

14 The Red Sea – Mediterranean link: unwanted effects of canals

24399

CHARLES F. BOUDOURESQUE

Université de la Méditerranée, Marseilles, France

Abstract

The opening of the Suez Canal in 1869 was the cause of the most important biogeographic phenomenon witnessed in the contemporary oceans. Nearly 300 species of Red Sea and Indo-West Pacific origin invaded and settled in the Mediterranean (the "Lessepsian migrants"). Most settlers were benthic and demersal species, including fishes. The migration was almost exclusively from the Red Sea to the Mediterranean.

Migration is easier since the deepening of the Suez Canal which has removed the hyperhalinity of the Bitter Lakes as a barrier. The reduction of the Nile flow has created more stenohaline conditions at the western Canal outlet. As a result there are no signs that the influx of Lessepsian migrant is nearing a plateau, and they now represent about 4% of the Mediterranean species diversity and 10% of the Levantine basin diversity. Several hypotheses to explain the success of Lessepsian migrants are discussed.

Little attention has been paid to the ecological impact of Lessepsian migrants, both at the species and at the ecosystem level. Some evidence suggests drastic changes in species abundance and niche displacement that can be attributed to the competition with Red Sea species. The presence of large herbivore fishes among the migrants has probably had a strong impact on the functional processes of the Mediterranean ecosystems, where herbivory was low. Some species (e.g. the jellyfish *Rhoptilema nomadica*) have exerted a significant negative impact on fisheries and tourism. Some migrant species are now of economic importance and are being exploited by local fisheries (e.g. off the Israeli coast, where migrant fishes constitute a third of the trawl catches).

Migration across a canal is probably difficult to control. Possible mechanisms capable of slowing down the invasion of Red Sea species (e.g. the setting up of a lock gate, and/or reactivation of haline barriers) should be studied.

Introduction

The access routes for exotic marine species to a new area are diverse (Zibrowius, 1991; Boudouresque and Ribera, 1994; Farnham, 1994; Verlaque, 1994; Ribera and Boudouresque, 1995; see also Carlton, 1998).

(i) They may occur by transportation of sessile (fouling) and vagile

(clinging) species on ship hulls or drilling platforms. (ii) Transportation of species in ballast water and formerly, transport with solid ballast such as sand and stones. Ballast water has been responsible of the introduction species such as the zebra mussel *Dreissena polymorpha* to North America (Carlton, 1993) and the medusa *Mnemiopsis leidyi* to the Black Sea (Travis, 1993). (iii) Intentional introductions of species for commercial use, for example the Japanese oyster *Crassostrea gigas* and the venerid *Ruditapes philippinarum* (Bodoy *et al.*, 1981). (iv) Accidental introductions of species accompanying intentionally introduced species, for example the importation of spat of *Crassostrea gigas* that resulted in the introduction of nearly 15 species of Japanese algae to the Mediterranean (e.g., Riouall, 1985; Riouall *et al.*, 1985; Rueness, 1989; Verlaque and Riouall, 1989; see reviews in Verlaque, 1994; Ribera and Boudouresque, 1995). (v) Discarding of intentionally imported live specimens from the market to the sea have included species used as bait and algae used as packing material (e.g., *Fucus spiralis* introduced from Brittany to a French Mediterranean brackish lagoon; Sancholle, 1988). (vi) Escape from aquaria, especially through open systems that do not have treatment. In the North-Western Mediterranean, the green tropical alga *Caulerpa taxifolia* was introduced this way (Boudouresque *et al.*, 1992, 1995; Meinesz *et al.*, 1993; Meinesz and Hesse, 1991). (vii) Species introduced in association with scientific research. Many scientists who use non-indigenous strains or species are often unaware of, or underestimate the risks of introduction. They fail to take the elementary precautions that are required to prevent these species from escaping from their cultures or breeding sites. An example of this is the red alga *Mastocarpus stellatus* introduced into Germany (Helgoland; North Sea) by a visiting scientist (Ribera and Boudouresque, 1995).

In the Mediterranean, the Suez Canal is an additional and unique route for the introduction of species. The canal, 163 km long running from Port Said to the Gulf of Suez (Egypt), was opened in 1869. It linked two biogeographical provinces, the Mediterranean and the Red Sea that had been partially separated since the early Miocene (ca 20 Ma) and completely separated since the late Miocene (Messinian), ca 5 Ma ago (Robba, 1987). The Suez Canal was deepened and widened several times and now reaches a navigational depth of 14.5 m and is 365 m wide (Halim, 1990). Mass migration of species from the Red Sea to the Mediterranean ("Lessepsian migrants"; Por, 1969) and on a much smaller scale from the Mediterranean to the Red Sea (referred to as "anti-Lessepsian migrants") are considered the most spectacular biological invasions witnessed in the contemporary oceans (Por, 1978, 1989, 1990; Spanier and Galil, 1991; Zibrowius, 1991; Galil, 1994).

Lessepsian migrants

An exhaustive inventory of Lessepsian migrants cannot be presented, because it would require the teamwork of many specialists. Furthermore, reliable inventories of the Mediterranean flora and fauna are not available for all taxonomic groups. Titles and abstracts of papers do not always provide an indication that aliens are mentioned in the text. The questions exist as to whether the identifications are reliable and previously known geographical ranges are representative (see discussion in Por, 1978; Zibrowius, 1991). As a result, our inventory of Lessepsian migrants (Table 14.1) does not intend to be exhaustive, but emphasises the scale of this unique inflow of migrants to the Eastern Mediterranean. Nearly 300 Red Sea species are known to have entered the Mediterranean through the Suez Canal.

