benthic taxa estimated on the basis of recent measurements within the Aegean, Marmara and Black Seas and the Istanbul Strait

	Number of Species				
Benthic Taxa	Agean Sea	Marmara Sea	Istanbul Strait	Black Sea	Data Sources
Crustacea/Decap	205	118		33	Özcan *et al.* (2010)
Polychaeta	592	203	152	192	Arvantidis(2000) Çınar (2010) Zaitsev (2008)
Echinodermata	71	51	19	14	Özgür and Öztürk (2010)
Pisces	389	253	118	192	Turan *et al* (2010) Keskin and Eryılmaz (2010)

~75% of the Marmara Sea zooplankton community structure is formed by the Black Sea species aggregated mainly in the lower salinity surface layer waters (Unal *et al*. 2000; Tarkan *et al*. 2005; Svetlichny *et al*. 2006; Isinibilir *et al*. 2008). This reflects a steady transport planktonic organisms to the Marmara Sea, extending even to the northern Aegean Sea, due to the permanent surface layer flow from the Black Sea to the Sea of Marmara (Tarkan 2000; Kovalev *et al*. 2001). Mediterranean species forming the remaining 25% are located within salty waters below the interface (Svetlichny *et al*. 2006). Thus, in terms of plankton community structure and species diversity, the Marmara Sea is not much different from the Black Sea except the confinement of Mediterranean species in a separate layer below the brackish surface layer. Such a salty Mediterranean layer does not however exist in the Black Sea.

An overview of TSS flow and stratification characteristics

The flow dynamics of TSS, explored by systematic observations carried out during the last three decades, have been documented by Unluata *et al*. (1989), Oguz and Sur (1989), Oguz *et al*. (1990), Oguz and Rozman (1991), Latif *et al*. (1991), Besiktepe *et al*. (1994), Di Iorio and Yuce (1999), Ozsoy *et al*. (2001), Gregg and Ozsoy (2002) and others cited in these publications. The description of physical characteristics given below constitutes a synthesis deduced from these studies. The main geometrical and morphological features relevant to this study are shown in Figure 1a-c. The schematic of its main flow and stratification features is depicted in Figure 2.

TSS constitutes a two-layer stratified system between a highly stratified Black Sea and a weakly stratified Aegean Sea. The location of its pycnocline varies from 50 m below the sea surface near the Black Sea end to 20-25 m within the Marmara Sea and 10 m near the Aegean end. The interfacial density changes, mainly accounted by the salinity differences, are very strong and occur typically on the order of 7.0-13.0 kg m^{-3}. We recall that this difference is typically an order of magnitude larger than the Mediterranean Sea. The degree of stratification changes seasonally depending on the local as well as remote conditions in the adjacent basins.

Upper layer water mass enters the Istanbul Strait from the Black Sea with salinity S~18.0-18.5 psu. It becomes subject to intense mixing at the constriction and southern sill regions and joins into the Marmara Sea with S~20.0-21.0 psu. Relatively uniform conditions prevail in the upper layer flow along the Sea of Marmara and the upper half of Canakkale Strait where it is characterized by the salinity range 22–26 psu and the temperature range varying from 5-6 ^{o}C in winter to 25-27 ^{o}C in summer. In the Marmara Sea, the upper 20 m layer is followed by an approximately 10 m transition zone with sharp temperature and salinity variations immediately above the Mediterranean water mass. The relatively narrow zone between the radiatively-heated surface layer and the interface is characterized by a relatively cold layer (10-12 ^{o}C) below as a remnant of the cold winter layer. The upper layer flow experiences intense vertical mixing at the elbow-shape Cape Nara section of the Canakkale Strait (Figure 1b) and joins the Aegean Sea as a thin layer of less than 10 m with S~25.0-28.0 psu while its temperature varies with seasons.

