A SEA CHANGE – EXOTICS IN THE EASTERN MEDITERRANEAN

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Abstract

The eastern Mediterranean is susceptible to biological invasions because of its placement between the Atlantic, Pontic and Erythrean regions, busy maritime traffic, and lagoons and bays that are crowded with fish and shellfish farms. However, the greatest influx of invaders resulted from the opening of the Suez Canal in 1869, which allowed entry of Indo-Pacific and Erythrean biota. Exotic macrophytes, invertebrates and fish are found in most coastal habitats in the eastern Mediterranean. Some invaders have outcompeted or replaced native species locally, some are considered pests or cause nuisance, whereas other invaders are of commercial value. However, at variance with other invaded seas, the invasion into the eastern Mediterranean has increased the region's biodiversity. The rate of marine biotic invasions has increased in recent decades; collectively they have significant ecological and economic impacts in the eastern Mediterranean. Some Erythrean invaders have already spread as far west as Malta and Sicily, and if global warming was to affect the Mediterranean sea-water temperature, then tropical invasive species would gain a distinct advantage over the native fauna.

Key words: biological invasions, Ionian, Aegean, Levantine, Suez Canal, Red Sea, shipping, mariculture

1 Introduction

1.1 TOPOGRAPHY

The eastern Mediterranean (EMED) comprises the Levantine, Aegean, Ionian and Adriatic Seas (see Occhipinti, this volume). The Ionian Sea connects with the western Mediterranean by the shallow (400 m) Strait of Sicily, with the Adriatic Sea by the

Otranto Passage, and with the Levantine Sea by the Cretan Passage. The Aegean Sea is connected to the Black Sea through the Dardanelles, Sea of Marmara and the Bosphorus (see Ozturk, this volume), and with the Ionian and Levantine Seas at the Cretan Arc Straits. The Levantine Sea is open to the Red Sea and Indian Ocean through the Suez Canal.

The EMED is more active in terms of plate tectonics and is characterized by more complex morphology than the western Mediterranean (Picco et al. 1999). The Ionian, Aegean and Levantine Seas are characterized by deep trenches and raised regions: the Ionian Abyssal Plain is enclosed by the Tunisian Plateau and by the Calabrian and Sirte Rise regions; the Mid-Mediterranean Ridge is bound to the south by the Herodotus Trough, and to the north by the Hellenic Trench. The greatest depth in the entire Mediterranean, 4 982 m, is located in the Ionian Sea, SW of Greece. Recent paleoclimatic data, collected in geologically stable areas, combined with archaeological or historical evidence, indicates that sea level increase might be 30 cm in the 21st century (EEA 1999).

1.2 EARLY HISTORY - IMPLICATIONS FOR THE EVOLUTION OF THE EMED BIOTA

The EMED is a remnant of the Tethys Ocean (Neev et al. 1985). The deep-water communication between the Mediterranean and the Indian Ocean was breached during the early Miocene (Robba 1987), though intermittent marine contacts continued well into the Messinian (Sonnenfeld 1985), and species of Indo-Pacific origin still inhabited the Pliocene Mediterranean (Sorbini 1988). During the Messinian, the Mediterranean was periodically cut off from the Atlantic and the Paratethys, divided into water bodies of varying salinities - freshwater, brackish or hypersaline - or, as some scientists argue, totally desiccated (Hsu et al. 1978). The Messinian Levantine basin may have been a shallow, hypersaline, evaporitic sea, or a brackish, Paratethys-related lago-mare. About 5 million years BP, Atlantic waters supporting tropical and subtropical Atlantic species, refilled the sea. During the Pliocene, the cooling of the sea prompted the substitution of temperate for tropical biota (Ruggieri 1967). The climatic fluctuations of the Pleistocene, accompanied by changes in salinity, temperature, and stratification patterns, have affected the biota as well (Zaccaria 1968).

The Suez rift cleaves the once continuous Arabo-African plate. The rift was formed by the Early Miocene, underwent subsidence and was inundated by the Mediterranean, forming the Clysmic Gulf. However, influx of seawater from the Mediterranean must have ceased during the Messinian (Garfunkel & Bartov 1977). In the lower Pliocene the Gulf of Suez and the Red Sea were settled by Indian Ocean biota. The Suez Canal was constructed (PLEASE RETAIN ORIGINAL WORDING)trough of the Suez rift.

Once a lake connected to the Caspian Sea, the Black Sea was joined to the Mediterranean after the opening of the Dardanelles during the interglacials (100,000-150,000 years BP). Following another period of isolation, the Black Sea was re-connected to the Sea of Marmara and the Mediterranean about 6,000 years BP (Zaitsev & Mamaev 1997).

