

## Impact of Red Sea Fish Migrants through the Suez Canal on the Aquatic Environment of the Eastern Mediterranean

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### ABSTRACT

The invasion of Red Sea organisms through the Suez Canal, known as "Lessepsian migration" (after Ferdinand de Lesseps, the Frenchman who directed the canal's construction), has profoundly modified the ecosystem of the Eastern Mediterranean. This migration, the result of major man-made changes in the area, has given us a unique opportunity to study the process of invasion and colonization by tropical biota of a sub-tropical region populated by temperate biota. The present research on Lessepsian fish focuses on three major areas: 1) identifying the characteristics distinguishing colonizer species from closely related non-colonizer species in the Red Sea; 2) assessing the colonizer populations' responses to the new environmental conditions; and 3) studying the impact of the Lessepsian migration on the Eastern Mediterranean ecosystem.

### INTRODUCTION

No zoogeographic marine area of the world has been affected more by man-made changes than the eastern Mediterranean. Two major projects have heavily influenced the Levantine marine ecosystem: the construction of the Suez Canal, completed in 1869, and, to a lesser extent, the Aswan High Dam. The dam, which became fully operational in 1964, resulted in the cessation of fluvial sedimentation and nutrients to the Mediterranean, leading to a sharp decrease in fish populations, mainly sardines (Aleem 1972); as a result, the Egyptian purse seine fishing industry today takes only 10% of the pre-dam catch. The Suez Canal, however, has had an even more significant and lasting impact.

The opening of the Canal in 1869 has had zoogeographic and ecological ramifications far beyond those envisioned by its designers, who only intended to provide a quick trade route from Europe to India and the Far East. Stretching from Port Said in the north, the Suez Canal continues southward for 162.5 km, crossing Lake Timsah and the Bitter Lakes on its way to the city of Suez and the Gulf of Suez. For most of its length, the canal is quite narrow, only 200–300 m, and very shallow, 10–15 m. The canal connects two major bodies of water, the Red Sea and the Mediterranean, which differ fundamentally both faunistically and hydrographically. The main abiotic difference between the two regions is the temperature regime, which is stable in the tropical Red Sea but experiences wide fluctuations in the subtropical Mediterranean. The fauna of the Red Sea is of tropical Indo-Pacific origin, while that of the Mediterranean is mainly of temperate Atlantic origin. In the wake of the

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opening of the Suez Canal, each sea was exposed to invasion of organisms from the other sea. However, the vast majority of migrational movement has been from the Red Sea to the Mediterranean. This influx of biota from the Red Sea into the Mediterranean has been termed "Lessepsian migration" (Por 1978), in recognition of Ferdinand de Lesseps, the engineer and spirit behind the creation of the Suez Canal. The minor migration in the opposite direction is known as "Anti-Lessepsian migration." This phenomenon encompasses all major taxa. It is interesting to note that in all studied taxa, the percentage of Lessepsian migrants in the Levant is quite high: 7.1% of Polychaeta (Ben-Eliyahu 1995); 22.9% of decapod crustaceans (Galil 1992); 9.4% of Mollusca (Barash 1992) and 13.2% of fish (Golani 1996). Among all taxa, the study of fish is advantageous, since their taxonomy is well known and, due to their commercial importance, constant information on quantitative and qualitative changes of migrant and native populations is available through the local fisheries (Golani and Ben-Tuvia 1995).

The phenomenon of Lessepsian migration provides a unique opportunity to investigate, on a large scale, processes of migration, invasion and colonization, processes which usually occur over a geological time scale.

Lessepsian fish research commenced shortly after the opening of the Suez Canal, with the monitoring of fish species in the canal itself (Keller 1882; Tillier 1902). Until the late 1970s, the vast majority of studies were limited to reporting new arrivals and creating inventories of migrant species (Ben-Tuvia 1966, 1978). In the 1980s and 1990s, a wider approach has been taken, emphasizing quantitative and qualitative ecological analyses (Ben-Tuvia 1985; Golani and Ben-Tuvia 1995). The present research on Lessepsian fish focuses on three major areas:

- identifying the characteristics distinguishing colonizer species from closely related non-colonizer species in the Red Sea;
- assessing the colonizer populations' responses to the new environmental conditions; and
- studying the impact of the Lessepsian migration on the Eastern Mediterranean ecosystem.