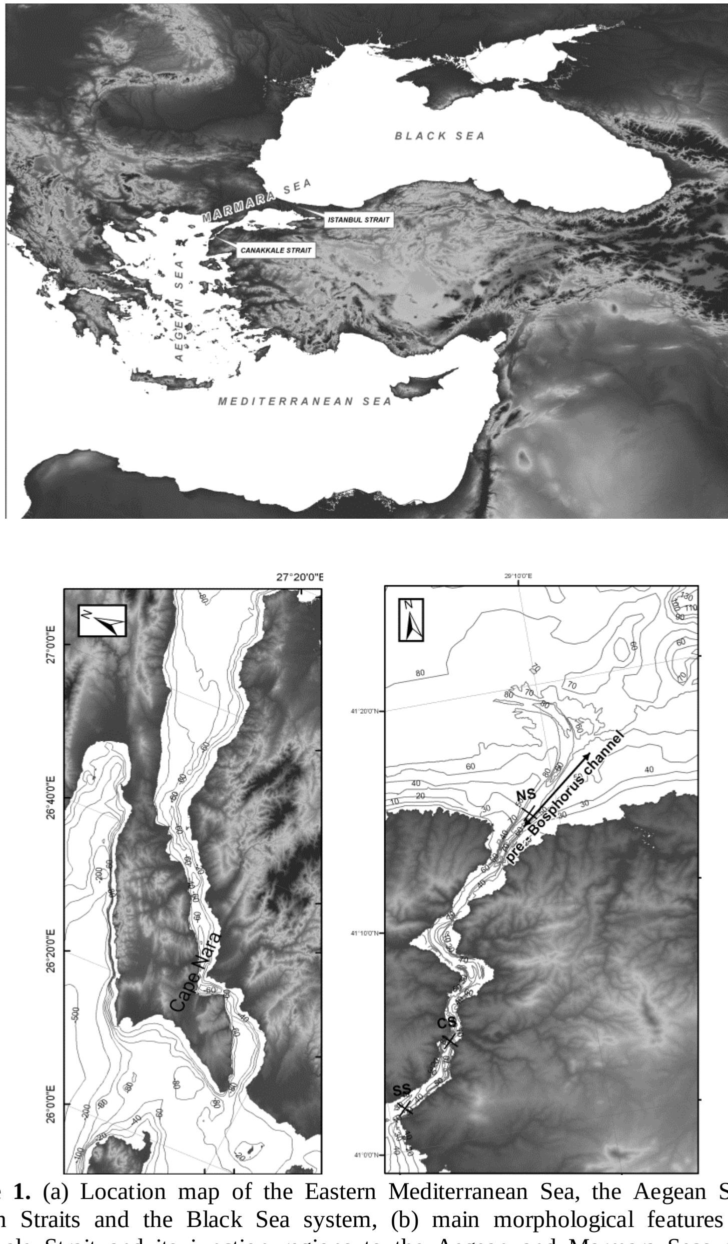

Figure 1. (a) Location map of the Eastern Mediterranean Sea, the Aegean Sea, the Turkish Straits and the Black Sea system, (b) main morphological features of the Canakkale Strait and its junction regions to the Aegean and Marmara Seas and the location of Cape Nara section, (c) main morphological features of the Istanbul Strait, the pre-Bosphorus channel and the Black Sea southwestern shelf region and the crosses with letters SS, CS and NS denoting the locations of the southern sill, the constriction section and the northern sill, respectively.

