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A review of changes in the fish assemblages of Levantine inland and marine ecosystems following the introduction of non-native fishes

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Summary

The arrival of non-native fishes in the Levant Basin began in the late 19th century. Whereas the presence of most of the 40 non-native freshwater fishes stem from intentional introductions, either for aquaculture or pest control, the 62 species of non-native marine fishes arrived by natural dispersal via the Suez Canal. Of the non-native freshwater species, five have established successful breeding populations (mosquitofish *Gambusia affinis*, common carp *Cyprinus carpio*, crucian carp *Carassius carassius*, swordtail *Xiphophorus hellerii* and rainbow trout *Oncorhynchus mykiss*), and seven are regularly stocked in natural habitats (thinlip mullet *Liza ramada*, flathead mullet *Mugil cephalus*, European eel *Anguilla anguilla*, grass carp *Ctenopharyngodon idella*, Asian silver carp *Hypophthalmichthys molitrix*, bighead carp *Aristichthys nobilis*, black carp *Mylopharyngodon piceus*). Some non-native species appear to have out-competed native species. *Gambusia affinis* may have caused the extirpation of two native cyprinid fishes from the Qishon River basin (Levant silver carp *Hemigrammocapoeta nana* and common garra *Garra rufa*) and the southern Dead Sea (endemic Sodom's garra *G. ghoerensis*). The opening of the Suez Canal in 1869 allowed entry into the eastern Mediterranean of Indo-Pacific and Erythrean biota, with the latter now dominating the community structure (50–90% of fish biomass) and function (altered native food web) of the Levantine littoral and infra-littoral zones. The process has accelerated in recent years concurrent with a warming trend of the seawater. Record numbers of newly discovered non-native species is leading to the creation of a human-assisted Erythrean biotic province in the eastern Mediterranean.

Introduction

Human-assisted changes to the Levantine landscape began in the Neolithic, with the onset of farming and husbandry, which altered vegetation cover and consequently the patterns of soil erosion. Modern land-use practices were not introduced until the late 19th century, resulting in marsh and wetland drainage as well as aggressive regulation of small Levantine Rivers. A similar sequence of change took place in the Mediterranean Sea in which seafaring and fishing practices appear to have begun in the early Mesolithic. For example, well-preserved fish remains discovered in the coastal pre-ceramic Neolithic site of Atlit-Yam, Israel, attest to size-dependent fish processing methods (Zohar et al., 2001). However, the greatest change in the Levantine marine environment took place during the industrial revolution (19th century), with the opening of the Suez Canal. The creation of a direct link between the Mediterranean and Indo-Pacific basins resulted in unintentional and intentional species introductions into the Levantine aquatic systems.

During the same period, most introductions of non-native fish into freshwater systems resulted from intentional introductions, either for aquaculture purposes or for pest control. To date, over 40 non-native freshwater species have been recorded for Israel (Goren and Ortal, 1999; Golani and Mires, 2000), and over 60 fish species of Indo-Pacific origin (Erythrean non-natives) have entered the Levantine Basin through the Suez Canal and established flourishing populations (Galil, 2000; Golani et al., 2002; Goren and Aronov, 2002). The aim of the present study was to review the information on demonstrated and suspected impacts of non-native fishes on Levantine inland and marine ecosystems so as to identify possible reasons for successful invasion.

Freshwater fishes

Freshwater ecosystems in arid and semiarid regions are variable by nature. They experience frequent predictable and unpredictable changes in water flow regime. During the wet season, river discharges can be 100–1000 times greater than in the dry season (Gasith and Resh, 1999). The structure of riverbeds often change during and after floods, and these modifications force the fishes to adapt continuously to new conditions. In Israel, as in many of its neighboring countries, most freshwater hydrosystems suffer from groundwater abstraction, channel modification and water pollution (Goren and Ortal, 1999). The combination of these adverse conditions and the presence of non-native species, most of them opportunistic and resistant to poor water quality, have led to local or regional extinction of fish species.

