

EXOTIC MOLLUSCS IN THE MEDITERRANEAN BASIN: CURRENT STATUS AND PERSPECTIVES

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Abstract An updated synthesis is presented for the records of introduced Mollusca in the Mediterranean basin. The rationale for taking molluscan records as significant is discussed. The Mediterranean Sea, with some 1800 native species of Mollusca, currently houses 139 exotic species, of which 85 form established populations, 52 are aliens recorded once or twice, and two are questionable. Ten species (the gastropods *Cerithium scabridum*, *Rhinoclavis kochi*, *Strombus persicus* and *Bursatella leachi* and the bivalves *Pinctada radiata* and *Brachidontes pharaonis* in the eastern Mediterranean, the gastropod *Rapana venosa* and the bivalves *Anadara inaequalvis*, *Musculista senhousia*, and *Xenostrobus securis* in the northern Adriatic and the western Mediterranean lagoons) are locally invasive.

The bulk of the introduced species (118 species, of which 70 are established, 46 aliens, and two questionable) are species of Indo–Pacific origin found mainly in the eastern basin of the Mediterranean. Among these species, some which live in the Suez Canal are most likely to have spread by their own means through this waterway (these are the “lessepsian immigrants” in the most restricted sense). For other species, the intervention of transport by ship hulls or ballast water can be suspected. Only two of these Indo–Pacific immigrants are found, very locally, in the western Mediterranean. The process of immigration has become unprecedented in magnitude since the 1970s and is not slowing down.

The remaining introductions of marine species are connected with mariculture and/or shipping. These vectors account for the occurrence or dissemination of only 29 exotic species in the Mediterranean basin, but four of these are invasive.

The data regarding the Mollusca do not support any substantial faunal change caused by an influx of subtropical faunal elements through the Straits of Gibraltar. Some local species boundaries may have changed slightly in the past decades but not a single newcomer to the Mediterranean basin by this route could be detected in this survey.

The open sea localities of the western Mediterranean remain virtually free of immigrant mollusc species. The areas most severely affected by the occurrence of exotic species (eastern Mediterranean, Adriatic and lagoons in the western Mediterranean) are those where the species richness of the native fauna is low. It is speculated that this low diversity is a crucial contribution to the success of the newcomers. In the affected areas, the impact on the local fauna is considerable in terms of species composition of the assemblages but so far no native Mediterranean species can be reported as endangered as an effect of a biological invasion.

Introduction

Molluscs are an important component of marine benthic fauna worldwide, and may make up to 15–25% of the benthic macrofauna both in number of species and in number of individuals. Thus, any important change in the species composition of molluscan assemblages will have a visible impact on the benthic community in general.

The exotic species, which are the subject of this review, are those which do not belong to the native fauna and have arrived recently (i.e. within historical times). An organism that has colonised an area outside its native range with human assistance, intentional or unintentional, is said to be introduced. Much attention has been given to introduced species, at first terrestrial (Elton 1958) but later also to marine species (e.g. Carlton & Geller 1993, Carlton 1996a), because it has been realised how much of a threat they are for the balance in native faunas. Other organisms extend their geographical range following natural or man-made changes in the environment (Vermeij 1996). Some species may thrive in their new environment, displace the original components of the biota, and be regarded as “invasive”.

The Mediterranean Sea holds approximately 1800 native species of molluscs (Sabelli et al. 1990). It is generally believed that the Mediterranean marine fauna vanished, or at least was greatly depleted, during the Late Miocene salinity crisis between 5.96 mya and 5.33 mya (Hsü et al. 1973, McKenzie 1999). During this time, marine species survived only in nearby areas of the Atlantic Ocean. Earlier during the Miocene, c. 12 mya, the connection between the Atlanto–Mediterranean realm and the Indo–Pacific was closed (Robba 1987), and was never restored until the opening of the Suez Canal in 1869. The opening of the Red Sea in the Pliocene brought the two realms very close but the threshold was impassable for the marine fauna, and allowed considerable divergence to take place. At the time of the planning of the Suez Canal, biologists were concerned about a possible dramatic merging of the Erythrean and Mediterranean faunas. Several surveys of the Bay of Suez (Fischer 1865, Vaillant 1865, Issel 1869, MacAndrew 1870) were conducted, pioneering what is today known as baseline studies. Fischer (1865) correctly concluded that the two shores of the Suez Isthmus do not share any species of their marine mollusc faunas. The only species to have crossed the isthmus by natural means was *Potamides conicus*, a paralic gastropod also capable of colonising landlocked waters (Plaziat 1989).

The communication between the Mediterranean and the Atlantic, nevertheless, was never interrupted since the beginning of the Pliocene. Without being aware of the salinity crisis, malacologists with a good knowledge of the Mediterranean fauna considered that it was derived from the Atlantic fauna. Pallary (1907), who gathered experience from the North African coast, wrote that “the Mediterranean having received its population from the Ocean, there is no such thing as a Mediterranean fauna” (in translation). The eastern limit, towards the Mediterranean, of those species occurring in the Ibero–Moroccan area of the Atlantic had time to reach an equilibrium position.

In the past decades, human activity has exposed the Mediterranean fauna to considerable factors of change. The invasion of exotic species in the Mediterranean basin is something that has been going on for some time but lately the number of reported species has increased dramatically; currently it amounts to 139 species and is certain to increase further. Three-quarters of these species have been recorded in the past three decades, in part because some conditions have changed, but also as a result of greater attention being given to micromolluscs in the eastern basin of the Mediterranean.

The most spectacular change in the Mediterranean fauna is the influx of Indo–Pacific

species through the Suez Canal, a process for which Por (1978) coined the term “lessepsian migration” (more accurately, immigration, see Vermeij (1996)). Important post-canal surveys of the Mollusca were published by Keller (1882), Tillier & Bavay (1905), Tomlin (1927) and O’Donoghue (1929). Moazzo (1939) provided a comprehensive survey of the Mollusca in the Suez Canal, based on original collections and on the reports of previous authors. His original material is currently in Goulandris Museum of Natural History, Kifisia, Greece, so that some specimens could be checked by the authors. The Hebrew University – Smithsonian Institution joint programme 1967–72, was aimed at understanding some of the characteristics of the successful migrants, and produced some collections.

It has been suggested in the past decade that the distribution of tropical or subtropical Atlantic species in the Mediterranean is in progress and that this may reflect a trend in climatic change. This viewpoint has been substantiated essentially by fish data (e.g. Francour et al. 1994, Bombace 2001, Golani et al. 2002), occasionally by invertebrate data (Morri et al. 2001) and has been termed the “tropicalisation” or “meridionalisation” of the Mediterranean Sea. This aspect is here addressed for the Mollusca, among which there is not yet any documented case of this effect.

Shipping and mariculture also brought their share of exotic species. Reports are scattered in a large number of publications, usually reporting single finds, and there have been few attempts at a synthesis of this information (e.g. Zibrowius 1992).

The purpose of this paper is to summarise and discuss the data gathered for the ongoing Atlas of Exotic molluscan species prepared by the International Commission for the Scientific Exploration of the Mediterranean Sea (CIESM), based in Monaco (Zenetos et al., in press, and online Internet version at <http://www.ciesm.org/atlas>; hereafter referred as “the CIESM Atlas”) to which we refer for details of species occurrences and distributions. Several questions require to be addressed.

- (1) Which processes are involved in the introduction of exotic species?
- (2) Is the rate of influx slowing down, stable, or accelerating? Does the influx meet geographical limits?
- (3) What are the reasons for the success of some particular species as invaders, or for the success of invaders in some particular environments?
- (4) What is the impact on the native fauna? Has any native species become extinct because of invaders?

Methods

Geographic scope

The CIESM Atlas covers the Mediterranean basin, including the Adriatic but not the Black Sea. In addition to the Atlas species, in the present review three cases of introductions from one area to another within the Mediterranean basin are considered. These are *Gibbula albida*, a north Adriatic endemic introduced into western Mediterranean lagoons (Clanzig 1989), *Siphonaria pectinata*, an eastern Atlantic species occurring naturally in the Alboran Sea and Algeria but introduced to Greece (Nicolay 1980), and *Perna picta*, also eastern Atlantic and western Mediterranean, reported from the Adriatic (De Min & Vio 1998).