1.3 HYDROGRAPHY, HYDROCHEMISTRY AND PRIMARY PRODUCTIVITY

The building blocks of the eastern Mediterranean upper thermocline circulation are subbasin scale gyres and permanent, or quasi-permanent, cyclonic and anticyclonic structures interconnected by intense jets and meandering currents (Malanotte-Rizzoli et al. 1999). The Levantine Sea is characterized by the cyclonic Rhodes and west Cyprus gyres, the anticyclonic Mersa-Matruh gyre, the Mid-Mediterranean Jet, and the Shikmona eddy south of Cyprus. In the Ionian sea the strong Mid-Ionian Jet crosses the basin in north-south direction before creating the Mid-Mediterranean Jet ().

The Nile, the largest river flowing into the EMED, passes 89 km³ a⁻¹ at Aswan, but only 5 km³ a⁻¹ flows into the sea. As evaporation exceeds precipitation and river runoff by an estimated 2500 km³ a⁻¹ (EEA 1999), the EMED is a 'concentration basin'. The annual salinity average of surface water ranges from 37.5 PSU in the Sicily Straits to 39.0 PSU in the Levantine Sea. Surface water temperatures show high seasonal variations and range from 14 °C during winter to 30 °C in summer in the Levantine Sea.

The EMED is ultra-oligotrophic: data collected in the past decade confirms earlier results concerning the progressive depletion of nutrients and chlorophyll from the Aegean to the Ionian and Levantine Seas (McGill 1961, 1965; Stergiou et al. 1997). Primary production rates are on average three times lower in the eastern basin than in the north-western basin (Turley 1999); rates integrated over the euphotic zone (maximum depth 120 m) were low (about 40, 78 and 155 mgC n² d⁻¹) in the eastern, central and western Mediterranean basins respectively (Gotsis -Skretas unpubl.). In summer, phosphate concentrations in the euphotic zone in the Levantine Sea are mostly below detection limit of 0.008 µmol and nitrate concentrations are less than 0.6 µmol (Krom et al. 1992); Chlorophyll-a concentrations are as low as $0.4 \ \mu g \ 1^{-1}$ nearshore, and decrease offshore to 0.05 µg Γ^1 (Berman et al. 1986; Yacobi et al. 1995).

Considerably higher nutrient concentrations (5 μ mol nitrate, 0.2 μ mol phosphate) are found beneath the nutricline (ca 200 m) and are injected into the upper layers by wintertime vertical mixing. The nutrient distribution and phytoplankton production in the EMED are principally determined by the duration and the intensity of deep water mixing in the quasi-permanent anticyclonic and cyclonic eddies (Yilmaz & Tugrul 1998). Levantine oligotrophy is attributed to the increasingly nutrient-depleted Atlantic inflow, further reduced by the Levantine intermediate water, the arid and semi-arid climate with low riverine discharge of nutrient-rich waters, limited atmospheric input, and the relatively narrow continental shelf that allows little benthic-pelagic coupling for nutrient recycling.

2 Vectors of invasion

2.1 THE ERYTHREAN INTRUSION

The Suez Canal, 163 km long, traverses a series of shallow lakes, the waters of which ranged from brackish to hypersaline: salinity in the Bitter Lakes was as high as 161 PSU

B. Galil & A. Zenetos

right after opening the canal in 1869 (Vadiya & Shenuda 1985). As sea water flowed through the Bitter Lakes the salinity fell to 70 PSU in 1870-1872, and measurements taken a century later were not much higher than in the northern Gulf of Suez (Morcos 1960, 1980). Another obstacle to invasion has been removed with the damming of the Nile at Aswan. The Nile floods coincided with the summer current inversion and the inflow of Mediterranean water into the canal, resulting in markedly decreased salinity, as low as 26 PSU, in the northern portion of the canal and in the adjacent Mediterranean, and 34 PSU as far as Haifa (Oren 1969; Vadiya & Shenuda 1985). Since the completion of the Aswan high dam, the Nile flow has been drastically reduced. When opened in 1869, the canal was barely 8 m deep and between 65 and 98 m wide. Deepened and widened several times the canal is now 345 m wide and its navigational depth is 20.5 m. Each increase in volume decreased temperature fluctuations within the canal, while increasing depth has probably facilitated the passage of infralittoral species.

Though ship passageways had been constructed since pharaonic times, the ancient waterways were routed through eastern branches of the Nile or extinct deltaic lagoons, which constituted a freshwater barrier for marine biota (Sneh et al. 1975). In contrast, the opening of the Suez Canal initiated the invasion of Erythrean and Indo-Pacific biota into the Mediterranean. Despite impediments such as the canal's length, shallowness, current regime, temperature and salinity extremes, hundreds of Erythrean species traversed the Suez Canal and settled in the Mediterranean, forming thriving populations along the Levantine coasts, with some invaders spreading as far west as Tunis, Malta and Sicily (www.ciesm.org/atlas/).