#### WHAT IS A SUCCESSFUL LESSEPSIAN FISH MIGRANT?

It has been observed in many taxa that some species have a high dispersal and colonization ability while other closely related species with similar ecological requirements do not. In the Red Sea, there are a number of fish families with several species, of whom only a few have established populations in the Mediterranean.

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For example, there are 14 Goatfish (Mullidae) species in the Red Sea (Goren and Dor 1994), but only two, *Upeneus moluccensis* and *U. pori*, have migrated to the Mediterranean. Similarly, there are 15 species of Squirrelfishes (Holocentridae) in the Red Sea but only one colonizer in the Mediterranean, namely, *Sargocentron rubrum*.

The question of how to distinguish a potential colonizer was first approached by Elton (1958). In the mid 1960s, Baker and Stebbins (1965) and MacArthur and Wilson (1967) were among the first to study this problem in a multidisciplinary manner. In the Red Sea, their approach was utilized in the study of mollusc migrants (Lavee 1983; Lavee and Ritte 1994). Selander and Kaufman (1973) noted that there are great differences between invertebrates and fish concerning their response to changes in the environment. In the current study, criteria which distinguish the successful colonizer were examined in four critical areas. The goatfish family (Mullidae) was the subject of this multidisciplinary approach. The four factors chosen for examining the correlation to successful colonization were:

- genetic variability;
- breadth of trophic niche;
- life history strategy; and
- relative importance in the fish assemblage in the source site (Red Sea).

#### GENETIC VARIABILITY

Since the conditions in the target area differ from those prevailing in the source area, the colonizer must respond rapidly to changes encountered in order to establish a sustainable population. Theoretically, an adequate response to the new selective pressure demands high genetic variability, so that within the given wide genetic repertoire, the appropriate genotype can be found, become dominant, and thus lead to successful adaptation. Five non-colonizer species of Mullidae, *Mulloides flavolineatus*, *Parupeneus forsskali*, *P. rubescens*, *P. macronema* and *Upeneus subvittatus*, were compared to two mullid colonizers, *Upeneus moluccensis* and *U. pori*. Genetic variability was tested by electrophoretic examination of allozymes; the results revealed no correlation between genetic variability and success in colonization (Golani and Ritte 1993). These results confirm the general findings of Gray (1986) and Barrett and Richardson (1986). However, Parsons (1983) claimed that examination of specific allozymes responsible for adaptation to new environmental conditions and facilitating success in colonization would reveal differences between colonizers and non-colonizers.

### TROPHIC NICHE BREADTH

The theoretical basis for examination of this factor resembles that for the previous factor, genetic variability, namely, that species which feed on a wide variety of food types (termed “generalist feeders”) will be better potential colonizers. Species with a narrow trophic niche breadth (“specialist feeders”) are less likely to find appropriate food in the new area. The feeding habits of three non-colonizer mullids, *Mulloidides flavolineatus*, *Parupeneus forsskali* and *P. rubescens*, were compared to that of the colonizer *Upeneus pori* (Ben-Eliahu and Golani 1990). No correlation was found between trophic niche breadth and success in colonization.

### LIFE HISTORY STRATEGY

This factor is defined as the sum total of demographic features that determine the species’ fitness. MacArthur and Wilson (1967) developed a model, by which a continuum of life history strategy is determined. One end of the continuum represents the “r-strategist,” which is characterized by rapid growth rate and a high reproductive potential (which is expressed by a high intrinsic rate of increase, early sexual maturity, small body size, a short longevity and usually only one reproductive season). On the other end is the “K-strategist,” which is characterized by the opposite features. MacArthur and Wilson (1967) and Safriel and Ritte (1980) predicted that r-strategists would be better colonizers. Their reasoning was based on the hypothesis that smaller populations have greater probability of random extinction. Since the pioneer group of invaders is usually small, not more than a few individuals, the invaders must have the ability for rapid population growth in order to avoid extinction. Moreover, in the case of invaders who perceive their new environment as unpredictable in contrast to the source environment to which they have been long adapted, the invaders are prone to ecological catastrophes that are liable to decrease their population, leaving a very small number of individuals.