Criteria for the selection of data

In the process of compiling data for the CIESM Atlas, records for nearly 200 species were reviewed, of which only 136 exotics (plus *Alvania dorbignyi*, a cryptogenic species reported in 1982) were accepted and given a full coverage. A list of spurious records that continue to exist in twentieth century checklists or identification guides or published in the past three decades, is presented in Table 1. For those 62 species, a statement of the reasons for which the record is not accepted is given in the Atlas. Faulty records (see below) from earlier than 1900 were omitted.

The rejected records can be classified under the following headings.

Table 1 Species excluded from the CIESM Atlas of Exotic Mollusca (62 entries). Abbreviations used for origin, RS: Red Sea; IP: Indo-Pacific, Carib.; Caribbean. Those entries where the Mediterranean citation is considered to proceed from a misidentification of a native species are denoted by (m). Some species with a native eastern Atlantic/Mediterranean range are listed here because they were explicitly presented as exotic in a published report.

Class GASTROPODA, subclass Prosobranchia	Origin	Date collected	Date published	Where found
<i>Clelandella infucata</i> (Gould, 1861)	IP		1982	Sicily
<i>Gibbula cineraria</i> (Linné, 1758)	NE Atlantic		1979	Malta
<i>Umbonium vestiarium</i> (Link, 1807)	RS, IP	1969	1970	Libya
<i>Littorina littorea</i> (Linné, 1758)	NE Atlantic		1982	Italy
<i>Littorina obtusata</i> (Linné, 1758)	NE Atlantic		1997	Alboran Sea
<i>Cerithium caeruleum</i> Sowerby G.B., 1855	RS, IP		1989	Israel
<i>Cerithium echinatum</i> Lamarck, 1822	RS, IP	1980	1986	Israel
<i>Cerithium erythraeoense</i> Lamarck 1822	RS, IP		1937	Israel
<i>Bittium proteum</i> (Jousseaume, 1930)	RS, IP		1977	Egypt
<i>Potamides conicus</i> (Blainville, 1824)	RS, S. Medit.		1824	S. Medit.
<i>Scaliola elata</i> Issel, 1869	RS, IP	1974	1977	Egypt
<i>Callostracum gracile</i> (Maltzan, 1883)	West Africa		1981	Israel
<i>Mesalia opalina</i> (Adams & Reeve, 1850)	West Africa		1967	Italy
<i>Rissoina chesneli</i> (Michaud, 1832)	Caribbean		1886	France
<i>Rissoina decussata</i> (Montagu, 1803)	Caribbean		1886	France
<i>Natica marochiensis</i> Gmelin, 1791	W. Africa, Carib.		1997	Alboran Sea
<i>Polynices lacteus</i> (Guilding, 1834)	W. Africa, Carib.		1970	Tunisia
<i>Cypraea pantherina</i> Solander in Lightfoot, 1786	RS endemic		1970	Lampedusa
<i>Erronea caurica</i> (Linné, 1758)	RS, IP	1932	1968	Greece
<i>Monetaria moneta</i> (Linné, 1758)	RS, IP		1886	France
<i>Monetaria annulus</i> (Linné, 1758)	RS, IP		1937	Israel
<i>Staphylaea nucleus</i> (Linné, 1758)	RS, IP		1993	Israel
<i>Strombus lentiginosus</i> Linné, 1758	IP		1934	Israel
<i>Bursa marginata</i> (Gmelin, 1791)	W. Africa		1997	Alboran Sea
<i>Rapana rapiformis</i> (von Born, 1778)	RS, IP	1976	1977	Israel
<i>Coralliobia madreporarum</i> (Sowerby, 1832)	RS, IP		1970	Italy
<i>Latirus polygonus</i> (Gmelin, 1791)	IP	1958	2000	Israel
<i>Mazatlanian cosentini</i> (Philippi, 1836)	Caribbean		1836	Sicily
<i>Vasum turbinellus</i> (Linné, 1758)	RS, IP	1956	1973	Israel
<i>Strigatella virgata</i> (Reeve, 1844)	RS, IP		1970	Italy

EXOTIC MOLLUSCS IN THE MEDITERRANEAN BASIN

Table 1 *continued*

Class GASTROPODA, subclass Prosobranchia	Origin	Date collected	Date published	Where found
<i>Vexillum depexum</i> (Deshayes in Laborde, 1834)	South Arabia	1984	1985	Israel
<i>Cymbium rubiginosum</i> (Swainson, 1822)	NW Africa		1991	Sardinia
<i>Lophiotoma indica</i> (Röding, 1798)	RS, IP		1939	Egypt
<i>Pusionella nifat</i> (Bruguière, 1789)	West Africa		1862	Algeria
<i>Conus arenatus</i> Hwass in Bruguière, 1792	RS, IP		1937	Israel
Class GASTROPODA, subclass Opisthobranchia				
<i>Cylichna</i> cf. <i>mongii</i> (Audouin, 1826)	(m)		1996	Cyprus
<i>Aglaia taila</i> Marcus & Marcus, 1966	E. Atlantic, Medit.		1976	Italy
<i>Melanochlamys seurati</i> (Vayssière, 1926)	Tunisia		1999	Israel
<i>Atys blainvilliana</i> (Recluz, 1843)	France		1992	Israel
<i>Aplysia juliana</i> Quoy & Gaimard, 1832	(m)			(no definite data)
<i>Notarchus indicus</i> Schweiger, 1820	IP		1970	Israel
<i>Petalifera gravieri</i> (Vayssière, 1906)	(m)		1970	(no definite data)
<i>Dolabrifera holboelli</i> Bergh, 1872	? Greenland		1972	(no definite data)
<i>Berthellina citrina</i> (Rüppell & Leuckart, 1828)	(m)		1970	Israel
<i>Sclerodoris</i> cf. <i>tuberculata</i> Eliot, 1904	(m)		1985	Italy
<i>Chromodoris clenchi</i> (Russell, 1935)	(m)		1983	Israel
Class BIVALVIA				
<i>Anadara notabilis</i> (Röding, 1798)	(m)		1974	Morocco
<i>Hochstetteria munieri</i> Bernard, 1879	(uncertain)		1879	France
<i>Arctinula groenlandica</i> (Sowerby, 1842)	(m)		1974	Italy
<i>Crassostrea virginica</i> (Gmelin, 1791)	NW Atlantic		1915	Italy
<i>Placopecten magellanicus</i> (Gmelin, 1791)	NW Atlantic		1973	Italy
<i>Spondylus spectrum</i> Reeve, 1856	IP		1934	Israel
<i>Spondylus limbatus</i> Sowerby, 1847	IP		1998	Israel
<i>Galeomma polita</i> Deshayes, 1855	(m)		1969	(no definite data)
<i>Linga aurantia</i> Deshayes, 1832	Caribbean		1992	Israel
<i>Hippopus hippopus</i> (Linné, 1758)	IP		1937	Israel
<i>Parvicardium haumiense</i> (Høpner-Petersen & Russell, 1971)	Baltic Sea		1992	France
<i>Laevicardium flavum</i> (Linné, 1758)	IP	1980	1986	
<i>Mactrinula tryphera</i> Melvill, 1899	IP		2000	Israel
<i>Saxidomus purpuratus</i> (Sowerby, 1852)	IP	1956	1999	Egypt
<i>Petricola hemprichii</i> Issel, 1869.	RS		1905	Egypt
<i>Penicillus vaginiferus</i> (Lamarck, 1818)	IP		1968	(no definite data)

Unsupported records

These are statements that an exotic species exists, or may exist in the Mediterranean, or even merely a name of an exotic species within a list of Mediterranean molluscs, which are not supported by data regarding locality of collecting and actual specimens.

Records based on mislabelled or misidentified material

This refers to a few cases where a genuinely Mediterranean species was misidentified as an exotic species.

Records of species finally regarded as native

The only case of a native Red Sea and Mediterranean range is that of the lagoon snail *Potamides conicus*. Otherwise, this important question regards the Atlanto–Mediterranean species which have an Atlantic type locality and recorded range, and were subsequently found in the Mediterranean. The reverse also occurs (i.e. “Mediterranean” species that were subsequently found in the Canaries or the Ibero–Moroccan area as the fauna became better known). In such cases there is no reason to suspect the authenticity of the records but the hypothesis that those species are “invaders” which have moved through the Strait of Gibraltar must be considered with a high degree of caution. Rare species may have been in both the Mediterranean and the Atlantic for a long time, and the apparent trend is only an artifact due to the timing of records. The possible influx of Atlantic species into the Mediterranean as a dynamic process has been kept under scrutiny; however, the authors retain as “introduced” only those species which have obviously been brought into the Mediterranean by human interference, an example being *Mya arenaria* (see Pelorce 1995).