Already Keller (1882) observed that "Der Isthmusdurchstich wurde ja vermuthlich auch als Karawanenstrasse für die thierischen Bewohner beider Meere benutzt", and Steinitz (1919) commented that "The Suez Canal ... connects two oceans having each a very different fauna from the other, which throws up a number of new problems: Does an exchange of fauna take place between the two oceans by means of this canal? Do the immigrants from the other side flourish on this or die? Has such an immigration caused important changes in the fauna of the eastern basin of the Mediterranean?". The 37 scientific publications resulting from the Cambridge Expedition to the Suez Canal in 1924 answered all three questions in the affirmative. Gruvel (1936) added "Mais si l'ensemble de ces mouvements d'espèces animals et végétales constitue, pour la Science, une fait fort intéressant, les passages définitifs de ces espèces à traverse la totalité du Canal présentent un résultat économique également très important".

Calman (1927), Monod (1932), Ben Tuvia (1970, 1983) and others used the term Erythræan to mark the northwards immigrants through the canal. Por (1971) proposed the term Lessepsian immigration in homage to the French engineer Ferdinand de Lesseps, who supervised construction (1859-1869). The term Erythrean invader refers here to marine organisms living in the Red Sea that have crossed the Suez Canal, as larvae or adults, autonomously or by natural phoresy, and have made their way into the Mediterranean. The occurrence of a species in the Red Sea and its distribution along the Levant coast are considered earmarks of an Erythrean invader.

A small mytilid bivalve, Brachiodontes pharaonis, widely spread throughout the Red Sea (Oliver 1992), was an early entrant into the Mediterranean - it was already in 1876 recorded from Port Said, where it soon became abundant (Pallary 1912). It has spread along the Levant coast from Egypt to Turkey, Cyprus and Greece (www.ciesm.org/atlas/), and even further (see below). Preliminary results of a molecular study have shown that the Mediterranean population possesses both Red Sea genotypes and non-Red Sea genotypes, the latter increasing in frequency with increasing distance from the Canal. This was interpreted as possible indication of ship transport from outside the Red Sea (A. Abelson, pers. comm.). Another early Erythrean intruder, the gastropod Cerithium scabridum, was reported from the Suez Canal by 1882, and has established large, stable populations from Egypt to south-eastern Turkey and Cyprus. C. scabridum too, has been reported from further afield: Naples, Sicily (Italy) and Tunisia (www.ciesm.org/atlas/). Lavie & Nevo (1986) found high levels of genetic variability in both Red Sea and Mediterranean populations of C. scabridum. A more recent, rapidly expanding invader, the gastropod Strombus persicus, was first sighted in Mersin Bay, Turkey, in 1978 (Nicolay & Romagna-Manoja 1983), and then in rapid succession off Israel (Mienis 1984), Rhodes (Verhecken 1984), Cyprus (Bazzocchi 1985) and Lebanon (Bogi & Khaizallah 1987). It was postulated that S. persicus may have arrived in Iskenderun in discharged ballast water from oil tankers coming from the Persian Gulf (Oliverio 1995). However, the gastropod has been found far from oil terminals, and because tankers at the time lacked segregated ballast tanks, oil-laden vessels would not carry ballast water. Off the Israeli coast the shallow sandy littoral is littered with them: 'one can speak of an invasion... hundreds of dead shells on the beaches and shoals of Strombus, of all sizes, colors and patterns, feeding on the sea floor up to 20 m depth' (Curini-Galletti 1988). In recent years it has been sold on the Jaffa fish market (Mienis 1999). The Indo-Pacific rock oyster Spondylus spinosus was recorded off Israel (Mienis et al. 1993) and later off Lebanon and south-eastern Turkey. Although it was not recorded from the Suez Canal, it is assumed to be an Erythrean invader, and it is unlikely that it spread by shipping as proposed by Lamprell (1998).