The association between life history strategy and success in colonization has been studied also in the family Mullidae. Table 1 summarizes demographic data on goatfishes in the source area of the Red Sea, obtained by Golani (1988) and others. From the data it can be concluded that the two colonizer species are indeed “r-strategists” as compared to the non-colonizers. However, Golani (1988) postulated that in the particular case of the eastern Mediterranean, which is a heterogeneous ecosystem as compared to the Red Sea, the r-strategists had an advantage in colonizing this unpredictable environment. Therefore, r-strategists are not necessarily

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always better universal colonists. For example, the rivers of North America are dominated by typical K-strategist (mainly Cich lidae) colonizers (Stauffer 1984).

#### Relative importance in fish assemblage in source site

It is evident that, in order for colonization to be successful, there must be some similarity between the environmental conditions of the source habitat and that of the target habitat. This overlap must be within the range of tolerance of the colonizer. Golani and Ben-Tuvia (1989) showed that the habitat in the eastern Mediterranean that is the most prone to Lessepsian colonization is shallow sandy or muddy substrates. The closest equivalent to this Mediterranean habitat in the Red Sea is the sandy shore. Examination of the fish assemblage in the Red Sea sandy shore revealed that the dominant species in this assemblage were Lessepsian migrants, who inhabited this habitat throughout all their life stages (Golani 1993 a). It was therefore concluded that dominance in the equivalent source habitat constitutes pre-adaptation to success in colonization of the Eastern Mediterranean by Lessepsian fish migrants.

Table I Some demographic data of colonizing and non-colonizing goatfishes (Mullidae) from the Red Sea and other native sites.

	COLONIZERS		NON-COLONIZERS			
	<i>U. mol.</i>	<i>U. pori</i>	<i>M. fla.</i>	<i>M. van.</i>	<i>P. for.</i>	<i>P. hep.</i>
Spawning season	Apr.- Dec. <sup>a</sup>	Mar.-Apr.	Mar.-Aug.	May-Sep. <sup>c</sup>	—	—
Size at benthic settlement (mm, SL)	45.0 <sup>b</sup>	27.2	50.0	—	50.0	—
Age at first reproduction (month)	12 <sup>b</sup>	9	36	—	24	—
Size at first reproduction (mm, SL)	104 <sup>b</sup>	61	130	—	115	—
Maximum attainable size (mm, SL)	170 <sup>b</sup>	135	328 <sup>c</sup>	363 <sup>c</sup>	230	444 <sup>c</sup>
Growth rate coefficient	0.303 <sup>b</sup>	0.663	0.213 <sup>c</sup>	0.160 <sup>c</sup>	0.261 <sup>d</sup>	0.208 <sup>e</sup>

<sup>a</sup> - Southern Red Sea (Ben-Tuvia 1968) <sup>b</sup> - Hong Kong (Lee 1974) <sup>c</sup> - Gulf of Aqaba (Wahbeh 1992)

<sup>d</sup> - " " (Wahbeh and Ajiad 1985) <sup>e</sup> - " " (Al-Absy and Ajiad 1988)

*U. mol.* = *Upeneus moluccensis*, *U. pori* = *Upeneus pori*, *M. fla.* = *Mulloidides flavolineatus*, *M. van* = *Mulloidides vanicolensis*, *P. for.* = *Parupeneus forsskali*, *P. hep.* = *Parupeneus heptacanthus*.