Records based on the accidental input of isolated specimens or shells, in a context which cannot, or did not, prove to be viable

This situation accounts for most rejections. Unsupported records are a particularly serious problem with Mollusca because their shells may last for a long time after the animal has died, having been transported by man for food or ornament, and left or lost in places where the animals do not live. Unfortunately, reports of molluscs based on empty shells are commonplace in the malacological literature. Petit de la Saussaye (1869) was already aware of the problem and warned, in the introduction to his Catalogue of European Shells that “these records are not more meaningful for biogeography than the finding of a crocodile in the river Seine or a monkey in the forest of Fontainebleau” (in translation).

In the eighteenth and nineteenth centuries, the occurrence of exotic shells on European shores was mainly a result of the discharge of ballast sand by ocean-going ships and these shells cannot be considered as introductions. Most of such exotic species in the early descriptive literature were reported without the authors being aware that the species were not native, so that several taxa were named with an erroneous European type locality.

Nowadays, the meaningless records of exotic shells derive mainly from the souvenir trade and from material brought in by fishermen operating in remote areas. The occurrence

of several Indo–Pacific species, including the spectacular *Cypraea tigris* (Linné 1758) and *Cymbiola vesperilio* (Linné 1758), was reported by Bini (1983) from the Caprolace lagoon on the coast of Latium. There, the occurrence of the shells was correctly interpreted as purely accidental inputs, which would not result in the introduction of these species in the Mediterranean. Other authors were not so cautious and presented such findings as “new records” without any evidence that the isolated shell(s) found had been the founders of locally-sustained populations. Some records are not tenable for biological reasons, like the alleged occurrence in the Mediterranean of the tridacnid bivalve *Hippopus hippopus*, based on a single record by Haas (1937). This species requires a coral reef environment that does not exist in the Mediterranean (Taviani 1994).

Some old records of exotic species have now fallen into oblivion (e.g. records of *Monetaria annulus*, a common Indo–Pacific cowry that has long been used as currency). Others are perpetuated in checklists based (often not explicitly) on the same, unconfirmed single original citation. Such species are sought after by some collectors who are eager to possess every species but do not have the background to decide if the occurrences are meaningful. If a species is listed as Mediterranean but does not actually live there, specimens of spurious origin will sooner or later show up, as has happened for a long time with the elusive Caribbean species *Mazatlaniana cosentini* (see Bouchet & Gofas 1983). The authors believe that there is a need to remove such species from checklists and guides, because otherwise their mention will trigger more unwarranted citations and finally give the impression that the species does exist in the region.

Also rejected are records of species which, though found alive, were later proved to be unable to establish populations or to spread. An example is a population of *Littorina littorea* reported by Barsotti & Campani (1982) but later reported as absent (Johannesson 1988). A similar case is that of a bushel of live *Patella vulgata*, a north Atlantic species, discarded from a nearby fish market in the harbour of Le Brusc, Mediterranean France, in 1968. Some individuals managed to crawl up the side of the pier but died after a few days (S. Gofas, pers. obs.).

Attributes of the species

The complete list of exotic species recorded in the Mediterranean basin, with the associated data, is presented in Table 2. For each species that has passed the selection criteria, information has been gathered under the following headings.

Year and place of first collection and year of first publication

This normally post-dates the actual time of introduction by several years, maybe decades, in the less-explored areas. Nevertheless, it is the only objective datum. In the case where the original publication does not state the year of collecting, the date of publication is taken by default.

Recorded Mediterranean range

This range is established from the compilation of all published data, museum material and personal communications from colleagues. In the case of established species (see below) it

Table 2 List of exotic species recorded in the Mediterranean Sea. This list includes all species treated in the CIESM Atlas except the cryptogenic *Alvania dorbignyi*, and three species (*Gibbula albida*, *Siphonaria pectinata*, *Perna picta*) not covered in the Atlas but for which intra-Mediterranean transfers have been reported. Abbreviations used: Date, Pub: Date of publication of first report; Rec: Actual collecting date, if mentioned. Current range, Can: Suez Canal; Lev: Levantine coast (Israel, Lebanon and Syria); T/C: Turkey and/or Cyprus; Egy: Egyptian Mediterranean coast. Ion: Ionian Sea,

	Date		Can.	Lev.	T/C	Range Egy.
	Pub.	Rec.				
Class POLYPLACOPHORA						
<i>Chiton hululensis</i> (Smith E.A. in Gardiner, 1903)	1974	1934		*		
Class GASTROPODA, Subclass Prosobranchia						
<i>Cellana rota</i> (Gmelin, 1791)	1967	1961	*	*		*
<i>Haliotis pustulata cruenta</i> Reeve, 1846	1971			*		*
<i>Diodora ruppellii</i> (Sowerby, 1834)	1948		*	*	*	
<i>Smaragdia souverbiana</i> (Montrouzier, 1863)	1994				*	
<i>Nerita sanguinolenta</i> Menke, 1829	1973	1968	*			*
<i>Trochus erythraeus</i> Brocchi, 1821	1973	1968	*	*	*	*
<i>Gibbula albida</i> (Gmelin, 1791)	1989					
<i>Pseudominolia nedyma</i> (Melvill, 1897)	1972	1966	*	*	*	
<i>Stomatella impertusa</i> (Burrow, 1815)	2000	1999			*	
<i>Cerithium nesioticum</i> Pilsbry & Vanatta, 1906	1977	1970		*	*	
<i>Cerithium scabridum</i> Philippi, 1848	1882		*	*	*	*
<i>Cerithium egenum</i> Gould, 1849	2001	1971		*		
<i>Rhinoclavis kochi</i> (Philippi, 1848)	1973	1963		*	*	
<i>Clypeomorus bifasciatus</i> (Sowerby G.B. II, 1855)	1985	1983	*	*		*
<i>Angiola punctostriata</i> (Smith E.A., 1872)	1977	1950		*		
<i>Planaxis griseus</i> (Brocchi, 1821)	1905		*	*		*
<i>Gibborissoa virgata</i> (Philippi, 1849)	1989	1970		*	*	
<i>Finella pupoides</i> Adams A., 1860	1977	1958	*	*	*	
<i>Clathrofenella ferruginea</i> (Adams A., 1860)	1977	1970	*	*	*	
<i>Diala varia</i> Adams A., 1860	1976	1935	*	*		*
<i>Cerithiopsis pulvis</i> (Issel, 1869)	1983	1978		*	*	
<i>Cerithiopsis tenthrenois</i> (Melvill, 1896)	1989	1982		*	*	
<i>Metaxia bacillum</i> (Issel, 1869)	1985	1978		*	*	
<i>Rissoina bertholleti</i> Issel, 1869	1973	1965		*	*	
<i>Rissoina spirata</i> Sowerby, 1825	1984	1974		*		
<i>Voorwindia tiberiana</i> (Issel, 1869)	1980		*	*		*
<i>Strombus persicus</i> Swainson, 1821	1983	1978		*	*	
<i>Strombus mutabilis</i> Swainson, 1821	2001	1991		*		
<i>Sabia conica</i> (Schumacher, 1817)	1986	1980		*		
<i>Crepidula aculeata</i> (Gmelin, 1791)	1992	1973				
<i>Crepidula fornicata</i> (Linné, 1758)	1982	1957				
<i>Erosaria turdus</i> (Lamarck, 1810)	1986	1980	*	*		*
<i>Purpuradusta gracilis notata</i> (Gill, 1858)	1983	1981		*	*	
<i>Palmadusta lentiginosa</i> (Gray, 1825)	1990	1989		*		
<i>Natica gualteriana</i> Récluz, 1844	1986	1966		*		*
<i>Cycloscala hyalina</i> (Sowerby, 1844)	1994	1992			*	

EXOTIC MOLLUSCS IN THE MEDITERRANEAN BASIN

including Malta but not the North African shores. Gab: Gulf of Gabès. Aeg.: Aegean Sea. Geographic origin, RS: Red Sea; IO: Indian Ocean; IP: Indo-Pacific. Status, E: Established; A: Alien; Q: Questionable. Mode of Introduction, Less: Lessepsian; L?: Suspected lessepsian; Ship.: Shipping; Aq.: Mariculture; ???: Unknown. Some species are scored for more than one mode. There are in total 139 exotic species, of which 85 are established, 52 alien and 2 questionable. The ten invasive species appear in boldface.