The native freshwater ichthyofauna of Israel comprises 32 species (Goren, 1974, 1983; Goren and Ortal, 1999). To date, 50 non-native species have been reported (Golani and Mires, 2000), which is relatively high considering the size of the country and the scarcity of natural water sources (Roll, 2004). Of these, five species have established successful breeding populations in natural habitats (mosquitofish *Gambusia affinis*, common carp *Cyprinus carpio*, crucian carp *Carassius carassius*, swordtail *Xiphophorus hellerii* and rainbow trout *Oncorhynchus mykiss*, authority of fish species in Table 1), and seven species are stocked regularly in natural habitats (thinlip mullet *Liza ramada*, flathead mullet *Mugil cephalus*, European eel *Anguilla anguilla*, grass carp *Ctenopharyngodon idella*, silver

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Table 1
List of fish species mentioned in the text with authority[a]

Acanthobrama telavivensis (Goren, Fishelson and Trewavas, 1973)
Alepes djedaba (Forsskål, 1775)
Anguilla anguilla (Linnaeus, 1758)
Aphanius dispar (Rüppell, 1828)
Aphanius fasciatus (Nardo, 1827)
Aphanius mento (Heckel, 1843)
Archocentrus nigrofasciatus (Günther, 1867)
Aristichthys nobilis (Richardson, 1845)
Astatotilapia flaviijosephi (Lortet, 1883)
Atherinomorus lacunosus (Forster *in* Bloch & Schneider, 1801)
Carassius carassius (Linnaeus, 1758)
Coryogalops ochetica (Norman, 1927)
Ctenopharyngodon idella (Valenciennes, 1844)
Cyprinus carpio (Linnaeus, 1758)
Dussumieria elopsoides (Bleeker, 1849)
Gambusia affinis (Baird & Girard, 1853)
Garra ghoerensis Krupp, 1982
Garra rufa (Heckel, 1843)
Hemigrammocapoeta nana (Heckel, 1843)
Herklotsichthys punctatus (Rüppell, 1837)
Huso huso (Linnaeus, 1758)
Hypophthalmichthys molitrix (Valenciennes, 1844)
Leiognathus klunzingeri (Steindachner, 1898)
Liza ramada (Risso, 1810)
Merluccius merluccius (Linnaeus, 1758)
Morone chrysops (Rafinesque, 1820)
Morone saxatilis (Walbaum, 1792)
Mugil cephalus (Linnaeus, 1758)
Mullus barbatus (Linnaeus, 1758)
Mylopharyngodon piceus (Richardson, 1846)
Oncorhynchus mykiss (Walbaum, 1792)
Oreochromis aureus (Stiendachner, 1864)
Oreochromis mosambicus (Peters, 1852)
Oreochromis niloticus (Linnaeus, 1758)
Oreochromis vulcani (Trewavas, 1933)
Pagellus erythrinus (Linnaeus, 1758)
Pempheris vanicolensis (Cuvier, 1821)
Petroscirtes ancylodon (Rüppell, 1838)
Sardina pilchardus (Walbaum, 1792)
Sardinella aurita (Valenciennes, 1847)
Sarotherodon galilaeus (Artedi, 1757)
Saurida undosquama (Richardson, 1848)
Sciaenops ocellatus (Linnaeus, 1766)
Scomberomorus commerson (Lacepède, 1800)
Siganus luridus (Rüppell, 1828)
Siganus rivulatus (Forsskål, 1775)
Sillago sihama (Forsskål, 1775)
Sphyraena chrysotaenia (Klunzinger, 1884)
Sphyraena sphyraena (Linnaeus, 1758)
Sphyraena viridensis (Cuvier, 1829)
Stephanolepis diaspros (Fraser-Brunner, 1940)
Synodus saurus (Linnaeus, 1758)
Upeneus moluccensis (Bleeker, 1855)
Upeneus pori (Ben Tuvia & Golani, 1989)
Xiphophorus hellerii (Heckel, 1848)

[a] In addition to the fish, the jellyfish *Rhopilema nomadica* Galil, 1990 and the aquatic plant *Ceratophyllum demersum* Linnaeus, 1758, are mentioned in the text.

carp *Hypophthalmichthys molitrix*, bighead carp *Aristichthys nobilis*, black carp *Mylopharyngodon piceus*).