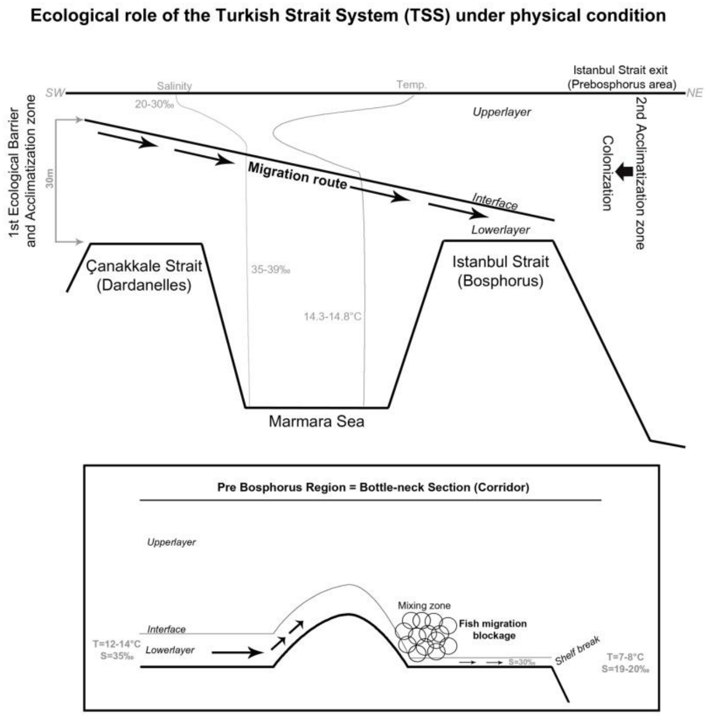

Figure 2. Schematic of the two-layer physical structure of the Turkish Strait System (upper figure) and of the pre-Bosphorus region representing the junction of the Istanbul Strait to the Black Sea (lower figure). The figure also depict important invasion processes as well as typical salinity, and temperature profiles as well as the position of the interface between the flow layers along the TSS.

The relatively dense Mediterranean underflow enters into the Canakkale Strait below the depths of 10-15 m with S~38.9-39.0 psu and temperature T~16-17 ^{o}C. It first undergoes gradual changes along the strait and its transition to the western Marmara basin. It then sinks into the deep basin as a dense water plume with S~38.5- 38.7 psu and T~15.0-16 ^{o}C up to the density levels where they reside, whereas a part of it continues to flow within a narrow oxygenated zone immediately below the density interface. The sinking plume subsequently takes part in the renewal of the sub-halocline waters of the Marmara Sea by spreading isopycnically in the form of intrusive layers. The underflow spends about 6–7 years in the deeper layers of the Marmara basin (Besiktepe *et al*. 1994).

Upon reaching the Bosphorus-Marmara junction region, the lower layer water characterized with T~14.0-15.0 ^{o}C and S~36-38 psu enters the Istanbul Strait through the submarine canyon. Thereafter, interaction of the underflow first with local topography at the southern sill and subsequently the constriction region ~5 km downstream of the sill (Figure 1c) introduce further mixing and dilution. The underflow then arrives at the northern exit typically with T~12.5-14.5 ^{o}C and S~35-37 psu. More importantly its thickness of about 40 m at the Aegean end of the system reduces to 5-10 m at most. Afterwards, strong entrainment process of the underflow into the upper layer introduces further dilution of the underflow on the downstream side of the northern sill, along the pre-Bosphorus channel, up to the shelf break zone of the Bosphorus-Black Sea junction region (Fig. 1c). When it arrives at the shelf break of the southwestern Black Sea, the underflow is identified as a thin plume with a thickness of less than 1 m and almost indistinguishable from ambient water of the region at same depths in terms of its temperature and salinity characteristics (Latif *et al*. 1991). This narrow shelf zone adjacent to the Istanbul Strait serves as a gate for eventual spreading of Mediterranean species over the entire Black Sea (Turan et al, 2009).

Biogeographic barriers along invasion route of Mediterranean species

Physical barriers: The Mediterranean planktonic species and fish larvae encounter their first barrier in the Nara Passage zone of the Çanakkale Strait. Strong vertical mixing may transfer a part of population close to the interfacial zone of the lower layer into the upper layer (Figure 2). This upward movement causes them to experience the strong counter flow structure and transport in the Aegean Sea direction until they are able to move back into the underflow again. The remaining species populations within the lower layer are subject to a second barrier within the junction region to the Sea of Marmara where the major part of the Mediterranean underflow sinks into intermediate and deep layers of the suboxic-anoxic western Marmara basin (Figure 2). Species present within these sinking plumes can not survive any more. Only those which are able to confine within the narrow sub-halocline layer immediately below the interface containing sufficient oxygen are able to survive and maintain their daily dietary characteristics up on their passage of the Sea of Marmara.