Ion.	Gab.	Aeg.	Others	Origin	Status		Mode of introduction				
							Less.	L?	Ship.	Aq.	???
				RS, IP	A		*				
		*		RS, IP	E	*					
				RS, IP	A		*				
				RS, IP	E	*					*
		*		RS endemic	A		*				
		*		RS endemic	E	*					
			W Med. lagoons	Adriatic	E					*	
				RS, IP	E	*					
				RS, IP	A						*
*	*			RS, IP	A		*				
				RS, IO	E	*			*		
				RS, IP	A		*				
				RS, IP	E		*				
				RS, IP	A	*					
				RS	A		*				
				RS endemic	A	*					
				RS, IP	E		*				
				RS, IP	E	*					
				RS, IP	E	*					
				RS, IP	E	*					
				RS, IP	E		*				
				IP	E		*				
				RS, IP	E		*				
				RS, IP	E		*				
				RS, IP	A						*
				RS, IP	A	*					
		*		IO, Persian Gulf	E						*
				RS, IP	A		*				
*				RS, IP	A		*				
			Spain	S. Atlantic	E				*		
		*	**	N. Atlantic	E				*	*	
				RS, IP	A	*					
				RS, IP	E		*				
				RS, IP	A		*				
				RS, IP	E		*				
				RS, IP	E						*

Table 2 *continued*

	Date		Can.	Lev.	T/C	Range Egy.
	Pub.	Rec.				
<i>Sticteulima</i> cf. <i>lentiginosa</i> (Adams A., 1861)	1994				*	
<i>Ergalatax obscura</i> Houart, 1996	1995				*	
<i>Thais lacera</i> (Born, 1778)	1939	1939	*	*	*	*
<i>Thais sacellum</i> (Gmelin, 1791)	2002	2000		*		
<i>Rapana venosa</i> (Valenciennes, 1846)	1974	1974				
<i>Murex forskoehlII</i> Röding, 1798	1905		*	*		*
<i>Nassarius arcularius plicatus</i> (Röding, 1798)	1977	1968		*		*
<i>Fusinus verrucosus</i> (Gmelin, 1791)	1905		*	*		*
<i>Zafra savignyi</i> (Moazzo, 1939)	1963	1954		*	*	
<i>Zafra selasphora</i> (Melvill & Standen, 1901)	1993	1980		*	*	
<i>Conus fumigatus</i> Hwass in Bruguière, 1792	1986					
Class GASTROPODA, Subclass Heterobranchia						
<i>Murchisonella columna</i> (Hedley, 1907)	1995				*	
<i>Chrysallida fischeri</i> (Hornung & Mermod, 1925)	1979	1974		*	*	
<i>Chrysallida maiiae</i> (Hornung & Mermod, 1924)	1963	1935	*	*	*	*
<i>Chrysallida pirintella</i> Melvill, 1910	1989	1982		*	*	
<i>Adalactaeon fulvus</i> (Adams A., 1851)	1981	1967		*	*	
<i>Adalactaeon amoenus</i> (Adams A., 1851)	1985	1978		*	*	
<i>Styloptygma beatrix</i> Melvill, 1911	1992	1989		*	*	
<i>Cingulina isseli</i> (Tryon, 1886)	1983	1980		*	*	
<i>Turbonilla edgari</i> (Melvill, 1896)	1989	1980		*	*	
<i>Syrnola fasciata</i> (Jickeli, 1882)	1987	1958		*	*	
<i>Syrnola cinctella</i> Adams A., 1860	1998	1994			*	
<i>Odostomia lorioli</i> (Hornung & Mermod, 1924)	1987	1974		*		
<i>Oscilla jocosus</i> Melvill, 1904	1989	1984		*		
<i>Iolaea neofelixoides</i> (Nomura, 1936)	1998	1994			*	
<i>Hinemoa cylindrica</i> (de Folin, 1879)	2001	1992			*	
<i>Leucotina</i> cf. <i>eva</i> Thiele, 1925	2001	1995			*	
Class GASTROPODA, Subclass Opisthobranchia						
<i>Acteocina mucronata</i> (Philippi, 1849)	1990	1986		*	*	
<i>Cylichnina girardi</i> (Audouin, 1826)	1976		*	*	*	*
<i>Pyrrunculus fourierii</i> (Audouin, 1826)	1987		*	*	*	
<i>Bulla ampulla</i> Linné, 1758	1982	1978		*	*	
<i>Haminaea callidegenita</i> Gibson & Chia, 1989	1993	1992				
<i>Haminaea cyanomarginata</i> Heller & Thompson, 1983	2002	2001				
<i>Chelidonura fulvipunctata</i> Baba, 1938	1961	1959		*	*	
<i>Bursatella leachi</i> de Blainville, 1817	1940			*	*	
<i>Pleurobranchus forskalii</i> Rüppell & Leuckart, 1828	1977	1975		*		
<i>Polycerella emertoni</i> Verrill, 1881	1965	1964				
<i>Polycera hedgpethi</i> Marcus Er., 1964	1991	1986				
<i>Plocamopherus ocellatus</i> Rüppell & Leuckart, 1828	1982	1977	*	*		
<i>Discodoris lilacina</i> (Gould, 1852)	1977	1974		*		

EXOTIC MOLLUSCS IN THE MEDITERRANEAN BASIN

Ion.	Gab.	Aeg.	Others	Origin	Status	Mode of introduction				
						Less.	L?	Ship.	Aq.	???
				IP	A					*
				RS, IP	E					*
				IP	E			*		
				RS, IP	E			*		
		*	**	NW Pacific	E			*		
				RS endemic	E	*				
				RS, IP	A		*			
				RS endemic	E	*				
				RS	E			*		
				RS, IP	E			*		
			Libya	RS, IP	A					*
				RS, IP	A					*
				RS, IP	E			*		
				RS, IP	E	*				
				RS, IP	E			*		
				RS, IP	E			*		
				RS, IP	E			*		
				RS, IP	E			*		
				RS, IP	E			*		
				RS, IP	E			*		
				RS, IP	E			*		
				RS, IP	E			*		*
				RS, IP	A			*		
				RS, IP	A			*		
				IP	A					*
				IP	A					*
				IP	A					*
	*	*		RS, IP	E			*		
		*		RS, IP	E	*				
		*		RS, IP	E	*				
		*		RS, IP	E			*		
			Venice lagoon	N Atlantic	E				*	
*				RS, IP	A					*
*	*			IP	E					*
*	*	*		RS, IP	E			*		
				RS, IP	A			*		
*			**	N Atlantic	E					*
			Italy	S Atlantic	A			*		
				RS, IP	E	*				
				RS, IP	E			*		

Table 2 *continued*

	Date		Can.	Lev.	T/C	Range Egy.
	Pub.	Rec.				
<i>Hypselodoris infucata</i> (Rüppell & Leuckart, 1830)	1977	1965		*	*	
<i>Chromodoris quadricolor</i> (Rüppell & Leuckart, 1830)	1986	1982				
<i>Dendrodoris fumata</i> (Rüppell & Leuckart, 1830)	1986	1980		*		
<i>Melibe fimbriata</i> Alder & Hancock, 1864	1984	1982				
<i>Cuthona perca</i> (Marcus Er., 1958)	1995	1977				
<i>Flabellina rubrolineata</i> (O'Donoghue, 1929)	1993	1988		*	*	
<i>Caloria indica</i> (Bergh, 1896)	1993	1986		*		
<i>Aeolidiella indica</i> (Bergh, 1888)	1968					
Class GASTROPODA, Subclass Pulmonata						
<i>Siphonaria crenata</i> Blainville, 1827	1972	1965	*	*	*	
<i>Siphonaria pectinata</i> (Linné, 1758)	1980					
Class BIVALVIA						
<i>Acar plicata</i> (Dillwyn, 1817)	1986	1978	*	*		
<i>Anadara demiri</i> (Piani, 1981)	1977	1972				
<i>Anadara inaequalis</i> (Bruguiere, 1789)	1973	1969				
<i>Anadara natalensis</i> (Krauss, 1848)	1937	1935	*	*	*	*
<i>Glycymeris arabica</i> (Adams H., 1871)	1977	1966		*		
<i>Limopsis multistriata</i> (Forsskål, 1775)	1977	1965	*	*		
<i>Perna picta</i> (Born, 1780)						
<i>Musculista perfragilis</i> (Dunker, 1857)	1971	1960	*	*		*
<i>Musculista senhousia</i> (Benson in Cantor, 1842)	1971	1964		*		*
<i>Modiolus auriculatus</i> (Krauss, 1848)	1937		*	*		
<i>Xenostrobus securis</i> (Lamarck, 1819)	1994	1992				
<i>Brachidontes pharaonis</i> (Fischer P., 1870)	1877		*	*	*	*
<i>Septifer forskali</i> Dunker, 1855	2001	1999	*		*	
<i>Crassostrea gigas</i> (Thunberg, 1793)	1964					
<i>Saccostrea commercialis</i> (Iredale & Roughley, 1933)	1985	1984				
<i>Saccostrea cucullata</i> (Born, 1778)	2001	1999	*		*	*
<i>Dendrostrea frons</i> (Linné, 1758)	2001	1998			*	
<i>Pinctada margaritifera</i> (Linné, 1758)	1974					*
<i>Pinctada radiata</i> (Leach, 1814)	1878	1874	*	*	*	*
<i>Malvufundus regulus</i> (Forsskål, 1775)	1931	1931	*	*	*	*
<i>Chlamys lischkei</i> (Dunker, 1850)	1985	1985				
<i>Spondylus spinosus</i> Schreibers, 1793	1993	1988	*	*	*	
<i>Spondylus groschi</i> Lamprell & Kilburn, 1995	1998			*		
<i>Spondylus</i> cf. <i>multisetosus</i> Reeve, 1856	2001	1992			*	
<i>Divalinga arabica</i> Dekker & Goud, 1994	1979	1956	*	*		*
<i>Trapezium oblongum</i> (Linné, 1758)	1980	1980		*		
<i>Diplodonta</i> cf. <i>subrotunda</i> Issel, 1869	1999		*	*		
<i>Chama pacifica</i> Broderip, 1834	1905		*	*	*	*
<i>Pseudochama corbieri</i> (Jonas, 1846)	1946		*	*		