The introduction of non-native fishes into Israel dates back to the 1920s when *Ga. affinis* was introduced as an antimalarial agent, and to the late-1930s when *Cy. carpio* was introduced for aquaculture purpose (Goren, 1983; Welcomme, 1988). As its introduction, *Ga. affinis* has spread throughout the Israeli aquatic systems, excluding the springs at the north-eastern end of the Dead Sea. *Gambusia affinis* is resistant to extreme environmental conditions such as pollution and eutrophication and is an efficient predator of invertebrates and fish larvae and post-larvae. In many clear water ponds *Ga. affinis* shares the habitat with the native killifish *Aphanius mento* whereby *Ga. affinis* dominates the open and near shore water and *Ap. mento* is restricted to areas with dense submerged vegetation such as *Ceratophyllum demersum* or *Potamogeton* sp. (Goren, 1983; Alevi, 2003). In most Israeli coastal rivers, *Ap. mento* has unfortunately been deprived of its natural refuge, submerged vegetation, which has disappeared because of pollution and eutrophication. Consequently, *Ap. mento* has disappeared virtually everywhere except in springs of the north-eastern Dead Sea, where *Ga. affinis* is absent and *Ap. mento* is found in open non-vegetated areas (Goren, 1983).

The presence of *Ga. affinis* in the Qishon River basin (Fig. 1), the largest coastal river in Israel, may have caused the disappearance of two native cyprinid fish, *Hemigrammocapoeta nana* and common garra *Garra rufa*. Until the early 1970s, both species coexisted with *Ga. affinis*. The riverbed was modified early in that decade to prevent floods during rainy winters. Both cyprinids were collected in Qishon River system 1975. However, both species were not found in the river during comprehensive surveys carried out in 1978, 2002, 2003 and 2004 (unpublished data). Although water quality is sufficient for these species (both are found in the Jordan River system in water of similar water quality), eutrophication and modification of the bed have deprived the larvae and post-larvae of shelter and exposed them to the *Ga. affinis*. In the southern Dead Sea area, the introduction of *Ga. affinis* probably caused the extinction of the endemic Sodom's garra *G. ghoerensis* from most of the system (unpublished data).

The cyprinid *Acanthobrama telavivensis* is another possible victim of *Ga. affinis*. This endemic species, which once dominated the coastal rivers, has disappeared from most of its distribution region because of its sensitivity to pollution (Elron et al., 2004). Two of the three last surviving populations of this species died out during the drought of 1999. A small population of 150 fish, from two different basins, was saved and is kept in a breeding centre at the Zoological Garden, Tel Aviv University. Half of the 10 000 individuals that were raised in the last 3 years, were restocked in their original basins in 2002 and 2003. However, it appears that although the released fish were in good physical shape and developed gonads during the breeding season, no juveniles were found (unpublished data). *Gambusia affinis* are suspected of preying upon the *A. telavivensis* larvae and post-larvae, and this issue will be examined in 2005 by stocking *A. telavivensis* fish into an artificial pond without *Ga. affinis*.

Cyprinus carpio was imported to the Levantine area from the former Yugoslavia. It has gradually dispersed throughout the country to become the most abundant fish species in the aquaculture industry. *Cyprinus carpio* is resistant of adverse water conditions (Gasith et al., 1998), and its negative effect on other fishes results from its feeding habits. *Cyprinus carpio* seeks food by digging in the riverbed, causing a turbidity that prevents the growth of submerged vegetations (Crivelli, 1983; Lougheed et al., 1997) recycles pollutants that affect sensitive fishes (unpublished data). This particularly acute in the coastal rivers of Israel, where water velocities are very slow during