Table 14.1 Lessepsian migrants from the Red Sea to the Mediterranean, as number of species per taxonomic unit. The caution taken by Por (1978) in separating "High probability" and "Low probability" Lessepsian migrants has no meaning in the present context, according to Por (1989).

* Including 10 species of serpulid Polychaeta. Zibrowius (1983, 1991) stated that considerably more serpulid species of Indo-Pacific origin had settled on the Levantine coast.

** According to Zibrowius (1991), Por's list of Lessepsian ascidians, mainly based on Pérès (1958), could provide an over-estimation of alien species

Taxon	No. of spp.	References
Algae	21-25	Por (1978), Ribera and Boudouresque (1995), Verlaque (1994)
Seagrasses	1	Hartog (1972), Hartog and Van der Velde (1993)
Porifera	7	Por (1978)
Hydroidea	3	Por (1978)
Scyphozoa	3	Zibrowius (1991)
Polychaeta	31*	Ben-Eliahu (1986), Por (1978), Zibrowius (1991)
Pycnogonida	1	Por (1978)
Crustacea Decapoda	35	Galil et al. (1989), Galil and Golani (1990), Por (1978, 1989)
Crustacea (others)	23	Lakkis (1976), Morri et al. (1982), Por (1978, 1989)
Mollusks	105	Barash and Danin (1986), Aartsen et al. (1989, 1990)
Bryozoa	8	Por (1978), Zibrowius (1991)
Chaetognata	1	Guergues and Halim (1973), Por (1989)
Echinodermata	5	Cherbonnier (1986), Por (1978)
Tunicata (ascidians)	7**	Por (1978)
Enteropneusta	1	Por (1978)
Pisces	45	Ben-Tuvia (1985), Fredj and Meinardi (1989), Golani (1987), Golani and Ben-Tuvia (1986), Spanier and Goven (1988)

Decapod crustaceans, mollusks and fishes are the principal taxonomic groups represented among the Lessepsian migrants (Por, 1989). It should be emphasised that this is unusual because fishes are seldom a major component of species introductions in the marine environment. Planktonic species, which are generally stenohaline, are more poorly represented among the Lessepsian migrants. The fluctuant and rather high salinity of the canal, especially the Bitter Lakes, remain barriers to many migrants (Godeaux, 1974; Kimor, 1990; Por, 1990).

Por (1978) expressed the view that Lessepsian migration will eventually approach a plateau. This is indeed to be expected, but has not yet happened. The number of introduced species continues to increase at an exponential rate (Figure 14.1). Of course, these figures are to be taken with some caution, because the first observation of an introduced species always occurs some time after its real introduction. In addition, these figures may be indicative of an increase in the intensity of observation and our knowledge of biogeography. Nevertheless, a similar kinetics of increase in the rate of marine species' introduction has been evident among other vectors of introduction than the Suez Canal (Boudouresque and Ribera, 1994; Ribera and Boudouresque, 1995).

Most of Lessepsian migrants are still confined to the Levantine coast (from Egypt to Syria). Some are also present in other parts of the Eastern Mediterranean basin. For example, the opisthobranch *Bursatella leachi* is now common not only in the Levantine basin, but also has progressed to Greece, the Aegean Sea, the Ionian Islands, Malta, Southern Italy and the Adriatic Sea (Zibrowius, 1991). Very few species extend to the Western Mediterranean, for example the mollusks, *Brachydontes variabilis* and *Pinctada radiata*, observed in Corsica (J. Godeaux, pers. comm.) and the green alga *Caulerpa racemosa* in Leghorn, Northern Italy (Piazzi *et al.*, 1994). Por (1983) proposed the delimitation of a biogeographical "Lessepsian province" (Figure 14.2). The limits of this province presently are the entrance to the Aegean Sea and the Eastern coast of Sicily.

Lessepsian migrants are not the only alien species in the Mediterranean. Other routes of access to the Mediterranean have occurred. For example, 60 macroalgae are considered as probably introduced to the Mediterranean (Ribera and Boudouresque, 1995), of which 21–25 species are Lessepsian migrants (Table 14.1).

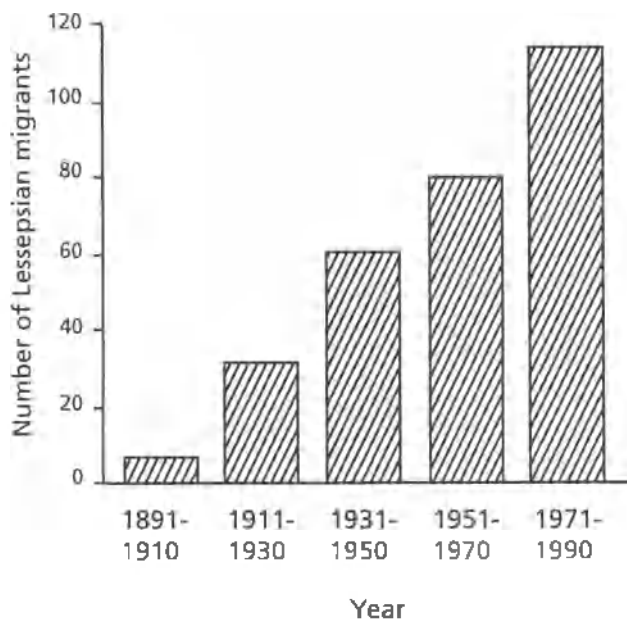


Figure 14.1 Number of Lessepsian migrants to the Mediterranean, by periods of 20 years (non-cumulative data), according to the date of first observation (or when not specified, the date of publication).