Each summer since the mid-1980s huge swarms of the invading jellyfish, *Rhopilema nomadica*, have appeared along the Levantine coast. In 1995 the jellyfish was recorded off the south-eastern coast of Turkey (Kideys & Gücü 1995), and in 1998 a specimen was collected near Izmir (A. Karatas pers. comm.). These massive swarms of voracious planktotrophs, some stretching 100 km long, must play havoc with the limited resources of this oligotrophic sea, and when the shoals draw nearer shore, they adversely affect tourism, fisheries and coastal installations. Local municipalities have reported a decrease in holiday makers frequenting the beaches because of the public's concern over the painful stings inflicted by the jellyfish. Coastal trawling and purse-seine fishing are disrupted for the duration of the swarming due to net clogging and inability to sort yield. Water intake pipes blocked with jellyfish pose a threat to cooling systems of port-bound vessels and coastal power plants: in summer 2001 Israel Electric removed tonnes of jellyfish from its seawater intake pipes at its two largest power plants, at estimated costs of 50,000 US\$ (M. Cohen, pers. comm.). Yet, the same jellyfish, *R. nomadica*, known to shelter the juveniles of a Red Sea carangid fish, *Alepes djeddaba*, among its nematocyst-

laden tentacles (Galil et al. 1990), may have precipitated the sudden population increase of this commercially important species (Grofit 1987).

Erythrean penaeid prawns make up most of the shrimp catches along both Egyptian and Israeli coasts (Galil 1993). The Erythrean prawns are highly prized and a small fleet of Israeli coastal "mini" trawlers has specialized in shrimping since the mid 1980s, bringing in a quarter of the total trawl catch volume and a third of the trawl gross income (Snovsky & Shapiro 1999). Marsupenaeus japonicus, Metapenaeus monoceros, and M. stebbingi compose most of the prawn catch off the Mediterranean coast of Egypt and in the Nile delta lagoons (Dowidar & Ramadan 1976; Bishara 1976). An early Erythrean invader, the swimming crab Portunus pelagicus, was recorded from Port Said in 1898 (Calman 1927), where it soon became abundant, and by the early 1900s it was offered in the markets of Port Said, Alexandria and Haifa (Fox 1924). Erythrean fish constitute nearly half of the trawl catches along the Israeli coast (Golani & Ben Tuvia 1995). In the 1990s both invading mullids, Upeneus moluccensis and U. pori, formed 87% of the mullid catch off the coast of Israel at depths of 20 m, and 50% at 55 m, whereas the native mullids were more abundant in deeper waters (Golani & Ben Tuvia 1995). The Red Sea obtuse barracuda, Sphyraena chrysotaenia, has outnumbered the native sphyraenids in inshore trawl and purse-seine catches along the Israeli coast (Grofit 1987). In addition, two of the four species of Erythrean clupeids that established populations in the Levant - Dussummieria acuta and Herklotsichthys punctatus - are of importance in the inshore-pelagic fishery. The growth of these invasive species, to the point where they are harvested commercially, is an excellent index of how prevalent they have become. This abundance is not limited to the south-eastern Levant, as Gücü & Bingel (1994) have estimated that invaders constitute 62% of the demersal fish biomass in the Gulf of Iskendrun, Turkey.

However, among the Erythrean invaders are several well documented cases of rapid increase followed by decline. In the late 1940s the invading goldband goatfish, Upeneus moluccensis, made up 10-15% of the total mullid catches off the Israeli coast. Following the exceptionally warm winter of 1954-55, its percentages increased to 83% but dropped later to 30% of the catch (Ben Tuvia 1973). Following the same winter, the brushtooth lizardfish, Saurida undosquamis, became a commercially important fish: its share in trawl catches rose to 25% in 1979 (Grofit 1987). The population then diminished and stabilized at about 5% of the total trawl catch (Ben Yami & Glazer 1974; Snovsky & Shapiro 1999). Leiognathus klunzingeri was "extremely common on trawling grounds at depths of 20-100 m in the early fifties", but its populations were decimated during 1960s (Ben Tuvia 1985). An extreme illustration is the case of the cerithiid gastropod Rhinoclavis kochi. It was first recorded off the Israeli coast in 1963, but in the early 1970s was recognized as "one of the abundant offshore species of the Mediterranean coast of Israel" (Barash & Danin 1973), and has spread rapidly to become one of the dominant species at depths between 20-60 m, peaking in the late 1970s (Galil & Lewinsohn 1981; Tom & Galil 1990). Samples collected a decade later contained solely empty shells.

2.2 SHIPPING

The eastern Mediterranean, fringed by major ports (Alexandria, Port Said, Haifa, Beirut, Limassol, Iskenderun, Izmir, Thessaloniki, Peiraias) and innumerable marinas, is susceptible to invasion of ship-borne organisms, whether the nonindigenous species occur in fouling communities or ballast.