## RESPONSE TO THE NEW ENVIRONMENT

Once the colonizers have established a population in the target area, they are presumably isolated from their source population and are exposed to new selective pressures which may result in phenotypic and genotypic changes in the new population (Parsons 1982). In order to test this hypothesis, a comparison was made between the source and target populations. Golani (1990) compared specimens from the source (Red Sea) and target (Eastern Mediterranean) populations of seven species of Lessepsian migrants. In most species, the spawning season was shortened in the Mediterranean, presumably due to the constraints of the colder temperature regime. In some species, changes were noted in some meristic counts, namely, number of dorsal and anal rays, number of lateral line scales and number of vertebrae. All these changes have been attributed to the prevailing temperature during spawning season (Golani 1990; also see Lindsey 1988).

Golani and Ritte (1993) compared allozymes of source and target populations of two Lessepsian fish migrants, *Upeneus moluccensis* and *U. pori*. No discernible genetic differences were found. It should be noted that this method of allozyme analysis is rather crude and is not sufficiently sensitive to discern small alterations. Current techniques such as DNA sequencing are able to detect minute changes and it is in this direction that research should progress.

Diet adaptations were studied in several species of Lessepsian migrants. As anticipated, the feeding habits of colonizers remained generally similar to those of the mother population. Some small differences were noted; for example, *Upeneus pori* feeds in the Mediterranean upon a wider size range of prey. The algal composition of the diet of the two rabbitfish, *Siganus luridus* and *S. rivulatus*, was altered in the Mediterranean. However, lack of quantitative data on trophic resources in both the source and target areas prohibits a determination of whether these changes are the result of selectivity or availability.

## IMPACT OF LESSEPSIAN MIGRANTS ON THE EASTERN MEDITERRANEAN

A total of 54 Lessepsian fish species have been recorded to date (Golani 1996), representing 37 families, of which 13 are new to the Mediterranean (Table 2). Out of these 37 families, 25 are represented by only one species; 8 by two species; three families by three species and one family (Clupeidae) by four species. The Lessepsian fish species constitute 13.2% of the total number of ichthyofauna in the Levant. These species have a qualitative and quantitative importance beyond their percentage in the composition of the local ichthyofauna; more than half of the species have become common in

*Almost half of the catch of trawl fishery in the Mediterranean coast of Israel can be attributed to Lessepsian migrant species.*

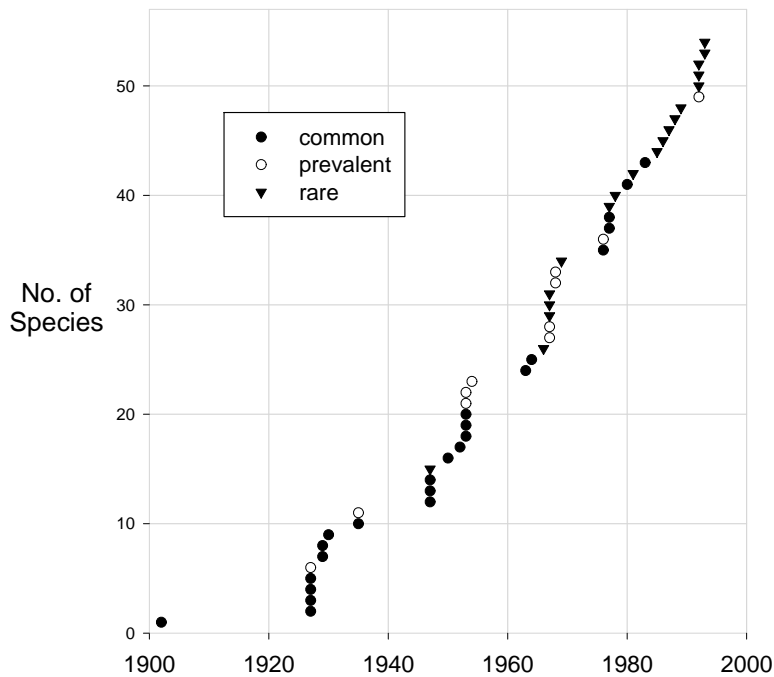


Figure 1 Cumulative count of Lessepsian migrant species as a function of the year of first record.

the eastern Mediterranean and at least 18 species contribute to the local fishery. Almost half of the catch of trawl fishery in the Mediterranean coast of Israel consists of Lessepsian migrant species (Golani and Ben-Tuvia 1995). It is difficult to determine precisely the percentage of Lessepsian migrants in the catch of other fishing methods, but it is estimated to be considerable.