Anti-Lessepsian migrants

The flow of migration through the Suez Canal is almost exclusively unidirectional from the Red Sea to the Mediterranean (Por, 1978). Very few Mediterranean species have moved in the reverse direction ("anti-Lessepsian migrants"), for example, the sea star *Sphaeriodiscus placenta* and the fishes *Liza aurata* and *Dicentrarchus punctatus* (Ben-Tuvia, 1975; Fouda and Hellal, 1987; Por, 1978, 1990). A total of 53 species at different times have been considered as Mediterranean immigrants to the Red Sea. A critical evaluation of the data leads to a reduction in the number of species to 10–20; most of them are still confined to the vicinity of Suez harbour and lagoons (Por, 1978).

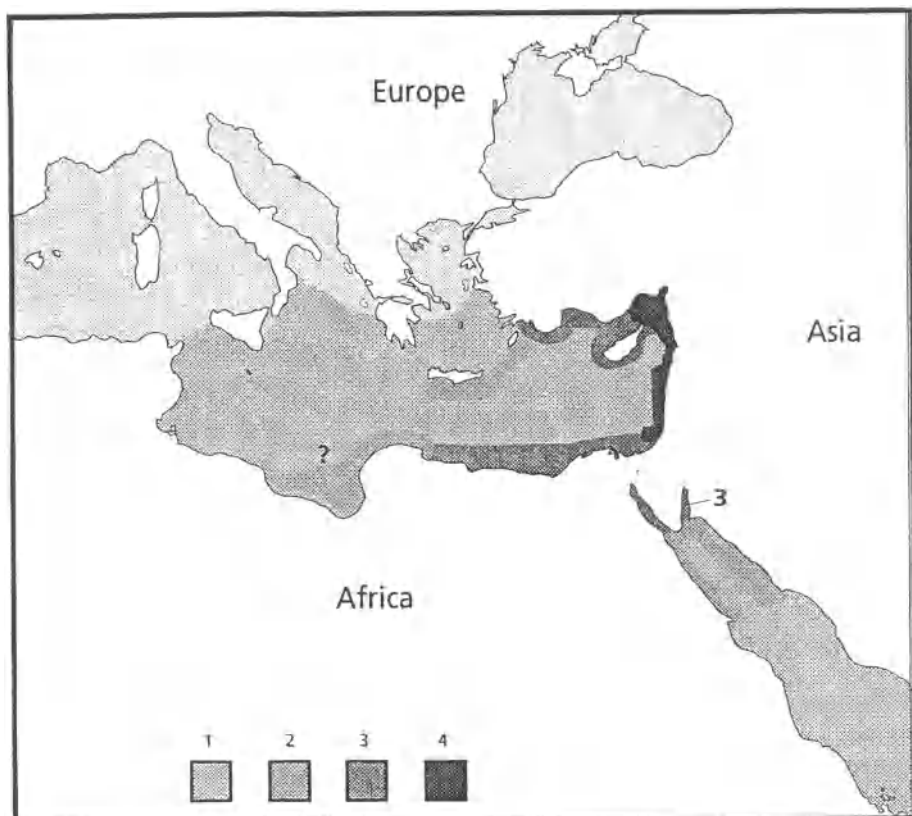


Figure 14.2 The Lessepsian province of the Mediterranean in relation to the Northern Red Sea. Four scales of shading depict the density of the settlement by migrants (from Por, 1990).

Why such a success for Lessepsian migrants?

The most important factors liable to hinder migrations through the Suez Canal are (Halim, 1990; Morcos, 1980; Spanier and Galil, 1991): (i) temperature fluctuations and turbidity of the canal water, which is higher than in the adjacent sea (this barrier has gradually disappeared); (ii) the degree of salinity of the hypersaline Bitter Lakes, which for a long time hindered migrations, but has gradually fallen from 70 to 43–48 *per mille* (similar to that of the Northern Gulf of Suez); and (iii) the Nile fresh-water dilution plume. Since the damming of the Nile at Aswan in 1965–1967, which drastically reduced the river's outflow, this barrier has almost disappeared.

Several causes can be put forward to explain the success of Lessepsian migrants. (i) A relatively low species diversity exists in the Levantine basin (when compared with the western basin), which probably results from its geological history. During the Messinian, the Mediterranean was periodically cut off from the Atlantic, resulting in hypersaline conditions until Atlantic waters refilled it 5 Ma ago (Hsu *et al.*, 1978). The effects on species diversity were severe, even if not as catastrophic as it appeared when it was first discovered (Por, 1990). Recolonization of the Mediterranean involved species of Atlantic origin, which still dominate the Mediterranean biota (Fredj *et al.*, 1992). (ii) The Pleistocene Glacial periods probably contributed to the shortage of thermophilic species in the Levantine basin. In some areas of the Levantine basin, summer surface temperatures can reach tropical conditions of 28–29 °C, and winter temperatures, always below 20 °C, are characteristic of warm temperate regions. The number of successful Lessepsian colonists demonstrates that habitats suitable for tropical species were available (Stephenson, 1948; Lüning, 1990; Spanier and Galil, 1991). (iii) The pre-adaptation of the Red Sea species to the Suez Canal salinity is to be considered. The Gulf of Suez, a shallow body of water with salinity values as high as 45 *per mille* and wide temperature fluctuations could act as a virtual lock chamber (Spanier and Galil, 1991). (iv) Finally, the water of the canal tends to flow towards the Mediterranean for ten months (the mean sea level of the Red Sea in Suez Gulf is 30–40 cm higher than at the Mediterranean canal outlet from January to June), reversing only in August–September (Morcos, 1967, 1980).