The oldest maritime pathway of dispersal and introduction is the transportation of fouling biota, sessile and adherent, on ship hulls. Many cosmopolitan members of the fouling community are quite possibly older introductions into the Mediterranean (Ryland 1967; Boudouresque & Ribera 1994). Scleractinian corals are not ordinarily considered members of ship fouling communities, yet the South American hermatypic coral Oculina patagonica was an early transoceanic arrival. Though first noted in 1966 in the Gulf of Genoa (Zibrowius 1974), it has been successively recorded near Egypt (1981), Lebanon (1992) and Israel (1993) (Bitar & Zibrowius 1997), where it is locally abundant. Serpulid polychaete worms of the genus Hydroides are frequently found in tropical fouling communities and are among the earliest documented invaders in the Mediterranean: Hydroides dianthus was documented in Izmir as early as 1865. Given the state of marine taxonomy in the 19th century, the Hydroides species may have arrived many years before they were first detected. They are now well established in ports and lagoons throughout the Mediterranean, where they cause major fouling problems on artificial substrates (Kocak et al. 1999). These worms are however absent from natural marine habitats (Zibrowius 1992).

The American blue crab, Callinectes sapidus, native to the Atlantic coast from Nova Scotia to Uruguay, was first recorded in the Mediterranean in the 1940s, in Egypt (Banoub 1963), and successively in Italy (Giordani-Soika 1951, as Neptunus pelagicus), Israel (Holthuis & Gottlieb 1955), the Aegean Sea (Kinzelbach 1965), and the southern coast of Turkey (Kocatas & Katagan 1983). Holthuis & Gottlieb (1955) suggested that C. sapidus was transported into the Mediterranean in ballast tanks. The veined rapa whelk, Rapana venosa, native to the Sea of Japan, was probably introduced into the Black Sea in the 1940s. It was first recorded in 1947 from the oil-exporting port of Novorossiysk; two specimens were collected near a natural oyster bank in 1986 in Thessaloniki Bay, northern Aegean (Koutsoubas & Voultsiadou-Koukoura 1991). Range extension is possibly mediated by ballast transport of larvae, or of egg masses transported with the products of marine farming. The western Pacific bivalve Musculista senhousia was introduced to the northwest coast of America in 1924 and to Australia in 1983, either with hull-fouling or in ballast. M. senhousia has spread into the French Mediterranean and Adriatic lagoons with imported shellfish mariculture. However, the Egyptian and Israeli records of *M. senhousia* may be either ship-transported or invaders from the Red Sea (www.ciesm.org/atlas). Similarly, the slipper limpet, Crepidula fornicata, has been transported into the Mediterranean with shellfish mariculture (see below), though a record from Saronikos Gulf (near Peiraias port) may be attributed to shipping as there is no oyster farming nearby (www.ciesm.org/atlas). A single specimen of the bivalve Petricola pholadiformis reported from the south Aegean Sea, is also thought to have been accidentally introduced with shipping (www.ciesm.org/atlas). The bivalve Anadara

demiri, a native of the China Sea, presumed to have arrived by shipping, was recorded from the central Ionian Sea (Solustri & Morello 2000). *A. demiri* dominated the highly polluted bottoms in Izmir harbour (Demir 1977), and Thessaloniki Gulf (Zenetos 1994), where its population is presently in decline, perhaps due to amelioration of the pollution. Of the 114 invasive molluscs in the EMED, six are presumed to have been ship-borne. Though the true mode of introduction remains unknown, shipping is assumed to be the most probable vector since their occurrence is patchy, they are frequently recorded from ports and some are known as fouling organisms.

Shipping may serve to transport invading Erythrean species further on. A small Erythrean mytilid, Brachiodontes pharaonis (see above), common in the Levantine Basin, where it settles in dense clusters on midlittoral and infralittoral rocks, piers and debris (Barash & Danin 1992), has spread as far west as Sicily (Di Geronimo 1971), perhaps through ship fouling. Similarly, the gastropod Cerithium scabridum (see above), reported from Naples, Sicily and Tunisia, was possibly transported there by shipping. The pearl oyster, *Pinctada radiata*, was one of the first Erythrean molluscs recorded in the Mediterranean (Monterosato 1878, as Meleagrina sp.). Thirty years after the opening of the canal, it was recorded as forming large banks off Tunis, prompting Monterosato (1899) to suggest it might be indigenous to the Mediterranean. P. radiata is abundant in the Levantine Basin (Barash & Danin 1992) and has spread as far west as the Tyrrhenian Sea, as well as off Sicily, Malta, Pantellaria Island, and France (Ricordi 1993; Di Natale 1982; Tomlin 1927; Sabelli 1969; Zibrowius 1979). Its rapid dispersal is attributed to ship-borne individuals (Zibrowius 1992), or marine turtles - P. radiata was recorded as an epibiont on a loggerhead turtle off Lampedusa Island (Oliverio et al. 1992). The bivalve Fulvia fragilis has been recorded from the Suez Canal (Tomlin 1927), Israel Barash & Danin 1977), south-eastern Turkey and Tunisia (Passamonti 1996). However, its recent finding in Saronikos Gulf (Peiraias port) suggests it may be shiptransported as well (Vardala-Theodorou 1999).