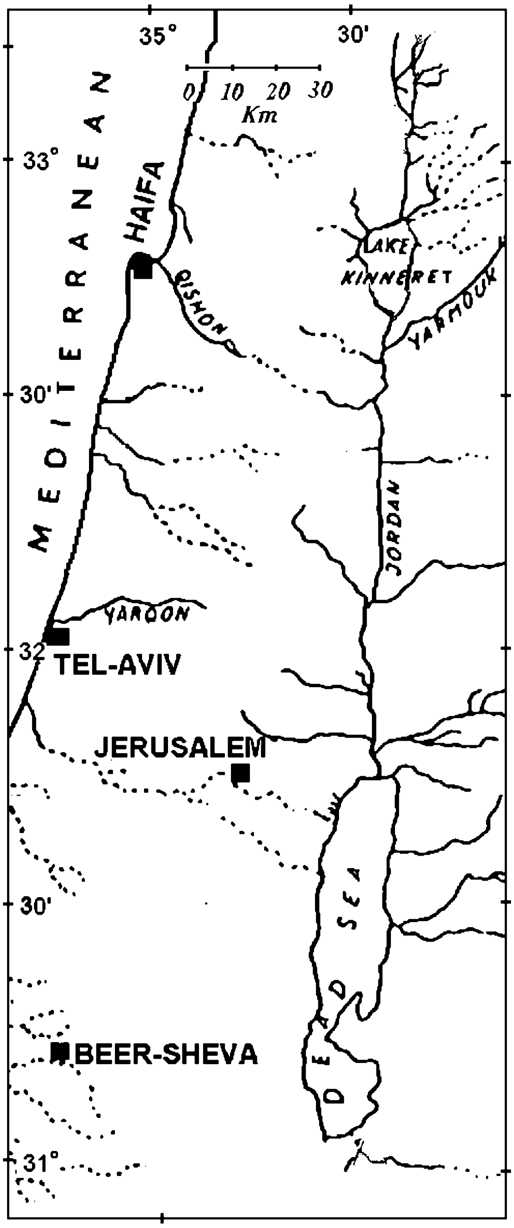

Fig. 1. The freshwater systems in south-east Levantine region

most of the year due to water abstraction and diversion, e.g. Yarqon River (S. Belkin, pers. comm.), Qishon River (B. Herut, pers. comm.). The sediments and pollutants sink to the bottom form particles, which adhere to the riverbed. These particles are continuously resuspended by the carp during their feeding activities.

Oncorhynchus mykiss was first introduced in the 1930s into the coastal rivers and later into a fish farm in the upper Jordan basin. *Oncorhynchus mykiss* failed to establish a population in the coastal river systems and eventually died off. The fish farm in the upper Jordan basin was destroyed during the Israeli war of independence in 1948, and the fish escaped into the wild. The fish farm was rebuilt in 1969. There is no reliable evidence that indicate reproduction of the fish during the 1950s. However, some 40–50% of the fishes in some sites along the Dan stream (near a fish farm outlet) were identified as *O. mykiss* (Krotman, 2004). In view of the wide range of sizes captured (40–374 mm total length), including ripe males and females, the claim by fish farmers that for more than 15 years only female *O. mykiss* have been imported and no male was ever observed in the fish farms, suggests that this species has established a self-sustaining population. Stomach content analysis has shown that the fish consume mainly crustaceans, insects and worms. In a system where 99% of the fish biomass is herbivore fishes (unpublished data 2002–2004), the presence of these non-native predators completely changes the food web.

Another introduced species that has had a similar effect is the swordtail *X. hellerii*. This species, which was introduced in 1940s (Golani and Mires, 2000), is found in some ponds together with *Ga. affinis*, but it also inhabits vegetated areas. The presence of both species in the same system creates a negative synergistic effect for other species (Krotman, 2004).

Four non-native fish species are regularly or unintentionally stocked into Lake Kinneret, which connects the upper Jordan River with the central Jordan River, and have a certain impact on its ichthyofauna. *Hypophthalmichthys molitrix*, of which about 200 000 are stocked annually, competes with some native cichlids for food. During the critical autumn period, when cichlid juveniles must gain maximal weight in order to survive the low winter temperatures, *H. molitrix* and the two native cichlid fish, *O. aureus* and *Sarotherodon galilaeus* compete for zooplankton (Sparatu, 1976; Gophen and Pollinger, 1985; Sparatu and Gophen, 1985a,b). Annual stocking of *L. ramada* and *Mu. cephalus* to Lake Kinneret varies between 0.5 and 1 million juveniles. In addition, an unknown number of *A. anguilla* has been introduced unintentionally into the lake. No study has been carried out on the impact of the introduced mullets on other fish or the environment.