There is a clear east-west gradient in the distribution of Lessepsian migrant species in the Mediterranean. There are 54 Lessepsian migrant fish species along the Levantine coast. This number gradually decreases along the gradient westward, up to the coasts of Tunisia and Sicily. Thirty Lessepsian migrant fish species inhabit the southern coast of Turkey and 32 inhabit the Mediterranean coast of Egypt. Only four Lessepsian species have been found along the southern coast of Italy, and no Lessepsian species have been found in the western basin of the Mediterranean.

From Table 2 and Figure 1, a clear correlation can be seen between the year of first record of individual Lessepsian migrant species in the Mediterranean and each species' current abundance along the Mediterranean coast of Israel. In general, those species that appeared earlier are currently more abundant. Although date of first record is not identical with the actual first arrival of a Lessepsian species to the Mediterranean, it is reasonable to assume that the chance of a species being collected and recorded increases with

Table 2 List of Lessepsian fish migrants. \* - new family to the Mediterranean; IP - inshore-pelagic, M - muddy, P - pelagic, R - rocky, S - sandy, V - vegetation; Abundance: + - rare, ++ - prevalent, +++ - common; 1<sup>st</sup> Year of Record - year of first record in the Mediterranean; BS - beach seine, N - trammel and gill nets, PS - purse seine, T - trawl.

Family	Species	Habitat	Abundance	1st Year of Record	Commercial
DASYATIDAE	<i>Himantura uarnak</i>	S&M	++	1955	T
CLUPEIDAE	<i>Dussumieria acuta</i>	PS	+++	1953	IP
	<i>Etrumeus teres</i>	P	+++	1963	PS
	<i>Herklotsichthys punctatus</i>	IP	+++	1976	PS
	<i>Spratelloides delicatulus</i>	IP	+	1978	—
CONGRIDAE	<i>Rhynchoconger trewavasae</i>	M	+	1993	—
MURAENESOCIDAE*	<i>Muraenesox cinereus</i>	M	+	1982	—
SYNODONTIDAE	<i>Saurida undosquamis</i>	S&M	+++	1953	T
EXOCEOETIDAE	<i>Paraexocoetus mento</i>	P	++	1935	PS
BELONIDAE	<i>Tylosurus choram</i>	P	+	1963	—
HEMIRAMPHIDAE	<i>Hemiramphus far</i>	P	+++	1927	PS
	<i>Hyporhamphus affinis</i>	P	+	1967	—
ATHERINIDAE	<i>Atherinomorus lacunosus</i>	IP	+++	1902	—
HOLOCENTRIDAE*	<i>Sargocentron rubrum</i>	R	+++	1947	N
SCORPAENIDAE	<i>Pterois miles</i>	R	+	1992	—
PLATYCEPHALIDAE*	<i>Papilloculiceps longiceps</i>	S	+	1990	—
	<i>Platycephalus indicus</i>	S	++	1953	—
	<i>Sorsogona prionota</i>	S	+	1947	—
SERRANIDAE	<i>Epinephelus coioides</i>	R	+	1969	—
	<i>Epinephelus malabaricus</i>	R	+	1969	—
TERAPONIDAE*	<i>Pelates quadrilineatus</i>	S	++	1970	—
	<i>Terapon puta</i>	S	++	1976	—
APOGONIDAE	<i>Apogon nigripinnis</i>	R	+++	1947	—
SILLAGINIDAE*	<i>Sillago sihama</i>	S	+++	1977	PS
RACHYCENTRIDAE*	<i>Rachycentron canadum</i>	P	+	1986	—
CARANGIDAE	<i>Alepes djedaba</i>	S&IP	+++	1927	BS&PS
LEIOGNATHIDAE*	<i>Leiognathus klunzingeri</i>	M	+++	1931	—
LUTJANIDAE*	<i>Lutjanus argentimaculatus</i>	R	+	1977	—
MULLIDAE	<i>Upeneus moluccensis</i>	S&M	+++	1947	—
	<i>Upeneus pori</i>	S&M	+++	1950	T
HAEMULIDAE	<i>Pomadasys stridens</i>	S	++	1969	—
SPARIDAE	<i>Crenidens crenidens</i>	S&V	++	1970	N
	<i>Rhabdosargus haffara</i>	S	++	1992	—
PEMPHERIDAE*	<i>Pempheris vanicolensis</i>	R	+++	1979	—
MUGILIDAE	<i>Liza carinata</i>	S&IP	+++	1971	BS&PS
SPHYRAENIDAE	<i>Sphyraena chrysotaenia</i>	P	+++	1930	T&PS
	<i>Sphyraena flavicauda</i>	P	+	1992	—
LABRIDAE	<i>Pteragogus pelycus</i>	S	+	1992	—
BLENNIDAE	<i>Petroscirtes ancyllodon</i>	S	+	1989	—
GOBIIDAE	<i>Monishia ochetica</i>	S	++	1927	—
	<i>Oxyurichthys papuensis</i>	S	+++	1983	—
	<i>Silhouettea aegyptia</i>	S	++	1991	—
	<i>Callionymus filamentosus</i>	S	+++	1953	—
SIGANIDAE*	<i>Siganus luridus</i>	V	+++	1964	N
	<i>Siganus rivulatus</i>	V	+++	1927	N&PS
SCOMBRIDAE	<i>Rastrelliger kanagurta</i>	P	+	1971	—
	<i>Scomberomorus commerson</i>	P	+++	1935	N&PS
CYNOGLOSSIDAE	<i>Cynoglossus sinusarabici</i>	S	++	1953	—
MONACANTHIDAE*	<i>Stephanolepis diaspros</i>	R&V	+++	1927	—
OSTRACIIDAE*	<i>Tetrosomus gibbosus</i>	S&V	+	1988	—
TETRAODONTIDAE	<i>Lagocephalus spadiceus</i>	S	+++	1953	—
	<i>Lagocephalus suezensis</i>	S	+++	1977	—
	<i>Torquigener flavimaculosus</i>	S	+	1987	—
DIODONTIDAE*	<i>Chilomycterus pilostylus</i>	S	+	1993	—