Besides taxa that have established sustainable populations in the Mediterranean, there are ship-transported species that fail to survive: a live specimen of the Brazilian giant barnacle *Megabalanus tintinnabulum* was found on a ship moored in Peiraias port, but not in subsequent surveys of the port (Zenetos 1997).

The Indo-West Pacific portunid crab *Charybdis hellerii* was first sighted in the Mediterranean off the Israeli coast in 1924-1925 (Steinitz 1929), and has since been reported off Egypt, Lebanon, Syria, Turkey and Cyprus (Galil 1993; Zibrowius pers. comm.) – a spread chronology common to Erythrean invaders. Shipping patterns ensure that the Mediterranean exports as well as imports biota. In 1987 *C. hellerii* was collected in Cuba (Gómez & Martinez-Iglesias 1990), and in rapid succession in Venezuela, Colombia, Florida, and Brazil (Campos & Türkay 1989; Lemaitre 1995; Carqueija & Gouvea 1996; Mantelatto & Dias 1999). Transport in ballast tanks is the most probable mode of dispersal because the crab's arrival corresponds to increased shipping contacts with the eastern Mediterranean (Campos & Türkay 1989).

2.3 MARICULTURE

Market-driven demands for exotic fish and shellfish have introduced mariculture farming into lagoons and bays along the shores of the eastern Mediterranean.

The Pacific oyster, *Crassostrea gigas*, native to north-eastern Asia, was introduced to Tunisia, the Ionian Sea (Minelli et al. 1995), to Patraikos, Greece (Dimitrakis 1989), and to Cyprus (Zibrowius 1992). *C. gigas* has established populations outside shellfish farms. A soft-shell clam, the common sand gaper, *Mya arenaria*, native of the North Atlantic, was reported from Saronikos Gulf, probably an accidental introduction as there are no shellfish farms in the vicinity (www.ciesm.org/atlas). The pearl oyster, *Pinctada radiata* (see above) was intentionally introduced to Greece for mariculture purposes, but has since established thriving populations in the wild (Serbetis 1963).

Transport and transplantation of commercially important alien oysters has resulted in numerous unintentional introductions of pathogens, parasites and pest species. Oyster farms have served as gateways into Mediterranean coastal waters for these nonindigenous camp-followers (Ribera & Boudouresque 1995). The slipper limpet, *Crepidula fornicata*, an invasive mollusc on the European Atlantic coast and the North Sea, is assumed to have been introduced with oyster farming. Its occurrence is more local in the Mediterranean. There are presumably separate introductions from the French Atlantic coast to the French Mediterranean lagoons, and from unknown origin to the Italian and Maltese sites (Cachia 1981; Di Natale 1982). The limpet was recorded from Saronikos Gulf (Peiraias port area), probably introduced through shipping as there are no shellfish farms in the vicinity (www.ciesm.org/atlas).

A widely distributed Indo-West Pacific penaeid prawn, *Marsupenaeus japonicus*, that has invaded the Mediterranean through the Suez Canal (see above), and established populations along the Levantine coast from Egypt to Rhodes (www.ciesm.org/atlas), has been successfully cultivated in the Central and Western Mediterranean (Tournier 1972; Lumare & Palmegiano 1980; Rodriguez 1987). Recently, experimental cultivation of the prawn was undertaken in Amvrakikos Gulf, Ionian Sea and in Vistonikos Gulf, N. Aegean Sea (Kevrekidis et al. 996). The widely distributed rock oyster *Saccostrea cucullata* was recorded from the Suez Canal, Egypt and Turkey. It had been imported into the Adriatic, but the cultivation efforts were unsuccessful (Cesari & Pelizzato 1985).

The American blue crab, transported to the Mediterranean in ballast tanks (see above) is found mainly near harbours, estuaries or lagoons (Holthuis 1961). The catadromous, euryhaline crab (Williams 1984) is occasionally caught in the Sea of Galilee, a freshwater lake, whence it was accidentally introduced with grey mullet spat collected in the Mediterranean and used to restock the lake (Snovsky & Galil 1990).