Other non-native species are frequently reported in water courses, some probably have negligible impact, but others may seriously affect it. The South American cichlid *Archocentrus nigrofasciatus* was found in a small stream (Nahal haKibbuzim) in the central Jordan River basin for a period of 10 years, from the mid-1980s. During this time, this species established a self-sustaining population and suppressed the native fish *Astatotilapia flaviijosephi*. For unknown reasons, this non-native fish disappeared from the river. A large specimen of a non-native predator *Sciaenops ocellatus*, weighing over 3.5 kg, was captured in this stream in 2000 and found to contain *Barbus* spp. in its stomach. The estimated total biomass of *Barbus* spp. in this river is 30–50 kg. Assuming that *Sc. ocellatus* had consumed about 35 kg fish to gain its weight, the damage caused to the local *Barbus* spp. population, before *Sc. ocellatus* was removed, was considerable.

Other predatory fishes, such as *A. anguilla*, the sturgeon fish (hybrid of *Huso huso*) and the hybrids of *Morone saxatilis* × *M. chrysops* that were released or escaped from fish farms and can survive in nature for many years, are presenting a new threat to a native fauna that is not adapted to efficient predators.

Another important aspect of these invasions is the genetic contamination of native species by non-native genes. Modern aquaculture relies to a large extent on hybrids, and the introduction of non-native genes through hybrids may be no less destructive than the introduction of a non-native fish. In Israel, hybrids of the native cichlid fish *O. aureus* with the non-native species *Oreochromis niloticus* (*O. vulcani* or *O. mosambicus*) constitute the second important commercial fish in Israel (after *Cy. carpio*). As there is a constant stream of escapee fish from the fish farms into the natural systems, it is reasonable to assume that after 30 years of continuous supply of fertile hybrids, most of the natural populations of *O. aureus* have been genetically contaminated.

In conclusion, the inland waters of Israel, non-native freshwater fishes appear to have caused the decline and even local extinction of native species, genetic contamination of native fish populations, and in addition to fundamental changes in the invertebrate communities, they damaged the water quality. The two worst offenders are *Ga. affinis* and *Cy. carpio*.

Non-native Erythrean fishes in marine ecosystems of the Levantine Basin

The presence of many of the high abundance invaders has resulted in competition for different resources or direct interference between the newcomers and the native species, the latter may be completely displaced from their habitat by the invading species. However, insufficient data are available on the life histories and ecological relationships of native and invasive species to determine which are the competing species, and there is no documented evidence of direct competition between Erythrean and native species. But, there are many instances of sudden changes in abundance and competition is one explanation. With the decline in some native species and the increased abundance of non-native fishes, changes have occurred in the commercial exploitation of fish stocks. Some Erythrean invaders constitute a nuisance or an economic burden, but many species (especially fish) are now exploited commercially.

Early in its existence, the Suez Canal Company sought to exploit the biota in the Canal, and hired Gruvel (1936), a fisheries expert who was familiar with the Levantine fisheries, as 'chef de mission' to identify possible commercially advantageous products. The resulting report, produced by Gruvel (1936), identified fish, decapods and molluscs of economic interest. Among the Erythrean fish fished commercially along the Suez Canal, Gruvel (1936) mentions the clupeids *Herklotsichthys punctatus* (as *Harengula punctata*) and *Dussumieria elopsoides* (as *D. productissima*; Gruvel, 1936), the carangid Erythrean jack *Alepes djedaba* (as *Caranx djedaba*), *Sphyraena chrysotaenia*, *Coryogalops ochetica*, *Petroscirtes ancylodon*, and the Erythrean mullids, *Upeneus pori* (as *Upenoides vittatus*) and *Up. moluccensis* (as *Mulloides flavolineatus*), which were known but uncommon in local markets. Gruvel (1936), a Frenchman, could not resist adding some gustatory advice concerning the filefish *Stephanolepis diaspros* (as *Monacanthus setifer*).