population growth upon arrival to the target area. Therefore, date of first record may be used as a baseline for initiation of a species' colonization. There are several explanations for this correlation. First, the longer the time elapsed since colonization, the better the opportunity to establish large, flourishing populations; in addition, the species may have undergone further adaptation to the new habitat during these years. Second, these species may have had a superior colonization and competitive ability that allowed them to arrive first into the Mediterranean and closely thereafter establish a population. Another explanation may be that the increase in ichthyological studies in the last few decades has revealed more first records, some of which may represent abortive colonization events which would not have been detected prior to the use of intensive research methods. It is interesting to note that the vast majority of species recorded since 1970 have been rare (see Figure 1); however, five species (*Herklotsichthys punctatus*, *Sillago sihama*, *Pempheris vanicolensis*, *Oxyurichthys papuensis*, and *Lagocephalus suezensis*) recorded in the late 1970s are very common in the eastern Mediterranean. There is no obvious common feature between these five species, yet together they constitute an exception to the pattern of gradual building of population size.

The success of Lessepsian migrant fish species in colonization of the Eastern Mediterranean has often been explained as the exploitation of unsaturated niches. For example, the success of the two herbivore siganids *Siganus luridus* and *S. rivulatus* was attributed to their entering temperate waters of the Mediterranean where there were scarcely any herbivores (Lundberg and Golani 1995). Similarly, the lack of nocturnal species facilitated the success of the colonization of three nocturnal Lessepsian migrants: *Sargocentron rubrum*, *Apogon nigripinnis* and *Pempheris vanicolensis* (Golani and Diamant 1991). One might conclude that penetration and colonization should be easier for species whose families have no or very few representatives in the target area; conversely, one might assume that species whose families are well represented by species in the target area would have a high resistance to confamilial colonization. Figure 2 offers four categories according to the percentages that the Lessepsian migrants represent among all species in a particular family in the Levant, as well as the composition of each category by the number of species in each family. In thirteen families, all species are Lessepsian migrants and in another eleven families, 50% or more are Lessepsian migrants. However, there are thirteen other Lessepsian migrant species which have succeeded in penetrating and colonizing the Mediterranean, despite many indigenous confamilial species already inhabiting the Mediterranean.