EXOTIC MOLLUSCS IN THE MEDITERRANEAN BASIN

Ion.	Gab.	Aeg.	Others	Origin	Status	Mode of introduction				
						Less.	L?	Ship.	Aq.	???
				RS, IP	E		*			
			Ligurian Sea	RS, IP	A					*
*	*	*		RS, IP	A		*			
			Adriatic	IP	E					*
				S. Atlantic	A			*		
				RS, IP	A		*			
*				RS, IP	A			*		
				RS, IP	A				*	
				RS, IP	E	*				
		*		Atlantic,	E			*		
				W.Med.	E					
		*	Adriatic	RS, IP	A	*				
			**	SE Asia	E			*		
				NW Pacific	E			*	*	
				RS, IP	E	*				
				RS, IP	A		*			
			Adriatic	RS, IP	A	*				
				Atlantic,	A			*		
				W.Med.	E	*				
		**		RS, IP	E	*				*
		**		SE Asia	E	*				*
*		*	**	SE Asia	E	*			*	
				RS, IP	E	*		*		
				RS	A					*
	*		**	NW Pacific	E				*	
				S Australia	A				*	
				RS, IP	A					*
				RS, IP	E					*
*	*	*		RS, IP	E	*			*	
		*		RS, IP	E	*				
			**	S. Atlantic	A					*
				RS, IP	E	*				
				RS, IP	Q		*			
				RS, IP	Q					*
				RS, IP	E	*				
				RS, IP	A		*			
				RS, IP	A	*				
				RS, IP	E	*				
		*		RS, IP	A	*				

Table 2 *continued*

	Date					Range Egy.
	Pub.	Rec.	Can.	Lev.	T/C	
<i>Fulvia australis</i> (Sowerby G.B., 1834)	1948			*	*	
<i>Fulvia fragilis</i> (Forsskål, 1775)	1973	1955	*	*	*	
<i>Afrocardium richardi</i> (Audouin, 1826)	1999	1999	*	*	*	
<i>Tellina valtonis</i> Hanley, 1844	1977	1970	*		*	*
<i>Psammotreta praerupta</i> (Salisbury, 1934)	1999	1992	*		*	
<i>Hiatula rueppelliana</i> (Reeve, 1857)	1905		*			*
<i>Mactra olorina</i> Philippi, 1846	1889		*	*		*
<i>Mactra lilacea</i> Lamarck, 1818	2001	1972		*		
<i>Atactodea glabrata</i> (Gmelin, 1791)	1977	1973	*	*		
<i>Gafrarium pectinatum</i> (Linné, 1758)	1905		*	*	*	*
<i>Circenita callipyga</i> (Born, 1778)	1986	1972	*	*		
<i>Clementia papyracea</i> (Gray, 1825)	1948		*	*	*	
<i>Paphia textile</i> (Gmelin, 1791)	1939		*	*	*	*
<i>Mercenaria mercenaria</i> (Linné, 1758)	1965					
<i>Ruditapes philippinarum</i> (Adams & Reeve, 1850)	1981	1981				
<i>Antigona lamellaris</i> Schumacher, 1817	1999	1992	*		*	
<i>Dosinia erythraea</i> Römer, 1860	1905		*			*
<i>Timoclea roemeriana</i> (Issel, 1869)	1999	1997	*	*		
<i>Petricola pholadiformis</i> Lamarck, 1818	1994					
<i>Sphenia rueppelli</i> Adams A., 1850	1986	1978	*	*		
<i>Mya arenaria</i> Linné, 1758	1976					
<i>Gastrochaena cymbium</i> (Spengler, 1783)	1973	1960	*	*	*	
<i>Laternula anatina</i> (Linné, 1758)	1905		*	*	*	*
Totals (questionable not included)			53	92	66	34

generally represents the current range at the time of publication, and is likely to expand. Conversely, for the species recorded as “alien”, records more than a few years old may represent occasional findings or failed introductions, and records do not imply that the species currently lives there.

Relation to current Mediterranean range

The geographical ranges of living organisms are subject to fluctuate both on a historical timescale and on a broader geological timescale. The “current” range is actually the summary of records over many years in historical times (some records dating back from the late eighteenth century) and ignores small short-term variations. The concept of an exotic species refers to new occurrences which clearly depart from this “current” range. The following categories can be considered.

Exotic (or *non-indigenous*) All species, in the broader sense, that are not native. This category encompasses species that have arrived within historical times with the help of human intervention or by their own means. Broadly, this grouping includes lessepsian immigration,

EXOTIC MOLLUSCS IN THE MEDITERRANEAN BASIN

Ion.	Gab.	Aeg.	Others	Origin	Status	Mode of introduction				
						Less.	L?	Ship.	Aq.	???
				RS, IP	E		*			
	*	*		RS, IP	E	*		*		
				RS, IP	E	*				
				RS, IP	E	*				
				RS, IP	A					*
				RS, IP	E	*				
				RS, IP	E	*				
				RS, IP	E		*			
				RS, IP	A	*				
				RS, IP	E	*				
				RS, IP	A	*				
				RS, IP	E	*				
			**	N. Atlantic	E				*	
			**	NW Pacific	E				*	
				RS, IP	A					*
				RS, IP	A	*				
				RS, IP	E	*				
		*		N. Atlantic	A			*		
		*	**	N. Atlantic	E			*		
		*		RS, IP	E	*				
				RS, IP	E	*				
10	7	21				47	43	17	12	25

the possible immigration of Atlantic species into the Mediterranean through the Straits of Gibraltar, and introduced species.

Introduced A term used here only for species which have been transported by man or his artifacts. These are clearly identified as not belonging to the native fauna, and have a known range from which a source area may be hypothesised. In most cases, there are reliable surveys indicating their absence at some particular time prior to introduction.

Cryptogenic Carlton (1996b) coined this term for species which cannot be readily determined as members of the native fauna, or as exotic ones. This usually includes species which, if introduced, have been brought in a long time ago (typically, before AD 1800) so that the history of introduction has not been witnessed. Reasons for suspecting introductions include historical texts, discrepancies with usual biogeographical patterns, and observations that the Mediterranean populations form a disjunct part of the total range. The cryptogenic species (except one, *Alvania dorbignyi* – see below) have been excluded from the CIESM Atlas for the reason of being long-established, but these will be discussed herein.

Native (or indigenous) Species, not considered in this survey, with a “current” Mediterranean range stable at least since historical times. Evidence for this status comes from early surveys (for the Mediterranean, prior to 1869) and museum material, and from fossil occurrences in Pleistocene or Holocene deposits.

Native range, as given by the literature

The worldwide native range, which includes the source area, was taken from literature data, referring as much as possible to first-hand data in revisions or reports with an actual material examined, not to general statements in identification guides.

Introduced range outside the Mediterranean

Reports of introductions in other parts of the world were also taken into account, since there are many cases of species prone to introduction worldwide.