In essence, Gruvel's (1936) report defined the economic importance of the Erythrean invasion, and the resulting fisheries activity was not limited to the Canal and the Egyptian coast. Bodenheimer (1935) witnessed the early penetration of Red Sea forms through the Suez Canal and noticed that quite a number of fishes have not only reached our (SE Levant) shores, but some of them have even increased in such numbers that they appeared regularly in the fish market. By the mid-1990s, Erythrean fishes had become an important part of Levantine fisheries. The rabbitfish *Siganus rivulatus*, which was first reported from the Levantine coast in 1929, had become an important staple of the coastal fishery off Port Said and Alexandria by 1937 (Faouzi, 1951). Insofar as the Israeli and south-eastern Turkish (Gulf of Iskenderun) fishing grounds were concerned, the bulk of the trawler catch from 1950 to 1955 was composed of three species: native red bream *Pagellus erythrinus*, hake *Merluccius merluccius* and the Erythrean yellow striped mullet *U. moluccensis*. The latter were fished commercially in the early 1940s along the southern coast of Israel only, but by 1946–1947 they were found all along the coast (Gottlieb, 1957), and by the late-1940s constituted an estimated 10–15% of the total mullid catch (Wirszubski, 1953). In 1955, Israeli fishermen noticed greater numbers of *U. moluccensis*, and data assembled by the Sea Fisheries Research Station, Haifa, indicated that their percentage in the mullid catch rose to 20%, and to over 83% in early 1956 (Oren, 1957a,b), and was considered the most important commercial fish in the Israel trawl catches (Gottlieb, 1957).

Although the total mullid catch remained constant during the early 1950s, *U. moluccensis* almost completely replaced the native red mullet *Mullus barbatus* in trawl catches (Perlmutter, 1956). Another Erythrean invader, the lizardfish *Saurida undosquamis*, was first recorded in 1953 along the Mediterranean coast of Israel (Ben Tuvia, 1953) as much rarer than the native Mediterranean lizardfish *Synodus saurus*. However, by 1955 *S. undosquama* had became an important part of the trawl catch, with commercial catches increasing steadily to a total of 266.5 tons in 1956, i.e. 20% of the total annual trawl catch (Oren, 1957a,b). The fisheries grounds opposite El-Arish were also dominated by *S. undosquamis* (misidentified as *S. tumbil*), which represented up 53% of the total catch in the spring of 1959 (Gorgy, 1966). In 1962, 652 tons of *S. undosquamis* were landed in the area stretching from Damietta eastward to Port Said (El-Zarka and El-Din Koura, 1965). The sudden increase in the populations of *Sa. undosquama*, *U. moluccensis*, *Sargocentron rubrum* and Erythrean penaeids was attributed to a rise of 1.0–1.5°C in sea temperature during the winter months of 1955 (Ben Yami, 1955; Chervinsky, 1959).

With the completion of the Aswan Dam in 1966, the outflow of Nile waters into the Mediterranean nearly ceased, reducing the phytoplankton bloom on which the sardines fed, and the sardine fisheries decreased from 18 200 tons in 1962 to 1200 tons in 1966 (Al-Kholy and El-Wakeel, 1975). Before the damming of the Nile, the clupeid catch was composed of the native sardines (*Sardina pilchardus*, *Sardinella aurita*), but studies in 1970–1971 revealed that the Erythrean *D. elopsoides* (misidentified as *D. acuta*) accounted for 54% of the clupeid yield on the Egyptian shelf (Al-Kholy and El-Wakeel, 1975). The remarkable penetration of this Erythrean species was considered to be the result of the increasing salinity of the coastal waters (Al-Kholy and El-Wakeel, 1975).

A survey of the *jaroofi* seine fishery in St George Bay (Lebanon) was undertaken to permit evaluation of the changes that are and will be taking place in the fish populations following the High Dam completion, and the salinity decrease in the Bitter Lakes (George and Athanassiou, 1967). Of the 101 species identified, 15% were Erythrean non-natives, but these Erythrean fishes dominated the Levantine near shore fishery. George and Athanassiou (1967) described *S. rivulatus* as one of the most firmly established erythraean immigrants, and one of the commonest fishes of St George Bay. It is taken in large numbers by trammel net, hook and line and seine fishermen. The Erythrean goatfish *U. pori* (described as *U. asymmetricus*) was thought to have already displaced a significant part of the indigenous *M. barbatus* population, Erythrean species like *U. moluccensis* and *S. chrysotaenia* found favour in the markets of Beirut and further north along the coast, respectively.