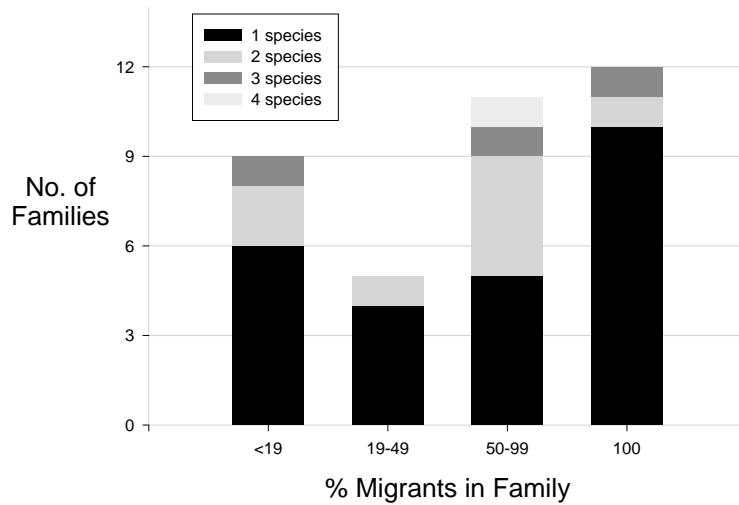


Figure 2 Percentage of Lessepsian migrant species in their families in the Mediterranean, with further breakdown according to the number of Lessepsian species per family.

There are very few studies which directly investigate the impact of Lessepsian migrants on the autochthonous species. The difficulty lies mainly in the lack of information available from the period prior to invasion. The method of investigating this relationship should be the study of the ecological requirements of closely related species (Ben-Yami and Glaser 1974). Such an investigation was conducted by Golani (1994) on Goatfishes (Mullidae), in which there are two migrant species, *Upeneus moluccensis* and *U. pori*, and two indigenous Mediterranean species, *Mullus barbatus* and *Mullus surmuletus*. A similar study (Golani 1993b) was conducted on Lizardfishes (Synodontidae,) which has a single Lessepsian migrant, *Saurida undosquamis*, and an indigenous species, *Synodus saurus*. The family Sphyraenidae was also studied (unpublished material). In all three families, the feeding habits of the colonizers and the local species were remarkably similar and niche partitioning was presumably accomplished along bathymetric axes. Among the goatfishes (Mullidae), the colonizer species occupied a shallower sector, while an opposite trend was observed among the lizardfish (Synodontidae). It is difficult to determine whether the colonizers displaced the local species or whether the latter occupied the same bathymetric niche prior to its confamilial's colonization. An examination of the bathymetric distribution of local species in those areas where colonizers have not penetrated will be of no avail in determining this question, since there are many other environmental factors which on one hand may be affecting the local species and on the other hand may be preventing the entrance of colonizer species.

It is important to note that no local species has disappeared since the study of Lessepsian migration. Nevertheless, there are two cases which deserve further study. The indigenous meager *Argyrosomus regius* was once one of the most common commercial species in Israel. Since the 1980s this species has almost completely disappeared in local catches, while simultaneously, the Lessepsian migrant narrow-barred Spanish mackerel *Scomberomorus commerson* has dramatically increased its population. Both species are piscivores and may utilize a similar niche. Similarly, the Lessepsian dragonet *Callionymus filamentosus* is one of the most common by-catch species in local fisheries. The other three confamilial indigenous species, who also occupy a similar shallow habitat, have almost disappeared from local catch. The only indigenous dragonet still being collected is *Synchiropus phaeton*, which inhabits much deeper waters (150–300 m).

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