Mediterranean species which manage to enter into the Bosphorus exercise four simultaneous shocks as in the case of Canakkale Strait. The first one is induced by the southern sill, the second one by the constriction region, the third one by the northern sill at the Black Sea exit, and the fourth one along the pre-Bosphorus channel (Figure 2). These shocks cause further reduction in Mediterranean species populations on their way to the Black Sea.

Under very strong winter northeasterly wind episodes, excessively large upper layer flow can temporarily fill all depths of the Istanbul Strait with cold waters of about 5-6 ^{o}C, and temporarily blocks the Mediterranean underflow. The abrupt mixing and sudden temperature changes between these two contrasting water masses lead to mass mortalities of planktonic organisms as well as commercial and migratory fish species such as bonito, bluefish, anchovy, horse mackerel. This phenomenon may even be extended into the southern half of the strait near the AnadoluHisar/Kandilli section in some particular years with severe winter conditions.

Physiological barriers: In addition to intense mixing zones along the TSS, the lack of sufficient food for Mediterranean species within the lower layer forces them to move into the upper layer for feeding. Species which move into the upper layer may experience a physiological shock due to abrupt temperature change of about 7-10 ^{o}C and salinity change of about 10-15 psu across the interface, which may be quite unfavorable for some species and especially for larvae. According to Mutlu (2005), Mediterranean species in the Marmara Sea perform limited diurnal vertical migration in order to avoid the strong and persistent salinity stress that affects their osmoregulation ability. They are however expected to do some up and down movements; for example they move upward if the oxygen concentration is below a threshold or move downward if the salinity is below a certain threshold.

In addition to these particular physical and physiological barriers, noise introduced by heavy ship traffic, oil spills, overfishing and chemical pollution are considered as other potential stressors that may further impede the range expansion of Mediterranean species.

Observations on natural alien species settlements into the Marmara and Black Seas

The Marmara Sea likely acts as a major transitional acclimatization - colonization zone prior to settlement of species in the Black Sea. For example, Katagan *et al*. (2004) and Tuncer *et al*. (2008) reported for the first time the settlements of a Lessepsian migrant stomatopod shrimp *Erugosquilla massavensis* and fish *Lagocephalus spadiceus*, respectively, into the Sea of Marmara whereas they have not been reported yet in the Black Sea. Other thermophilic species recorded recently in the Sea of Marmara include the wrass *Thalassoma pavo* and the sea urchine *Arbacia lixula* (Ozturk 2006). These thermophilic species may be considered as a signal of global warming within the region (Francour *et al*. 1994).

The recent observations also support the importance of narrow southwestern Black Sea shelf zone as the acclimation region and a gateway for colonization in the Black Sea. The survivors which are able to reach this region may have a chance for settlement and acclimization to the Black Sea conditions prior to their spreading and colonization depending on their evolving physiological properties. The role of this narrow shelf zone as an area of *holocoenose sui generis* on the physiological adaptation of Mediterranean species into the lower salinity and temperature Black Sea conditions have been emphasized as early as Pusanov (1967), Caspers (1968), Bacescu (1977), and later by Kovalev *et al.* (1999).

The recent example of successful natural invasion was the introduction of pelagic copepod species *Acartia tonsa* during 1990 from the Mediterranean Sea (Kovalev *et al*. 1998). Its success is likely related to its high range of salinity tolerance (between 0 psu and 52 psu) and well-adapted behavior to instantaneous salinity increase up to 10-15 psu whereas it is not sensitive to decreases in salinity (Cervetto *et al*. 1999). Moreover, the alien starfish species *Asterias rubens* has been observed in the Marmara Sea – Istanbul Strait in 1996 (Albayrak 1996) and then for the first time in the Black Sea during August 2003 (Unsal *et al*. 2007). Similarly, the shrimp *Palaemon longirostris* was reported in the Black Sea in July 2005 following its earlier observation in the Marmara Sea in 2003 (Sezgin *et al*. 2008). Inanmaz *et al*. (2002) reported jelly fish *Chrysaora hysoschella* in the central Marmara Sea which was later found in the Istanbul Strait in June 2009. Some fish species like sardine, bogue and salema and the Indo-Pacific species blunt barracuda *Syhyraena obtusata* also extended their distribution ranges to the Black Sea in recent years (Boltachev *et al*. 2002).