Could the possible recent warming of Mediterranean waters resulting from global climate change contribute to the explanations of such a success? Temperatures in deep waters of the Western Mediterranean basin have risen by 0.12°C since 1960 (Béthoux *et al.*, 1990). Some species of fishes and algae with established thermal preferences have recently extended their distribution area toward the north-western Mediterranean, where a warming trend for surface water temperatures exists (Bianchi and Morri, 1993, 1994; Francour *et al.*, 1994). Nevertheless, these changes could prove to be simple oscillations, which may have already existed since the opening of the Suez Canal. The kinetics of invasion (Figure 14.2) do not show any conspicuous changes with time, and the rise of surface temperatures in the Eastern Mediterranean basin has not been clearly established.

According to Por (1990), the conclusions reached by Safriel and Ritte (1985) that Lessepsian migrants are usually "r-strategists" should be re-examined.

As far as the anti-Lessepsian migrants are concerned, the reasons why they were so unsuccessful could be the same as above, but taken on the

reverse way. According to Por (1978), no favourable preconditions exist for the Levantine Mediterranean fauna (which is already impoverished) to migrate even further along an increasing salinity and temperature gradient. Moreover, the Red Sea fauna is particularly rich.

Unlike the Suez Canal, the opening of the Panama Canal, which links the Pacific to the Atlantic across Central America, has only resulted in the passage of a limited number of euryhaline species. According to Hay and Gaines (1984), it is not the lock system that segments the canal, or the freshwater lakes along its course that explain the low exchange of flora and fauna between the two oceans. Many Caribbean species can attach themselves to the hulls of ships and withstand a 6 to 12 hour passage through fresh water. As far as algae are concerned, the primary barrier to successful transport and establishment of these Caribbean species appears to be herbivore activity and lack of reef-generated refuge areas on the Pacific coast.

Ecological and economic consequences

Most attention has focused on environmentally damaging consequences and short-term economic losses resulting from alien invasive species in terrestrial and freshwater environment (see Mooney and Drake, 1986; Drake *et al.*, 1989; Pieterse and Murphy, 1990; Groves and di Castri, 1991). On the other hand, the marine environment, especially the Mediterranean one, has not been examined extensively.

Little attention has been paid to the ecological impact of Lessepsian migrants, both at the species and at the ecosystem levels. There is a common empirical opinion that the Red Sea species invasion has not resulted in Mediterranean species depletion, but instead in species enrichment. This simplistic interpretation (likely to appeal to politicians) whose logical result would be the world-wide standardisation (referred to as "mcdonaldisation" by Boudouresque, 1996) is diametrically opposed both to the concept of biodiversity and to the ethics of conservation of the environment. If this were in fact the case, zoos and botanical gardens would be the paradigm of biodiversity.

The hypothesis that Lessepsian migrants enrich the Mediterranean biodiversity is poorly founded on scientific data. The fate of native species has been poorly studied. On the contrary, evidence exists of drastic changes in abundance and niche displacement of native species that can be attributed to competition with Red Sea species. It is highly probable that a strong impact on the functional processes of the ecosystems of the Mediterranean, a sea characterised by a low herbivory, exists because of the presence of

large herbivorous fishes (the rabbit fishes, *Siganus rivulatus* and *S. luridus*) among the migrants.

The arrival of many Red Sea species has had a great impact on the composition of the south-eastern Mediterranean fish fauna. According to Fredj and Meinardi (1989) and Ben-Tuvia (1985), they represent 7% of the 648 fish species known from the Mediterranean, about 10% of the 469 species reported from the Eastern basin and 12% of the species of the Levantine basin. In benthic hard bottom ecosystems of the south-eastern shelf, they contribute nearly half of the total fish abundance and biomass (Spanier *et al.*, 1989), with the dominant species now being the rabbit fishes, and the red soldier fish, *Sargocentron rubrum*. Lessepsian species represent 9% of polychaetes, 9% of mollusks and 20% of decapod crustaceans along the Levantine coast (Barash and Danin, 1986; Ben-Eliahu, 1989; Galil, 1986). The microplankton communities of the northern Red Sea and of the Levantine basin now share a number of basic characteristics (Kimor, 1990). Currently, Lessepsian migrants represent about 4% of the Mediterranean species diversity and 10% of the Levantine basin diversity (Por, 1978, 1990).

Most settlers are benthic or demersal species and found at intermediary depths, between 20–40 m, on mixed sandy-muddy bottoms. This is a result of the cooling of the shallow waters in the winter and the exposure to cold at higher intertidal levels. Usually, the depth limit of the Lessepsian migrants is 70–80 m. A year-round temperature of 18 °C exists at this depth (Por, 1978).

The large aplisiid opisthobranch *Bursatella leachi* does not seem to have a native competitor (Zibrowius, 1991). The introduced asteroid *Asterina wega* appears to have locally replaced the native, ecologically similar *Asterina gibbosa*. The native prawn *Penaeus kerathurus*, which supported a commercial fishery throughout the 1950s, has nearly disappeared; it has been replaced by *P. japonicus* (Geldiay and Kocatas, 1972; Spanier and Galil, 1991). The recent decrease of the previously prevalent indigenous jellyfish *Rhizostoma pulmo* may also be a case of competitive displacement by the Lessepsian *Rhopilema nomadica*, which belongs to the same family (Spanier and Galil, 1991). Several native species have been competitively displaced to greater depths by introduced competitors. For example, the red snapping shrimp *Alpheus glaber*, the red mullet *Mullus barbatus* and the hake *Merluccius merluccius* have been displaced respectively by the shrimp *Alpheus rapacida*, the goldband goatfish *Upeneus moluccensis* and the brushtooth lizardfish *Saurida undosquamis* (Por, 1978). According to Por (1990), the conclusions reached by Safriel and Ritte (1985) that there is a smooth gene-flow between conspecific populations on both sides of the Suez Canal should be rechecked. Golani (1990) showed that some species of

Lessepsian fishes show significant morphologic differences compared with their Red Sea source populations. The causes of these differences could stem from species' spawning season, differences in the annual temperature regime at the source and target sites, and founder effects.