Establishment status

This entry considers the success of invasion and perenniality of introduced populations. Because the recorded species are not usually monitored continuously through time, the following standards have been used.

Established when documented by at least three reliable records, or when the available information shows that there are perennial populations in the Mediterranean. Several records or observations at the same site but at least one year apart are counted as separate records (e.g. *Crepidula aculeata*).

Alien based on one or two records. Among these, most records more than a few years old do not imply current occurrence of the species at the reported sites (otherwise, they would probably qualify as “established”).

Questionable This has been used for a few taxa for which there are unsettled taxonomic issues, and which may in the future be placed in synonymy. The species with this status will not be considered further in the species counts and evaluation of trends.

Mode of arrival

The mode of arrival is seldom known with certainty. Usually, it is surmised from the distribution data and the circumstances of the earliest record. The following categories were considered in this review.

Lessepsian The term was proposed by Por (1978) for species which have penetrated from the Red Sea into the Mediterranean, via the Suez Canal using their natural means of dispersal. This pathway is verified for species that have become established in the Suez Canal prior to their settlement in the Mediterranean, and have penetrated progressively along the

shores of the Suez Canal and the eastern Mediterranean. Species that are recorded in the Red Sea, in the Suez Canal, *and* in Egypt or the Levantine coast are scored as lessepsian. The species that occur in the Red Sea and first showed up in Egypt or along the Levantine coast but are not recorded from the Canal were scored as probable lessepsian. Conversely, species of Indo–Pacific origin that first showed up in more distant Mediterranean localities (e.g. Turkey, Ionian Sea) were scored with unknown mode of introduction.

Shipping Species that were first noticed as isolated populations in a major harbour are scored as introduced by shipping.

Mariculture Species that were voluntarily introduced to be cultivated or species that were first observed in areas dedicated to mariculture were scored as introduced with mariculture. The species maintained exclusively in artificial conditions, or in aquaria, are not considered.

For species suspected to have arrived in the Mediterranean after previous introductions to intermediate areas, and not directly from their native range (e.g. *Mya arenaria*, *Rapana venosa*), it is the final step that is taken into account. In a few cases more than one mode is considered for the same species, regarding different subranges within the Mediterranean.

Type of larval development

The larval stage is known to be crucial for dispersal in the Mollusca. Species that have a long planktonic larval stage are likely to be transported to remote sites by currents but also in ballast water of ocean-going ships.

In shelled gastropods, the type of larval development can be inferred from shell morphology (Jablonski & Lutz 1980, Levin & Bridges 1995). The type of larval development has been scored for all the prosobranch species involved, because in this group the interpretation of protoconch features is quite straightforward. All vetigastropods have been scored as “acteplanic”, because they release short-lived larval stages that stay a few days in the plankton but do not feed prior to metamorphosis.

Sources of the exotic species

Cryptogenic species

The authors view as cryptogenic five molluscan species of the Mediterranean, which are discussed hereafter but are not considered in the species counts. Only one of them was treated in the CIESM Atlas, complying with the editorial policy of not considering very old records.

Littorina saxatilis (Olivi, 1792) was originally described from Venice, which is part of a limited subrange of the species in the northern Adriatic. It also occurs in small subranges in the Gulf of Gabès, Tunisia, in the Straits of Gibraltar, and currently has its main range in the North Atlantic from Canada, Greenland and northern Norway south to Portugal. Two conflicting hypotheses can be considered for the Mediterranean occurrences (Reid 1996: 331): that it is a relict from a former range that included the Mediterranean at the time of

Pleistocene cold spells, or an old introduction through navigation. The relict hypothesis is tenable because the localities involved are those in the Mediterranean with a substantial tidal range, and at least one reliable fossil occurrence is known in Pleistocene deposits off Marseille, France (one shell in Muséum National d'Histoire Naturelle, Paris, unpubl. datum). A genetic analysis attempted to investigate the latter hypothesis but remained inconclusive (Janson 1985). A tenable alternative is a natural airborne introduction by wading birds (see Rees 1965), which could also explain the occurrences in Tunisia and southern Morocco.

There are some uncertainties regarding the small rissoid *Alvania dorbignyi* Audouin, 1826 (see Mienis 1985). In favour of accepting it as a native Mediterranean species, it belongs to a species group including several well-known Mediterranean natives, for example, *A. discors* (Allan 1818), *A. lanciae* (Calcara 1841) and *A. consociella* di Monterosato, 1884. All these species live among brown algae in clean, shallow open sea locations. Conversely, all undisputed native Indo-Pacific Rissoidae belong to different genera or, at least, different species groups. The origin of Audouin's specimen is uncertain, because that material included Mediterranean as well as Red Sea species, and the subsequent records of *A. dorbignyi* in the Gulf of Suez (Moazzo 1939) are well after the opening of the Suez Canal. The point is that there are no documented introductions of Mediterranean molluscs into the Red Sea. There is no reason to believe that this species, rather rare on the Levantine coast and not particularly hardy, would be one of the few exceptions. A further support for holding this species as Indo-Pacific is that a very similar, if not conspecific, form has been found living on the coast of New Caledonia (S. Gofas, pers. obs. 1993).

Barash & Danin (1973, 1992) suggested *Aspella anceps* (Lamarck 1822) as an Indo-Pacific species immigrating into the Mediterranean. The same species is also found in Pleistocene deposits bordering the Red Sea at Hurghada, Egypt (Houart & Vokes 1995), indicating that it is definitely native in the Indo-Pacific realm. However, the Mediterranean populations were recorded very early by di Monterosato (1880) who described it as a new species *Epidromus gladiolus* from specimens collected in sponges of undetermined origin, and from two specimens dredged in the harbour of Alexandria, Egypt (Gaglioli 1987). Pallary (1912) recorded as two separate entries di Monterosato's species and a "*Ranella* sp." which, judging from the description given and source, is the same. Modern records (Houart & Vokes 1995) do not extend beyond the eastern basin of the Mediterranean. It is very unlikely that this rare, sublittoral species, not recorded from the Suez Canal, could be one of the pioneer migrant species, whereas all the other early migrants (see below) are euryhaline species well installed in the canal. One possibility is that it has been brought into the Mediterranean in historical times (independently from the opening of the Suez Canal) with the trade of commercial sponges from the Red Sea, or that all Mediterranean records are based on discards from the sponge trade. The alternative interpretation, also unproved, is that the Mediterranean population is native, and that there is a morphologically indistinguishable sibling species in the Indo-Pacific.

Mytilus galloprovincialis Lamarck, 1819 has its type locality in the French Mediterranean, but is prone to introductions worldwide and is recorded as one of the "top 100 invasive species". There are reasons to suspect that some Mediterranean populations are introduced, particularly where the species is cultured. For the populations found in the western Mediterranean, particularly in the Alboran Sea, there is a continuity of the range with the Atlantic Ibero-Moroccan area, and there is little doubt that in this area the species is native.

Teredo navalis (Linné 1758) first appeared around 1730 in the North Sea where it severely affected the Dutch maritime constructions (Selli 1733, Reise et al. 1999, Hoppe

2002). It was probably brought from SE Asia by wooden ships (indiamen). The extent and origin of its occurrence in the Mediterranean is not easy to determine, and there are few positive records (e.g. the Venice lagoon, see Olivi 1792: 197).

Immigrants from the Indo–Pacific

The bulk of the exotic species recorded from the Mediterranean is of Indo–Pacific origin (marked IP, RS or Persian Gulf on Table 2). There are 47 species classified as lessepsian, 43 more as probable lessepsians, which makes a total of 65% of the exotic species. To this list may be added the 17 tropical Indo–Pacific species which are not found near the Mediterranean entrance of the Suez Canal but occur on the coasts of Turkey, one species (*Pinctada margaritifera*) introduced deliberately, two species (*Thais lacera* and *T. sacellum*) introduced by shipping, scattered occurrences of unknown pathway (*Rissoina spirata*, *Conus fumigatus*, *Melibe fimbriata*, *Haminaea cyanomarginata*, *Chromodoris quadricolor*), and the two questionable species of *Spondylus*, bringing the share of tropical Indo–Pacific exotics to a total of 118 (85%).

The data in Table 3, comparing current results with Moazzo’s (1939) survey, demonstrate that having established populations in the Suez Canal is an efficient launching pad for subsequent settling in the Mediterranean. Of the 57 species recorded by Moazzo as established in the Suez Canal (scored as “common” or “quite common” at least in one section of the Canal), about half are now present in the Mediterranean. The other half never made the move. Conversely, of the 152 species recorded from the Gulf of Suez but not in the Suez Canal, only 15 (10%) are now found in the Mediterranean. The percentage is only slightly higher (23%) if one considers species that do occur in the Suez Canal but are scarce.