A contrary example for an unsuccessful invasion event into the Black Sea is the spreading of *Posidonia oceanica.* Its isolated patches observed today along the northern coast of the Marmara Sea have been genetically related to its relic populations adapted to brackish water conditions during at least the last five thousand years following the formation of the Marmara Sea (Meinesz *et al*. 2009). But they have been unable to move further north into the Black Sea up to now.

TSS as a corridor for fish migrations

The TTS serves as a biological corridor for cetaceans and migratory pelagic fishes of the Black Sea and the Aegean Sea origin. Their different adaptation characteristics with respect to invertebrates allow them to surpass the salinity and other physiological barriers and to live efficiently both in the low salinity environment of the Black Sea and high salinity environment of the Aegean Sea. Some fish species (e.g. horse mackerel, bluefish) and the cetacean harbour porpoise have even been able to develop genetically different populations in the Black Sea and the Marmara Sea as compared to the Aegean Sea (Turan *et al*. 2006, 2008; Martinez-Viaud *et al*. 2007). The migration of cetaceans and large fishes such as bluefin tuna between the Aegean Sea and the Black Sea follows the migration of their main prey fish species such as anchovy, horse mackerel, sprat, bonito, mackerel, and sardine. Currently, however, the heavy marine traffic along the TSS limits severely the cetacean migrations.

Water temperature is a critical environmental parameter that controls the timing of fish migrations. For example, the spring migration of blue fish, bonito and mackerel from the Marmara Sea for spawning to the Black Sea occurs at surface temperature of 11^{o}C (Acara 1957; Demir and Acara 1958) whereas they migrate in autumn back to their feeding grounds in the Sea of Marmara. On the other hand, small pelagic fishes start their migration at 9^{o}C (Oral *et al*. 2008).

Similarly, some Aegean fish species come to the more productive Marmara Sea in spring for feeding and spawning and return to the Aegean Sea in autumn for overwintering.

Observations on major human-mediated bio-invasions

In the Black Sea, the low species diversity and absence of many local competitors provided unoccupied ecological niches for exotic invaders and therefore made biodiversity extremely sensitive to bio-invasions. This is apparent by a progressive rate of increase of alien introductions from 3 to 7, to 11 and finally to 17 in each quarter of the previous century, respectively (Zaitsev and Mamaev 1997). Among the human-mediated alien invasions, those occurring through ballast waters of commercial vessels or as fouling organisms on ship hulls have been becoming a primary mean of bioinvasion. This general view has indeed been firmly supported by the observation of 36 new Mediterranean copepod species during the monthly biodiversity monitoring program in the Novorossiysk Bay located along the northeastern Black Sea coast (with a very busy port) during 2004–2006 (Selifonova 2009). Obviously, not all of these species are expected to become established in their new environment as they may be subject to various threats. Similarly, appearance of 33 new Mediterranean copepod taxa in the western Black Sea (Selifonova *et al.* 2008) and 69 alien species in the Sea of Marmara (Çınar *et al*. 2011) cannot solely be a consequence of natural migration process. Their major portion should be transported by various forms of shipping activities. In addition, according to Çınar *et al.* (2011), there found 20 alien species in the Turkish part of the Black Sea, but this number is less than those in the other seas surrounding Turkey.

Among the introduced species, the mollusc *Rapana venosa*, bivalve species *Mya arenaria* and *Anadara inaequivalvi,* gelatinous carnivores *Mnemiopsis leidyi* and *Boreo ovata* have developed mass populations and gave rise to considerable impacts on functioning the pelagic and/or benthic food webs of the Black Sea during the last several decades of severe ecosystem transformations (see chapters 6 and 8 in BSC, 2008). For example, the bivalve *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 peak abundance in 1972. It was later affected adversely by regular hypoxia-anoxia crisis that destroyed the entire benthos in the 1980s. But it still retains considerable abundance in western coastal waters. Another bivalve of Indo-Pacific fauna *Anadara inaequivalvis* has spread to the whole basin following its first detection in the Black Sea in 1968. The gastropod mollusc *Rapana venosa*, a native of the Sea of Japan, was first discovered in 1947 in the Black Sea. It has settled quickly along the entire coastal zone and reached high biomass and has had serious consequences on oyster and mussel beds.