It is not unusual for an introduced species to present an early exuberant development and then decline. This is the case for the gastropod *Rhinoclavis kochi*, which was first reported in the mid-1960s and became one of the dominant species in the late 1970s, but has since become relatively rare (Galil and Lewinsohn, 1981; Spanier and Galil, 1991). Nevertheless, there are no known examples of disappearance of a Lessepsian species in the Mediterranean (Por, 1978). As for other species, changes in abundance seem related to climatic fluctuations. For example, the fishes *Saurida undosquamis* and *Upeneus moluccensis* experienced peaks of abundance following an exceptionally warm winter (Oren, 1957; Ben-Tuvia, 1973; Ben-Yami and Glaser, 1974). Finally, the exponential expansion phase of several species reached a plateau, but a decline has not yet occurred. This is exemplified by the prawn *Penaeus japonicus* and by the swimming crab *Charybdis longicollis*, which dominate the macrobenthic fauna of silty sand bottoms, forming up to 70% of the biomass in certain places (Galil, 1986; Spanier and Galil, 1991).

Some migrant species are now of economic importance, being exploited by local fisheries (Oren 1957; Galil 1986; Spanier and Galil 1991; Zibrowius 1991). The crab *Portunus pelagicus* has become the dominant crab in commercial catches throughout the eastern Mediterranean, especially in Egypt. The prawns *Penaeus japonicus* and *P. monoceros* are commercially fished, making up most of the shrimp catches in Israel and Egypt. Off the Israeli coast, migrant fishes constitute a third of the trawl catches (e.g. the brushtooth lizardfish *Saurida undosquamis*). The migrant goldband goatfish, *Upeneus moluccensis*, represents a third of the mullet catches (up to 83% in 1954–1955). It is unclear, however, whether the total prawn and fish stock has increased or decreased. The economic benefits of an introduction should not be assessed simply on the basis of strict sale price, but should also take into account losses from other business activities and the costs of any damage that may result. Furthermore, some species (e.g. the jellyfish *Rhopilema nomadica*) have exerted a significant negative impact on fisheries and tourism. *Rhopilema nomadica*, whose umbrella measures 20–60 (100) cm, can assemble in "jellyfish belts" at a distance of 1–5 km offshore from the Israeli coast, especially in summer. Maximal density was estimated at 25 individuals per m³. For several weeks in the summer of 1990, the coastal fishing was disrupted due to damage to nets and inability to sort the yield. Local municipalities reported a decrease in beach frequentation, due to the painful stings inflicted by the jellyfish. Nets

strung along bathing beaches proved ineffective, since jellyfish fragments passed through (Spanier and Galil, 1991). In Cyprus, an introduced green alga of the genus *Cladophora* (perhaps *C. patentiramosa*) proliferated off the beaches, and its flotsam accumulated on the beaches themselves, hindering bathing (Demetropoulos and Hadjichristophorou, in Ribera and Boudouresque, 1995).

Possible mechanisms of control

The complete or partial eradication of an introduced marine species is certainly very difficult, if not impossible given the present state of our knowledge and techniques. In addition, there has been little research in this field. So, the introduction of a species is to be considered as a probably definitive act that we impose on future generations.

Migration across a canal is probably the most difficult to control, especially the Suez Canal which handles some 20% of the world maritime traffic. Nothing has been done to study possible mechanisms capable of slowing down the invasion of Red Sea species. The setting up of a lock gate in the course of the canal should be considered. The possibility of technically treating the lock water (chemical or other treatment) in order to reduce its biological load should be examined. The reactivation of the saline barriers (Bitter Lakes) could also be studied, for example through the coupling with a desalinisation plant.

Conclusions

The Suez Canal has been compared to a thin capillary tube connecting two huge marine basins (Halim, 1990). Although its role in the exchange of water has been insignificant, it became the site of an immense biological invasion from the Red Sea to the Mediterranean.

Migration through the Suez Canal is an ongoing process, and there are no signs that the influx is nearing a plateau. Most of Lessepsian migrants are concentrated in the Eastern Mediterranean basin (especially along the Levantine coast). The area, therefore, could be considered as a "Lessepsian biogeographical province". The fauna and flora, as well as the functional processes at the ecosystem level have already dramatically changed in this part of the Mediterranean, even if the magnitude and the consequences of these changes have not been measured. No concentrated effort to follow the deployment of this unique biogeographical phenomenon exists. New records

of Lessepsian migrants are generally the result of occasional observations (Por, 1989).

The rate of marine species introduction in most parts of the world's oceans is rapidly increasing. What will happen if the introduced species become the majority, overwhelm the indigenous species, and build new communities whose composition, structure and functioning we are incapable of predicting? Carlton and Geller (1993) refer to this as "ecological roulette". Lessepsian migration and the south-eastern Mediterranean could prefigure the fate of other seas. It should be of interest to carefully study such a model and to try to slow or stop the invasion.

Acknowledgments

The author wishes to thank Michèle Perret-Boudouresque who provided documentation and Simone Fournier and Lorraine Fleming for checking the English text.