The influx of Indo–Pacific species into the Mediterranean is a dynamic process. The early settlers have expanded their first ranges, and both the number of species and the affected areas have been increasing since 1869.

There are only four Indo–Pacific molluscan species which were proved to be established in the Mediterranean prior to 1900. These are *Cerithium scabridum*, *Brachidontes pharaonis*, *Pinctada radiata*, and *Maetra olorina*. All four were recorded in the Suez Canal by Tillier & Bavay (1905) and later authors, and three of them are now at the forefront of the penetration of lessepsians in the eastern basin of the Mediterranean.

Cerithium scabridum was mentioned from Port Said, Egypt by Keller (1882). By the end of the nineteenth century, it had reached the Levantine coast. There are specimens from

Table 3 Status of molluscan species in the Suez Canal according to Moazzo (1939) and previous records cited therein, compared with current status in the Mediterranean Sea according to CIESM Atlas data.

Suez Canal data (Moazzo 1939)		Current status in the Mediterranean		
		Established	Alien	Not recorded or questionable
Established in the Canal	57	22	7	28
Others present in Canal	79	10	8	61
Recorded in Gulf of Suez but not in Canal	152	11	4	137

Jaffa (now Yafo, near Tel Aviv) in the Vignal collection, Muséum National d'Histoire Naturelle, Paris, collected in 1899. Pallary (1938) later mentions it as well established on the coasts of Syria and Lebanon. The species was found on the east coast of Sicily in the late 1970s (Di Natale 1978), in the harbour of Porto Megarese. An extensive survey of molluscan faunas around Djerba, Tunisia carried out in 1982 by P. Bouchet and colleagues (unpublished material in Muséum National d'Histoire Naturelle, Paris) did not detect *C. scabridum*, but our own collecting in October 1999 yielded large numbers at several sites around this island. This means that the Sicilian population was introduced at one or more point sources, possibly by ships calling at Porto Megarese, and not by progressive spreading along the North African coast and across the Sicily straits.

Pinctada radiata was first recorded by di Monterosato (1878, 1884) from Alexandria (collected in 1874) and the Mediterranean populations were later named as a new species *Meleagrina savignyi* di Monterosato 1884. It was recorded in the Gulf of Gabès, Tunisia, by 1890 (Seurat 1929) but had not been found there in a previous survey in 1882. It was also established in Cyprus in the late nineteenth century (di Monterosato 1899).

Brachidontes pharaonis was recorded very early at Port Said but only later along the Mediterranean coast. It had reached the Levantine coast by 1931, and now extends to Cyprus, southern Turkey and a few Aegean localities. It was reported from Sicily in 1969 (Di Gerónimo 1971) and is now well established there. As with *Cerithium scabridum*, the most likely cause for this latter occurrence is transportation by ships from the Middle East. The species was not found in the Gulf of Gabès in any of the previously mentioned samplings.

The fourth early settler, *Maetra olorina*, is extremely common in the Suez Canal but, possibly due to the lack of suitable habitats, the established Mediterranean populations remain mainly confined to the Egyptian coast.

The progress of the Indo-Pacific immigrants in the first half of the twentieth century is difficult to assess, because there were no data for the coastline of Turkey and Cyprus. Tillier & Bavay (1905) confirmed the occurrence of the above four species, and reported seven additional immigrants in the harbour of Port Said and one more at Alexandria. It is noteworthy that the very thorough survey of Pallary (1912) for the Mediterranean coast of Egypt did not reveal any novel immigrant. This finding means that the figures published at that time are realistic, and that no more than 12 Indo-Pacific species had a foothold in the Mediterranean in the early twentieth century (see Fig. 1). At the same time, the molluscan fauna of the Gulf of Gabès was quite well known (Pallary 1904–6) and by then *Pinctada radiata* was the only Indo-Pacific species to occur there.

The reports of Haas (1937, 1948) and Pallary (1938) brought new data for the Levantine coast, and at the same time Moazzo (1939) provided an update for the Egyptian coast. Moazzo confirmed all previous records except *Planaxis griseus*, and added *Paphia undulata* and *Thais lacera*. *Malvufundus regulus*, now well established on the Levantine coast, was first recorded there by Gruvel & Moazzo (1931). Haas reported from Palestine *Anadara natalensis*, *Modiolus auriculatus*, and O'Donoghue & White (1940) added the opisthobranch *Bursatella leachi*. A few more species (*Chiton hululensis*, *Diala varia* and *Chrysalida maiiae*) were mentioned in later literature from specimens collected in the 1930s. Several records by Aharoni (1934), Haas (1937) and Steuer (1939) have been rejected in the present review because they are based on shells only; their records are for species which were never found again and require environments that are not found in the Mediterranean. These are *Cerithium erythraeoense*, *Strombus lentiginosus*, *Lophiotoma indica*, *Conus arenatus* and *Hippopus hippopus*. The detailed survey of the Levantine fauna by Pallary (1938)

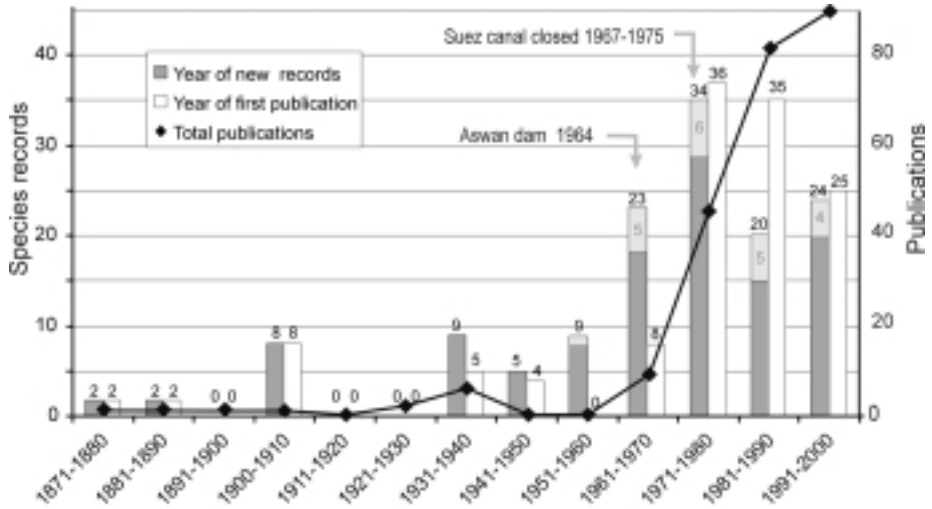


Figure 1 Numbers, per decade, of newly recorded immigrant molluscan species in the Mediterranean basin, and of publications regarding the subject (based on the reference list of the CIESM Atlas, Zenetos et al. in press). For each decade, the right column shows the years when the species was first reported in a publication, the left column the year of actual collecting (by default, same as year of publication). The questionable and cryptogenic species are not counted. Dark grey: species of tropical Indo–Pacific origin, light grey: others.

did not involve any previously unrecorded species. The number of Indo–Pacific molluscs in the eastern Mediterranean at that time, when pruned of unwarranted occurrences, amounted to 21 species. Of these, only four (*Cerithium scabridum*, *Pinctada radiata*, *Brachidontes pharaonis*, *Malleus regulus*) had significantly spread out and became common, whereas 10 (*Fusinus verrucosus*, *Thais lacera*, *Planaxis griseus*, *Chama pacifica*, *Hiatula rueppelliana*, *Mactra olorina*, *Dosinia erythraea*, *Gafrarium pectinatum*, *Paphia textile*, *Laternula anatina*) were still confined to the Egyptian coast. Data are totally wanting for the coastlines of Turkey and Cyprus in the same period but a realistic number of exotics in that region could have comprised between four (the four species whose range is expanding) and 12 (the total number of species then mentioned for the Levantine coast). It is after 1950 that many species were reported from the Levantine coast. The number of new reports increased dramatically in the 1970s (Fig. 1), but if dates of collecting are considered rather than dates of first publication, the histogram is less skewed to the right. Two major events have been invoked to explain the acceleration in the rate of immigration: the construction of the Aswan high dam in 1964 (Oren 1969, El Sayed & van Dijken 1995), which dramatically reduced the freshwater outflow from the Nile, and the closure of the Suez Canal from 1967 to 1975, which allowed marine life to develop in the canal without disturbance. The data indicate that some important immigrants (*Finella pupoides*, *Rhinoclavis kochi*, *Zafra savignyi*, *Syrnola fasciata*, *Chrysallida maiae*, *Fulvia fragilis*) were already in the Mediterranean prior to those events. Nevertheless, it cannot be disputed that the bulk of the immigrants post-date them.