3 Ecological impact of bioinvasions in the eastern Mediterranean

Many of the high-abundance invaders constitute neither a nuisance, nor have commercial value, yet their presence is overwhelming: autochthonous species are outcompeted wholly or partially displaced by the invaders. Though there is no B. Galil & A. Zenetos

documentation of direct competition between Erythrean and indigenous species, there are many instances of sudden changes in abundance; competition is one explanation. Decimation of the indigenous sea star Asterina gibbosa populations along the Israeli coast coincided with the rapid increase of its Erythrean cogener A. burtoni (Achituv 1973). However, recently, after a long absence, a small population of A. gibbosa was detected (Achituv 1999) at a single locality. Between 1992 and 1997 the Erythrean alga Caulerpa racemosa has replaced the native sea grass meadows of Posidonia oceanica in Moni Bay, Cyprus, and prompted significant change in the benthic macrofauna: the abundance of gastropods and crustaceans decreased, whereas that of polychaetes, bivalves and echinoderms increased (Argyrou et al. 1999). A native penaeid prawn, Melicertus kerathurus, was commonly caught by trawlers along the Israeli coastal shelf on sandy or sandy mud bottoms, and supported a commercial fishery throughout the 1950s (Holthuis & Gottlieb 1958). This native prawn has since nearly disappeared, and its habitat has been overrun by the Erythrean penaeid prawns. d'Udekem d'Acoz (1999) reported that M. japonicus "has almost evicted the native P. kerathurus from the easternmost part of the Mediterranean". The rapid advent of Metapenaeus monoceros into the Gulf of Gabes, Tunisia, has raised concerns over the fate of M. kerathurus fisheries (Chaouachi et al. 1998). The Erythrean snapping shrimps, Alpheus lobidens and A. edwardsiiare more common now in the south-eastern Levantine rocky littoral than the native A. dentipes (Lewinsohn & Galil 1982). The decrease in numbers of the once prevalent indigenous jellyfish, Rhizostoma pulmo, along the Levantine coast, has coincided with the massive presence of Rhopilema nomadica.

Competitive displacement may also cause bathymetric changes among populations of Erythrean and indigenous species. The local red mullet, *Mullus barbatus* and the native hake, *Merluccius merluccius* were both displaced into deeper, cooler waters by their respective Erythrean competitors, *Upeneus moluccensis* and *Saurida undosquamis* (Oren 1957). The Erythrean mantis shrimp *Erugosquilla massavensis* was recorded from Alexandria, Egypt in 1933 (as *Squilla africana*) (Steuer 1936), and successively from Israel (Steuer 1938), Turkey (Holthuis 1961), Lebanon (Holthuis 1961), Cyprus (Ingle 1963), and Rhodes (1996, Kevrekidis pers. comm.). *E. massavensis* is common in the south-eastern Levant, and considered to be a "most successful Red Sea immigrant" (Por 1971). Though on occasion it is taken together with the indigenous Spottail mantis shrimp *Squilla mantis*, generally the latter occurs in deeper waters than *E. massavensis*. In the north-western Mediterranean, *S. mantis* is fished commercially at 10-25 m, off the Israeli coast at 70-90 m. Lewinsohn & Manning (1980) questioned "whether temperature, bottom type, or pressure from *O. massavensis*, or a combination of these please retain original as it is a quote are responsible for its depth distribution".

Increase in the number of Erythrean species has coincided not only with displacement of indigenous species but, in some cases, resulted in apparent competition among the invaders themselves. The prawn *Trachysalambria curvirostris* was first recorded in the Mediterranean in 1924 (Balss 1927), already so abundant that it was sold in the Haifa fish market (Steinitz 1929). It was the most common penaeid on sandy mud bottoms until the mid-1980s (Galil 1986). In 1987 another Erythrean prawn, *Metapenaeopsis aegyptia* was

detected in that same habitat (Galil & Golani 1990). By 1993 *M. aegyptia* outnumbered *T. curvirostris* 3 to 1, and by 1996 the native prawn was outnumbered 25 to 1 in samples collected off the Israeli coast. Another Erythrean prawn, *M. mogiensis consobrina*, appeared on the sandy mud bottoms in 1996 (Galil 1997).

It has been suggested that biocontrol, involving the introduction of a predator, parasite or pathogen, may present an option for marine pests management, in particular invasive species (Thresher et al. 2000). Kuris (1997) suggested the use of endoparasitic rhizocephalan castrators, as they may be important regulators of host population density. The Erythrean invasion presented in the last decade an interesting "field experiment". The swimming crab Charybdis (Goniohellenus) longicollis, first recorded in the Mediterranean in 1959 off Turkey (Holthuis 1961), has since spread from Egypt to Cyprus (Lewinsohn & Holthuis 1986); it can form as much as 70% of the benthic biomass on sandy-silt bottoms off the Israeli coast (Galil 1986). Of the thousands of specimens collected over three decades, none showed evidence of parasitism until 1992, when a few bore the sacculinid rhizocephalan Heterosaccus dollfusi - another Erythrean invader (Galil & Lützen 1995). Within three years H. dollfusi had spread as far as the eastern Anatolian coast (Øksnebjerg et al. 1997). The parasite affects the growth, morphology and behaviour of the host, and castrates both male and female crabs. The infection rate in Haifa Bay rose to 77% in 1995 (Galil & Innocenti 1999). Yet, six years later, in spite of high levels of infestation there is no noticeable reduction in the host population.