References

- Aartsen, J.J., van Barash, A. and Carozza, A. (1989) Addition to the knowledge of the Mediterranean Mollusca of Israel and Sinai. *Bolletín Malacologia*, **25**, 63–76.
- Aartsen, J.J., van Carozza, F. and Lindner, G. (1990) *Acteocina mucronata* (Philippi, 1849), a recent Red Sea immigrant species in the eastern Mediterranean. *Bolletín Malacologia*, **25**, 285–288.
- Barash, A. and Danin, Z. (1986) Further additions to the knowledge of Indo-Pacific Mollusca in the Mediterranean Sea (Lessepsian migrants). *Spixiana*, **9**, 117–141.
- Ben-Eliahu, M.N. (1986) Red Sea serpulids in the Eastern Mediterranean, in *Proceedings of Second International Polychaete Conference*, Copenhagen.
- Ben-Eliahu, M.N. (1989) Lessepsian migration in Nereidae (Annelida: Polychaeta): some case histories. in *Environmental Quality and Ecosystem Stability*, (eds E. Spanier, E. Steinberger and M. Luria), ISEEQS Publications, Jerusalem, Israel, volume IV-B, pp. 124–134.
- Ben-Tuvia, A. (1973) Man-made changes in the Eastern Mediterranean sea and their effect on the fishery resources. *Marine Biology*, **19**, 197–203.
- Ben-Tuvia, A. (1975) Comparison of the fish-fauna in the Bardawil lagoon and in the Bitter Lakes. *Rapports P.V. Réunions Commission internationale Exploration scientifique Méditerranée*, **23**, 125–126.
- Ben-Tuvia, A. (1985) The impact of the Lessepsian (Suez Canal) fish migration on the eastern Mediterranean ecosystem, in *Mediterranean Marine Ecosystems*, (eds M. Moraitou-Apostolopoulou and V. Kiortsis), Plenum Press, pp. 367–375.
- Ben-Yami, M. and T. Glaser (1974) The invasion of *Saurida undosquamis* (Richardson) into the Levant Basin – an example of biological effect of interoceanic canals. *Fishery Bulletin*, **72**, 359–373.
- Béthoux, J.P., Gentili, B., Raunet, J. and Taillez, D. (1990) Warming trend in the Western Mediterranean deep water. *Nature*, **347**, 660–662.

- Bianchi, C.N. and Morri, C. (1993) Range extensions of warm-water species in the northern Mediterranean: evidence for climatic fluctuations? *Porcupine Newsletter*, **5**, 156–159.
- Bianchi, C.N. and Morri, C. (1994) Southern species in the Ligurian Sea (Northern Mediterranean): new records and a review. *Bolletino Museo Istituto Biologia Università Genova*, **58–59**, 181–197.
- Bodoy, A., Maître-Aillain, T. and Riva, A. (1981) Croissance comparée de la palourde européenne *Ruditapes decussatus* et de la palourde japonaise *Ruditapes philippinarum* dans un écosystème artificiel méditerranéen. *Vie marine*, **2**, 39–51.
- Boudouresque, C.F. (1996) *Impact de l'Homme et Conservation du Milieu Marin en Méditerranée*. 2^e édition. GIS Posidonie Publishers, Marseille.
- Boudouresque, C.F., Meinesz, A., Ribera, M.A. and Ballesteros, E. (1995) Spread of the green alga *Caulerpa taxifolia* (Caulerpales, Chlorophyta) in the Mediterranean: possible consequences of a major ecological event. *Scientia Marina*, **59** (suppl. 1), 21–29.
- Boudouresque, C.F., Meinesz, A., Verlaque, M., and Knoepffler-Peguy, M. (1992) The expansion of the tropical alga *Caulerpa taxifolia* (Chlorophyta) in the Mediterranean. *Cryptogamie-Algologie*, **13**, 144–145.
- Boudouresque, C.F. and Ribera, M.A. (1994) Les introductions d'espèces végétales et animales en milieu marin. Conséquences écologiques et économiques et problèmes législatifs, in *First International Workshop on Caulerpa taxifolia*, (eds C.F. Boudouresque, A. Meinesz and V. Gravez), GIS Posidonie Publishers, Marseilles, pp. 29–102.
- Carlton, J.T. (1993) Dispersal mechanisms of the zebra mussel (*Dreissena polymorpha*), in *Zebra Mussel: Biology, Impact and Control*, (eds T.F. Nalepa and D.W. Schloesser), Lewis publ., Boca Raton, Florida, USA.
- Carlton, J.T. (1998) The scale and ecological consequences of biological invasions in the World's oceans, in *Invasive Species and Biodiversity Management*, (eds O. T. Sandlund, P. I. Schei and Å. Viken), Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Carlton, J.T. and Geller, J.B. (1993) Ecological roulette: the global transport of non-indigenous marine organisms. *Science*, **261**, 78–82.
- Cherbonnier, G. (1986). Holothuries de Méditerranée et du Nord de la Mer Rouge. *Bulletin du Muséum national d'Histoire naturelle, Sér. 4*, **8**, 43–46.
- Drake, J.A., Mooney, H.A., di Castri, F., Kruger, F., Groves, R., M. Rejmanek and Williamson, W., eds (1989) *Biological Invasions: a Global Perspective*. SCOPE **37**, John Wiley and Sons, Chichester, UK.
- Farnham, W.F. (1994) Introduction of marine benthic algae into Atlantic European waters, in *Introduced Species in European Coastal Waters*, (eds C.F. Boudouresque, F. Briand and C. Nolan), European Commission publications, Luxemburg, pp. 32–36.
- Fouada, M.M. and Hellal, A.M. (1987) The Echinoderms of the north-western Red Sea, Asteroidea. *Fauna and Flora of Egypt*, **2**, 1–71.
- Francour, P., Boudouresque, C.F., Harmelin, J.G., Harmelin-Vivien, M.L. and Quignard, J.P. (1994) Are the Mediterranean waters becoming warmer? Information from biological indicators. *Marine Pollution Bulletin*, **28**, 523–526.
- Fredj, G., Bellan-Santini, D. and Meinardi, M. (1992) Etat des connaissances sur la faune marine méditerranéenne. *Bulletin de l'Institut océanographique*, num. spec. **9**, 133–145.
- Fredj, G. and Meinardi, M. (1989) Inventaire faunistique des ressources vivantes en Méditerranée: intérêt de la banque de données MEDIFAUNE. *Bulletin de Société Zoologique de France*, **114**, 75–87.