The most dramatic human-mediated invasion event was the introduction of *Mnemiopsis leidyi* that attained a massive basin-wide bloom in 1989-1990 following its first seen in 1982. The appearance of yet another invasive species gelatinous ctenophore *Beroe ovata* during 1998, a predator of the ctenophore *M. leidyi*, led to a partial recovery of the planktonic food web structure by compensating negative impacts *M. leidyi* on the food web structure.

Mugil so–iuy, a freshwater fish living in Amu Darya River Basin of Far East Asia, is a eurybiontic, eurythermal and euryhaline species with a rapid growth characteristic. It was first introduced to the area around the coast of Azov Sea for fish farming but, a large stock of several tons was released into the Sea of Azov in 1989-1990 after the advent of heavy mortalities in the breeding areas (Kaya *et al*. 1998). It then first migrated to the eastern Black Sea coast of Turkey, and spreaded to the western Black Sea coast of Turkey reaching the Sea of Marmara few years later. Its observation along the Turkish coasts of the Aegean Sea in the second half of 1995 and during 1996 demonstrates its acclimation to the Aegean Sea conditions (Kaya *et al*. 1998).

Discussion

A range expansion of any species requires first dispersal from its native environment and then colonization of the new environment. The present study focuses specifically on the dispersal process of Mediterranean species from the Aegean Sea to the Black Sea in order to offer a mechanistic understanding for inherently low species biodiversity of the Black Sea. We identify a suite of physical and physiological gradients along the TSS perceived by Mediterranean organisms moving toward the Black Sea. The central premise of our explanation is high degree of vulnerability of Mediterranean pelagic and benthic plankton species and fish larvae to long-distance natural expansions due to prevailing strong physical and physiological barriers along the TSS. The physical barriers include (1) very high inter-basin contrasts of temperature (15-16 versus 7-8 ^oC in winter) and salinity (39 versus 18-19 psu) between the Aegean and Black Seas, (2) two layer counter-flow system along TSS, (3) sharp horizontal and vertical temperature and salinity contrasts accompanying the two-layer flow structure, (4) very strong vertical mixing and hydraulic adjustment processes imposed by successive geometrical/morphological controls along the Canakkale and Istanbul Straits. The physiological barriers arise from the temperature, salinity, and oxygen stresses that species may experience during their dial migration and/or their physically-forced vertical displacements. These biogeographical breaks across TSS profoundly constrain the northeastward expansion of Mediterranean species more than southwestern expansion of Black Sea species. Only selected populations which are able to overcome these barriers may ultimately establish self-sustaining populations in the Black Sea.

Survival of some Mediterranean-Aegean Sea species in the Black Sea depends on their ability to adapt to a twice lower salinity range. Thus, the Mediterranization requires long-term physiological adaptation processes with specific behavioral, ecological, and evolutionary aspects for each species (Dingle and Drake 2007). On the basis of available data it is therefore conceivable to propose a two step process of species transfer from the Aegean to the Black Sea. First stage entails crossing of Mediterranean populations the Canakkale Strait and acclimatization of their survivals in the Marmara Sea to establish new upstream ‘source’ populations. Their eventual crossing of the Istanbul Strait and the adjacent pre-Bosphorus underwater channel constitutes the second stage. The Marmara Sea appears to be serving as an acclimatization zone for marine organisms migrating to the Black Sea. Some species can successfully acclimatize the Marmara Sea conditions but they are unable to do so for the Black Sea. As the Marmara Sea serves as an intermediate buffer zone between the two basins, the adjacent narrow and shallow straits on its both sides serve as true bottle-necks for dispersal of pelagic and benthic plankton species and fish larvae. These barriers however do not apply to fish migrations. Organisms which traverse the Bosphorus bottle-neck generally spend an adaptation phase in the southwestern shelf zone before they ultimately disperse within the Black Sea basin.