Examination of the Israeli fisheries statistics since the mid-1980s underscores the growing prominence of the Erythrean non-natives along the Levantine coast. The dominant fishes in the inshore fisheries (trammel-netting and hook-and-lining) are the siganids *S. rivulatus* and *S. luridus*, *S. chrysotaenia*, and *A. djedaba*. The above species, together with *Sillago sihama* and *Scomberomorus commerson*, two species that underwent population explosion in the early 1980s, are common in purse-seine landings (Pisanty and Grofit, 1991; Snovsky and Shapiro, 1999). The sudden increase in the population of *A. djeddaba* may have been precipitated by the massive shoals of the nomadic jellyfish *Rhopilema nomadica*, as the former takes shelter among the latter's nematocyst-laden tentacles (Galil et al., 1990).

Nearly half of the trawl catches along the Israeli coast consist of Erythrean fish (Golani and Ben Tuvia, 1995), as well as half the fish biomass in shallow rocky habitats (Goren and Galil, 2001), and between 50 and 90% of the fish in shallow sandy habitats (unpublished data). The annual catch of *S. undosquamis*, which reached 400 tons in 1960 soon after its arrival, declined to 100 tons in the mid-1960s, but has since increased, and catch fluctuations are correlated with Catch Per Unit Effort (CPUE). Catch statistics for mullids do not distinguish between the native (*M. barbatus*, *M. surmuletus*) and the Erythrean non-native species (*U. moluccensis*, *U. pori*). However, a study in the mid-1980s of the composition of trawl catches revealed that non-native species formed 87% of the mullid catch off the coast of Israel at depths of 20 m, and 50% at 55 m, whereas in deeper waters (> 70 m) the native mullids form over 80% of the catch (Golani and Ben Tuvia, 1995). The percentage of the Erythrean mullids in the total mullid catch has been increasing steadily, from 30% in 1980, 42% in 1984, to 47% in 1989 (Golani and Ben Tuvia, 1995).

Similarly, catch statistics of sphyraenids do not distinguish non-native Red Sea *Sp. chrysotaenia* from the native *S. sphyraena* and *S. viridensis*. However, examination of the landed catch showed that *S. chrysotaenia* had outnumbered the native sphyraenids in inshore trawl and purse-seine catches (Grofit, 1987). In addition, two of the four species of Erythrean clupeids (*D. elopsoides* and *He. punctatus*) that established populations in the Levant are of importance in the inshore-pelagic fishery. The increasing exploitation of Erythrean non-native species meant a shift in trawling grounds to the near shore, because their densest populations occur at depths up to 50 m – between 1980 and 1986, Israeli trawlers doubled their activity in shallow waters (Pisanty and Grofit, 1991). The shoreward displacement of the fishing grounds, coupled with the inexorable gain of Erythrean non-natives, has increased the ratio of non-native to native taxa in Levantine trawl landings.

The prominence of Erythrean species in trawl catches is not limited to the south-eastern Levant. Already in the mid-1940s, *U. moluccensis* was common off the southern Aegean Turkish coast (Laskarides, 1948). By 1952, it constituted a significant portion of the trawl catch in the Bay of Mersin, on the south-eastern Turkish coast (Gottlieb, 1957), concurrent with a decline in numbers of the previously common native *M. barbatus* (Oren, 1957a). By the mid-1960s, non-native *S. undosquamis* formed the main catch of trawlers off Mersin (Ben Tuvia, 1966). A study conducted in 1980–1984 in the Gulf of Iskenderun, Turkey, showed that Erythrean fishes constituted up to 74.5% of fish landings in the fall months (Gücü and Bingel, 1994). At depths of 14–59 m, Erythrean fishes (mainly *Leiognathus klunzingeri* and *S. undosquamis*) accounted for 51.9% and 67.6% of the biomass in October of 1983 and 1984, respectively. The importance of non-native species for the Anatolian fishery is increasing. *S. undosquamis* and *U. moluccensis* are the most abundant and commercially utilized fish species found in nearly every haul (Gücü et al., 1993; Gücü and Bingel, 1994).