- Galil, B. (1986) Red Sea Decapods along the Mediterranean coast of Israel: ecology and distribution, in *Environmental Quality and Ecosystem Stability*, vol. III A/B, (eds Z. Dubinsky and Y. Steinberg), Bar Ilan University Press, Ramat Gan, Israel, pp. 179–183.
- Galil, B.S. (1994) Lessepsian migration. Biological invasion of the Mediterranean, in *Introduced Species in European Coastal Waters* (eds C.F. Boudouresque, F. Briand and C. Nolan), European Commission publications, Luxemburg, pp. 63–66.
- Galil, B.S. and Golani, D. (1990) Two migrant Decapods from the eastern Mediterranean. *Crustaceana*, **58**, 229–236.
- Galil, B. and Lewinsohn, C. (1981) Macrobenthic communities of the Eastern Mediterranean continental shelf. *Marine Ecology, PSZN*, **2**, 343–352.
- Galil, B.S., Pisanty, S., Spanier, E. and Tom, M. (1989) The Indo-Pacific lobster *Panulirus ornatus* (Crustacea : Decapoda): a new lessepsian migrant to the eastern Mediterranean. *Israel Journal of Zoology*, **35**, 241–243.
- Geldiay, R. and Kocatas, A. (1972) *A Report on the Occurrence of Penaeidae (Decapoda Crustacea) along the Coast of Turkey from Eastern Mediterranean to the Vicinity of Izmir, as a Result of Migration and its Factors*. 17^e Congrès international de Zoologie, Monte Carlo.
- Godeaux, J. (1974) Thaliacés récoltés au large des côtes égyptiennes de la Méditerranée et de la mer Rouge (Tunicata, Thaliacea). *Beaufortia*, **22**, 83–103.
- Golani, D. (1987) The Red Sea pufferfish *Torquigener flavimaculosus* a new Suez Canal migrant in the Eastern Mediterranean (Pisces : Tetraodontidae). *Senckenberg. Mar.*, **19**, 339–343.
- Golani, D. (1990) Environmentally-induced meristic changes in Lessepsian fish migrants, a comparison of source and colonizing populations. *Bulletin de l'Institut océanographique de Monaco, N.S., num. spéc.* **7**, 143–152.
- Golani, D. and Ben-Tuvia, A. (1986) New records of fishes from the Mediterranean coast of Israel, including Red Sea immigrants. *Cybium*, **10**, 285–291.
- Groves R.H. and di Castri, F., eds (1991) *Biogeography of Mediterranean Invasions*. Cambridge University Press, Cambridge, UK.
- Guergues, S.K. and Halim, Y. (1973) Chétognathes du plancton d'Alexandrie. II. Un spécimen mûr de *Sagitta neglecta* Aida en Méditerranée. *Rapports P.V. Réunions Commission internationale Exploration scientifique Méditerranée*, **21**, 497 pp.
- Halim, Y. (1990) On the potential migration of Indo-Pacific plankton through the Suez Canal. *Bulletin de l'Institut océanographique de Monaco, N.S., num. spéc.* **7**, 11–27.
- Hartog, C. den (1972) Range extension of *Halophila stipulacea* (Hydrocharitaceae) in the Mediterranean. *Blumea*, **20**, 154 pp.
- Hartog, C. den and Van der Velde, G. (1993) Occurrence of the seagrass *Halophila stipulacea* (Hydrocharitaceae) along the Mediterranean coast of Turkey. *Posidonia Newsletter*, **4**, 5–6.
- Hay, M.E. and Gaines, S.D. (1984) Geographic differences in herbivore impact: do Pacific herbivores prevent Caribbean seaweeds from colonizing via Panama Canal? *Biotropica*, **16**, 24–30.
- Hsu, K.J., Montadert, L., Bernouilli, D., Cita, M.B., Erikson, A., Garrison, R.E., Kidd, R.B., Melieres, F., Muller, C., and Wright, R. (1978) History of the Mediterranean salinity crisis. *Initial Reports of DSDP*, **42**, 1053–1078.
- Kimor, B. (1990) Microplankton of the Red Sea, the Gulf of Suez and the Levantine basin of the Mediterranean. *Bulletin de l'Institut océanographique de Monaco, N.S., num. spéc.* **7**, 29–38.