4 A sea change

Shipping is considered the largest single vector for the movement of nonindigenous marine species across the globe (Ruiz et al. 1997). However, in the eastern Mediterranean, vessel-transported exotics and intentional and unintentional mariculture transfers lag far behind the Erythrean invasion in the number of species introduced – 80%, 87% and 88% of the exotic fish, decapod crustaceans and molluscs respectively are Erythrean invaders (www.ciesm.org/atlas) (). Por (1978) tallied 30 fish, 31 decapods and 44 mollusc species as Erythrean invaders in the Mediterranean, their numbers at present increased to 56, 40 and 101 respectively (www.ciesm.org/atlas).

With over 300 species, mainly molluscs, fish, decapod crustaceans, polychaetes and algae, the Erythrean intrusion is mainly confined to the Levantine Sea and the southeastern Aegean Sea. If earlier passage through the canal might have been restricted to euryhaline, eurythermal and generally hardy littoral species, it is now mainly depthrestricted. Lately, investigations of the Suez Canal biota pointed to intensification of the Erythrean invasion (Halim & Messih 1999). The recently announced plans by the Egyptian government to widen and deepen the Suez Canal to permit passage of super tankers are of grave importance (The Times of India, 18.8.2000). The expansion will increase the canal width to 400 m and its depth to 25 m. Following the amelioration of the salinity barriers, depth is the most important physical impediment to invasion. Most Erythrean invaders occupy at present the Mediterranean littoral and infralitoral to a depth of 50 m, and are hardly found in deeper waters. Thus, an effective increase in canal B. Galil & A. Zenetos

depth of 5 m will allow invasion of species whose upper depth range (as adults or larvae) did not permit passage until now, and cohorts of new invaders will gain admittance to the Levantine Sea.

The Levantine Sea has less than half the number of the benthic species found in the whole of the Mediterranean. This profound faunal impoverishment has been attributed to its comparatively late recolonisation after the Messinian crisis, to pleistocenic climatic fluctuations and to the Basin's extreme oligotrophy (Fredj 1974; Yacobi et al. 1995). Sarà (1985) conjectured that the high temperature and salinity prevailing in the Levant made it unsuitable for many Atlantic-Mediterranean species. The present-day Levantine fauna is not truly representative of the water temperature, since the tropical Atlantic species are mostly barred and their niche is only partially occupied (Türkay 1989), with many of the taxa present presumably at the limit of their ecological tolerance, leaving this part of the Mediterranean vulnerable to invasion. Consequently, when tropical species arrived, there were few ecological obstacles to prevent their successful implantation.

The mariculture introductions are mostly restricted to lagoonar or estuarine habitats, and the vessel-transported exotics to polluted harbours (Zibrowius 1992) - environments known for their low biodiversity. The lagoonar environments differ from the adjacent coastal regions in their hydrography and less diversified biota (Sacchi et al. 1989). The shallow, brackish coastal lagoons, formed by recent changes in sea level and in the pattern of sediment-laden coastal currents, are transitory and unstable environments. This instability may explain their rather limited species diversity. Ionian and Aegean lagoons have been exploited for mariculture of nonindigenous species, and the commercially valuable shellfish have proved successful in establishing reproducing populations. Polluted or physically-degraded environments are prone to invasion more than pristine sites. A recent study of macrofouling organisms discovered that many more species were found in a polluted than in a nonpolluted marina, and that the cosmopolitan serpulid worm, *Hydroides elegans*, which comprised 65% of the population in the polluted marina, was only infrequently found in the nonpolluted marina (Kocak et al. 1999).

The eastern Mediterranean, open to the Atlantic, Pontic and Erythrean biotas, is particularly prone to invasions. The littoral and infralittoral biota of the Levantine Sea is undergoing a profound change due to the influx of Erythrean invaders. Already some Erythrean invaders have spread as far west as Malta and Sicily; if global warming were to affect the Mediterranean sea water temperature, then tropical invasive species would gain a distinct advantage over the native fauna.

The rapid increase in human population density and urbanization along its shores has brought about coastal development, increased levels of agricultural run-offs and industrial wastes, unsustainable fishing practices and mariculture. These changes have caused wide spread disruption of the littoral ecosystem and decimation of the biota. Low indigenous biodiversity is certainly another factor in determining the success of these biotic invasions. The large number of exotic species in the eastern Mediterranean may have resulted from synergy between its geological history, environmental factors and anthropogenic activities.

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