The first known case of a complete replacement of a native fish by a non-native species is that of *A. fasciatus*, which was replaced by *A. dispar* within 40 years. The first *A. dispar* was collected off Tel Aviv, Israel, in the winter of 1943/1944 (Mendelssohn, 1947), and the last specimens of the native *A. fasciatus* were collected at Dor on 13 August 1976 (preserved in the National Collections, Tel Aviv University, access number 6319). *Aphanius dispar* is a notably euryhaline species, occurring in freshwaters as well as in saline waters up to four times the salinity of seawater. Whereas, *A. fasciatus* occurs mostly in brackish lagoons (Maltagliati, 1999). Both *Ap. dispar* and *A. fasciatus* were described from the Suez Canal and its lakes (Tillier, 1902; Norman, 1927). Both Norman (1927: p. 386) and Tortonese (1954) suspected the species interbred. Indeed, of the 4600 killifish collected between 1973 and 1975 in the hypersaline Bardawil Lagoon (coast of Sinai, Egypt), 45% were *A. dispar*, 17% *A. fasciatus* and 38% were hybrids (Lotan and Ben Tuvia, 1996). Naturally occurring hybrids of the two killifish species have been described as common, and in some locations (Ashdod Harbour, southern coast of Israel), parts of Bardawill Lagune, etc. the two populations include a large proportion of hybrids (Goren and Rychwalski, 1978). Villwock (1985) also described hybrids from Bardawil Lagoon and al-Qanatir, Egypt.

The two herbivorous siganid species (*S. rivulatus*, *S. luridus*), comprise a third of the total fish biomass in the Shiqmona reef and other rocky habitats along the Israeli coastline (Goren and Galil, 2001). Prior to their arrival, the role of herbivore fish in the food web in the Levantine rocky habitats had been negligible. The original food web had two components, and the algal contribution to the web was mainly through the decomposers (bacteria, fungi and protozoa) that in turn constituted the main source of food for the upper level of consumers. The arrival of the siganids brought on fundamental changes that 'normalized' the food web (e.g. Christensen and Pauly, 1992; Pauly and Christensen, 1993) by increasing the rate of recycling of large amounts of algal material, from weeks or months (by decomposition) to hours (via the fish gastrointestinal system), and by provision of prey for larger predators (e.g. groupers), which may have up to 70% of their diet composed of siganids (Aronov, 2002). The siganids have also altered the structure of the algal community; it seems that they have nearly eradicated locally some of their favorite types of algal prey (Lundberg et al., 2004).

Dietary shift is another interesting strategy. Two of the most common Erythrean planktivores now inhabiting the Mediterranean Sea, *Atherinomorus lacunosus* (sandy bottoms), and the nocturnal *Pempheris vanicolensis* (rocky shores), took mostly zooplankton in the Red Sea. But in the Levantine Basin, they feed almost exclusively on zoobenthos (Ogorek, 1999), and as such they compete with the native benthivorous fish species.

The fundamental changes caused by non-native species in the Levantine Basin of the Mediterranean Sea have gone far beyond recorded impacts in other marine ecosystems. The community structure and function in the Levantine Basin littoral and infra-littoral are dominated by Erythrean species; these non-native species comprise 50–90% of the fish biomass and have altered the native food web. The process has accelerated in recent years, with record numbers of newly discovered Erythrean species (CIESM, 2005). The draft of the Suez Canal in 1869 was 7.0 m and its width 22 m, and it traversed a series of shallow lakes, the waters of which ranged from brackish to hypersaline (Vadiya and Shenuda, 1985). Deepened and widened several times, the canal is at present between 300 and 365 m wide and its maximum permissible draught is 58 ft (IMSALEX, 2005). Earlier passage through the canal might have been restricted to euryhaline, eurythermal and generally hardy littoral species, but at present it is restricted mainly by water depth.

The plans underway to widen and deepen the Suez Canal to permit passage of larger oil tankers is of grave importance. An effective increase in canal depth of 5 m will allow invasion of species whose upper depth range (as adults or larvae) did not permit passage until now (e.g. sand dwelling gobies, blennies), and cohorts of new invaders will gain admittance to the Levantine Sea. One would expect that in an age of heightened environmental concern plans to deepen the Suez Canal, which had served as a conduit for over 80% of the known non-native taxa in the Mediterranean, would raise a great deal of attention, controversy and a discussion on environmental accountancy. Unless a salinity barrier (such as an hypersaline lock) is installed in the Suez Canal, the Eastern Mediterranean countries would find the biota in their part of the sea subject to even further fundamental change. The continuous invasion of species through the Suez Canal, accompanied by climate change, is leading to the establishment of an Erythrean province in the eastern Mediterranean.

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