- Lakkis, S. (1976) Sur la présence dans les eaux libanaises de quelques Copépodes d'origine Indo-Pacifique. *Rapports P.V. Réunions Commission internationale Exploration scientifique Méditerranée*, **23**, 83–85.
- Lüning, K. (1990) *Seaweeds? Their Environment, Biogeography and Ecophysiology*. John Wiley and Sons Inc., New York.
- Meinesz, A. and Hesse, B. (1991) Introduction et invasion de l'algue tropicale *Caulerpa taxifolia* en Méditerranée nord-occidentale. *Oceanologica Acta*, **14**, 415–426.
- Meinesz, A., de Vaugelas, J., Hesse, B., and Mari, X. (1993) Spread of the introduced tropical green alga *Caulerpa taxifolia* in Northern Mediterranean. *Journal of Applied Phycology*, **5**, 141–147.
- Mooney H.A. and Drake, J.A., eds (1986) *Ecology of Biological Invasions of North America and Hawaii*. Ecological studies, 58, Springer Verlag, Berlin.
- Morcos, S.A. (1967) The chemical composition of sea water from the Suez Canal region, Part I: the major anions. *Kieler Meeresforschung*, **23**, 80–91.
- Morcos, S.A. (1980) Seasonal changes in the Suez Canal following its opening in 1869: newly discovered hydrographic records of 1870–1872, in *Oceanography: the Past*, (eds M. Sears and D. Merriman), Springer, New York, pp. 290–305.
- Morri, C., Occhipinti Ambrogi A., and Sconfiati R. (1982) Specie nuove o critiche del bentos lagunare nord adriatico. *Progetto final – Prom. Qual. Amb.*, Roma, CNR, **35**, 1–4.
- Oren, O.H. (1957) Changes in temperature of the Eastern Mediterranean Sea in relation to the catch of the Israel trawl fisheries during the years 1955/55 and 1955/56. *Bulletin de l'Institut océanographique de Monaco*, **1102**, 1–12.
- Pérès, J.M. (1958) Ascidiées récoltées sur les côtes méditerranéennes d'Israël. *Bulletin of the Research Council of Israel*, **7B**, 143–150.
- Piazzi, L., Balestri, E., and Cinelli, F. (1994) Presence of *Caulerpa racemosa* in the north-western Mediterranean. *Cryptogamie-Algologie*, **15**, 183–189.
- Pieterse, A.H. and Murphy, K.J., eds (1990) *Aquatic Weeds. The Ecology and Management of Nuisance Aquatic Vegetation*. Oxford University Press, Oxford, UK.
- Por, F.D. (1969) The Canuellidae (Copepoda, Harpacticoida) in the waters around the Sinai Peninsula and the problem of "Lessepsian" migration of this family. *Israel Journal of Zoology*, **18**, 169–178.
- Por, F.D. (1978) *Lessepsian migrations. The Influx of Red Sea Biota into the Mediterranean by Way of the Suez Canal*, Springer Verlag, Berlin.
- Por, F.D. (1983) The Lessepsian biogeographic province of the Eastern Mediterranean. *Rapports P.V. Réunions Commission internationale Exploration scientifique Méditerranée, Journées Etudes Systématique et Biogéographie méditerranéenne, Cagliari*, pp. 81–84.
- Por, F.D. (1989) *The Legacy of Tethys. An Aquatic Biogeography of the Levant*. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Por, F.D. (1990) Lessepsian migrations. An appraisal and new data. *Bulletin de l'Institut océanographique*, **7**, 1–10.
- Ribera, M.A. and Boudouresque, C.F. (1995) Introduced marine plants, with special reference to macroalgae: mechanisms and impact, in *Progress in Phycological Research*, volume 11 (eds F.E. Round and D.J. Chapman), Biopress Ltd., Bristol, UK, pp. 187–268.
- Riouall, R. (1985) Sur la présence dans l'étang de Thau (Hérault, France) de *Sphaerotrichia divaricata* (C. Agardh) Kylin et *Chorda filum* (L.) Stackhouse. *Botanica Marina*, **27**, 83–86.

- Riouall, R., Guiry, M.D., and Codomier, L. (1985) Introduction d'une espèce foliacée de *Grateloupia* dans la flore marine de l'étang de Thau (Hérault, France). *Cryptogamie-Algologie*, **6**, 91–98.
- Robba, E. (1987) The final occlusion of Tethys: its bearing on Mediterranean benthic mollusks, in *Shallow Tethys 2*, (ed. K.G. McKenzie), Balkema, Rotterdam, Netherlands, pp. 405–426.
- Rueness, J. (1989) *Sargassum muticum* and other introduced Japanese macroalgae: biological pollution of European coasts. *Marine Pollution Bulletin*, **20**, 173–176.
- Safriel, U.N. and Ritte, U. (1986) Suez Canal migration and Mediterranean colonization. Their relative importance in Lessepsian migration. *Rapports P.V. Réunions Commission internationale Exploration Méditerranée*, **29**, 259–263.
- Sancholle, M. (1988) Présence de *Fucus spiralis* (Phaeophyceae) en Méditerranée occidentale. *Cryptogamie-Algologie*, **9**, 157–161.
- Spanier, E. and Galil, B.S. (1991) Lessepsian migration: a continuous biogeographical process. *Endeavour N.S.*, **16**, 102–106.
- Spanier, E. and Goven, M. (1988) An Indo-Pacific trunkfish *Tetrosomus gibbosus* (Linnaeus): first record of the family Ostracionidae in the Mediterranean. *Journal of Fish Biology*, **32**, 797–798.
- Spanier, E., Pisanty, S., Tom, M. and Almog-Shtayer, G. (1989) The fish assemblage on a coralligenous shallow shelf off the Mediterranean coast of northern Israel. *Journal of Fish Biology*, **35**, 641–649.
- Stephenson, T.A. (1948) The constitution of the intertidal fauna and flora of South-Africa. Part III. *Annals of the Natal Museum*, **11**, 207–324.
- Travis, J. (1993) Invader threatens Black, Azov Seas. *Science*, **262**, 1366–1367.
- Verlaque, M. (1994) Inventaire des plantes introduites en Méditerranée: origine et répercussions sur l'environnement et les activités humaines. *Oceanologica Acta*, **17**, 1–23.
- Verlaque, M. and Riouall, R. (1989) Introduction de *Polysiphonia nigrescens* et d'*Antithamnton nipponicum* (Rhodophyta, Ceramiales) sur le littoral méditerranéen français. *Cryptogamie-Algologie*, **10**, 313–323.
- Zibrowius, H. (1983) Extension de l'aire de répartition favorisée par l'homme chez les invertébrés marins. *Oceanis*, **9**, 337–353.
- Zibrowius, H. (1991) Ongoing modification of the Mediterranean marine fauna and flora by the establishment of exotic species. *Mésogée*, **51**, 83–107.