The decline of species diversity and biological invasions from the Mediterranean to the Black Sea resemble the poleward decline of species biodiversity because of unfavorable conditions of survivorship, reproduction, and population growth as consequences of decreasing temperature. For example, low temperature environment of the Antarctic is considered to be responsible for low diversity of many taxanomic groups through geologic times and is thought to continue operating today as a potential barrier to colonization (Barnes *et al*. 2006). On the contrary, the eastern Mediterranean basin has been experiencing an accelerated rate of tropicalization by the invasion of Indo-Pacific species (also known as the ‘Lessepsian migration’) through the 168 km long Suez Canal. This phenomenon is supported by the unidirectional flow towards the Mediterranean and weak contrasts of flow and stratification characteristics between the Northern Red Sea and Levantine Seas (Galil and Zenetos 2002). However, even for this case, Indo-Pacific species from the more distant populations (i.e. southern Red Sea, 2000 km) are rarely observed in the Mediterranean.

In conclusion, Mediterranization of the Black Sea is an ongoing process under the prevailing physical dispersal and physiological limitations driven by peculiar horizontal and vertical variations of temperature, salinity, and dissolved oxygen concentration along the TSS. Climate change may have been a facilitating factor for a recent increase in new species observations in the TSS and the Black Sea. Future observational studies require building up a cross-disciplinary cooperation in order to elucidate the impacts of physical environment on the biology of invasion events and to advance our present understanding of the Black Sea biodiversity change through natural and human-mediated processes.

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Karadeniz faunasının doğal Akdenizleşme sürecini önleyen mekanizmalar

Özet

Akdeniz'dekinin ancak yaklaşık üçte biri kadar olan biyolojik tür çeşitliliği, Akdeniz türlerinin Karadeniz'deki başarısız biyolojik adaptasyon ve yerleşme sürecinin bir göstergesidir. Bu olay Türk Boğazlar Sistemi (TBS) kolonizasyon yolu boyunca güçlü fiziksel etkileri ve bunlara katılan bazı fizyolojik kısıtlamaları temel alan bir hipotez ile açıklanmaktadır. Havzalar arası güçlü sıcaklık ve tuzluluk zıtlıkları, TBS boyunca iki katmanlı ters akıntı ve tabakalaşma, oldukça güçlü dikey karışım ve hidrolik sıçramalar fiziksel engelleyiciler olarak Akdeniz pelajik ve bentik plankton türleri ve balık larvalarını uzun mesafeli doğal yayılmalara karşı hassas kılmakta ve engellemektedir. Önemli fizyolojik engelleyiciler ise güçlü ve ani sıcaklık, tuzluluk ve oksijen değişimleri sonucu ortaya çıkan büyüme, ölüm ve üreme özelliklerindeki olumsuz etkilerdir. Bu engellerin aşılarak türlerin Karadeniz'e yayılmalarında, Marmara Denizi davranışsal, ekolojik ve evrimsel aklimizasyon süreçleri açısından bir geçiş havzası özelliği taşımaktadır. Burada fizyolojik olarak adaptasyon sürecini tamamlayan yeni "kaynak" popülasyonlar arasından sadece güneybatı Karadeniz sahanlık bölgesine varmayı başarabilenlerin Karadeniz'e aklimize olma ve ardından kendine yetebilen popülasyonlar oluşturma şansı bulunmaktadır. Bu tür güçlü fiziksel ve fizyolojik stresler yıllar arası değişen iklim ve ötrofikasyon kaynaklı olaylardan etkilenmemektedir. Ancak, geçtiğimiz yüzyılın ikinci yarısından itibaren TBS yoğunlaşan gemi trafiği aracılığıyla yabancı türlerin girişleri için de ideal bir geçiş koridoru işlevi görmektedir.

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