The species which now have the widest distribution are those that have been in the Mediterranean for a long time. The seven species present in Gulf of Gabès and/or Sicily had, by 2001, a mean of 74 yr in the Mediterranean, compared with the 39 yr mean residence of the 90 species present on the Levantine and/or Egyptian coast but not in the outposts of Gabès or Sicily. Figures are not given for Turkey as these would be of little value because of the lack of data before 1980.

Figure 2 shows the progress in numbers of Indo–Pacific immigrants in the last quarter of the twentieth century. The data for Figure 2A are essentially the same as those considered by Por (1978: 138). The counts are slightly at odds with Por's because in the present review the authors (a) counted as Mediterranean the species established at Port Said, whereas Por classified them as Suez Canal species, (b) rejected several of the records considered in Por (1978), here listed in Table 1, and (c) added species which had been collected before 1975 but published later.

The very low number of immigrants (the bivalves *Pinctada radiata*, *Malvufundus regulus* and the opisthobranch *Chelidonura fulvipunctata*) registered for Turkey and Cyprus by 1975 may be an artifact, since this coastline was virtually unexplored until the 1980s. Otherwise, the figures show that the number of immigrants has approximately doubled in 25 yr and that the incidence of immigrants has extended to other areas of the eastern Mediterranean. The Gulf of Gabès, which for a long time housed only *Pinctada radiata*, today features also *Cerithium scabridum*, *Bursatella leachi*, *Melibe fimbriata*, *Acteocina mucronata* and *Fulvia fragilis*.

Among the Indo–Pacific immigrants reported from the Mediterranean in the 1980s and 1990s, there is a pool of species recorded from the southern coast of Turkey and from Cyprus, but not from the Levantine coast nor from Egypt. The most noteworthy is *Strombus persicus*, first sighted in the Mediterranean in 1978 (Nicolay & Romagna-Manoja 1983) from SW Turkey, and today invasive in several areas. It rapidly expanded its range to include Israel (Mienis 1984), Rhodes (Verhecken 1984), Cyprus (Bazzocchi 1985) and Lebanon (Bogi & Khairallah 1987). It is now invasive in most of these places and was sold on the Yafo fish market (Mienis 1999). This species, which is native to the Persian Gulf and southern Arabia and does not occur in the Red Sea, has been presented as an example of “non lessepsian” immigration (Oliverio 1995). It was postulated that *S. persicus* may have arrived in Iskenderun in discharged ballast water from oil tankers coming from the Persian Gulf. However, the gastropod has been found far from oil terminals, and because tankers at the time lacked segregated ballast tanks, oil-laden vessels would not carry ballast water.

Other species which present a distributional gap between the Suez Canal and their Mediterranean subrange are the prosobranchs *Smaragdia souverbiana*, *Stomatella imper-tusa*, *Cycloscala hyalina*, *Sticteulima* cf. *lentiginosa*, *Ergalatax obscura*, five species of heterobranchs, and the bivalves *Saccostrea cucullata*, *Dendrostrea frons*, *Septifer forskali*, *Psammotreta praerupta* and *Antigona lamellaris*. These species have not been seen on the Levantine coast despite appropriate attention in the same period, or have been recorded there later than in Turkey. Thus, their pattern of spreading is unlikely to be a progression along the shore starting from the Suez Canal.

Two conflicting hypotheses may be considered:

- (1) they have been introduced by other means, probably shipping (the tanker terminal at Iskenderun has been proposed as a possible source, but Mersin is also a major port in this area);

EXOTIC MOLLUSCS IN THE MEDITERRANEAN BASIN

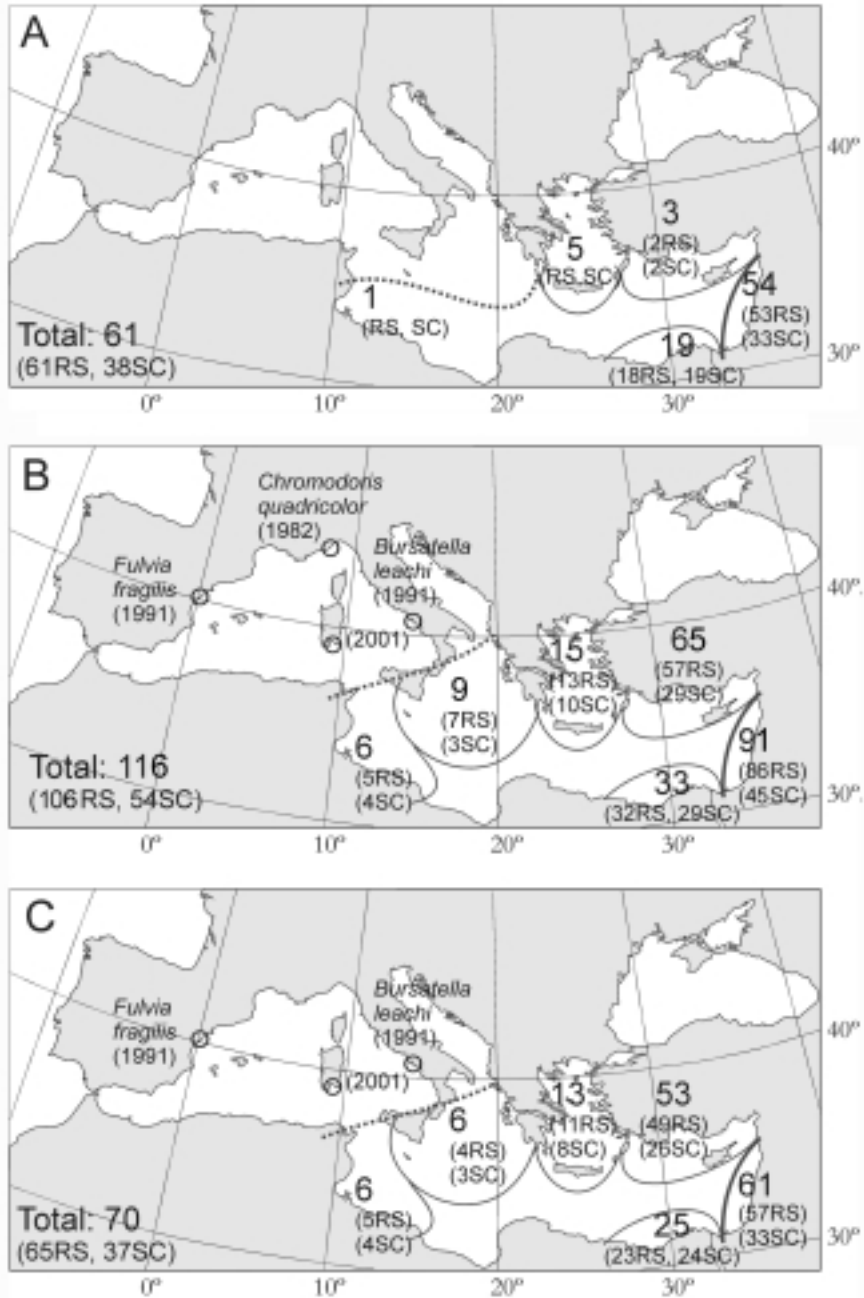


Figure 2 (A) Situation by year 1975 of the exotic species of tropical Indo–Pacific origin. (B) Situation by year 2001 of the exotic species of tropical Indo–Pacific origin. (C) Same, considering only the established species. For each area, the numbers in parenthesis indicate species occurring also in the Red Sea (RS) and within the Suez Canal (SC). The questionable, cryptogenic and cultivated species are not included in the counts.

- (2) these species came through the Suez Canal as larvae, which could find appropriate environments to settle in southern Turkey but not in Egypt nor on the Levantine coast. As a support for the latter hypothesis, five of the gastropods cited above have multispiral larval shells indicating planktotrophic development, and the other species have planktonic, albeit short-lived, larvae.

Other records may remain unexplained. The isolated live specimen of the Indo-Pacific nudibranch *Chromodoris quadricolor* collected in 1982 in the Ligurian sea (Cattaneo-Vietti 1986) may have escaped from a tropical aquarium – a pathway that contributed to the Mediterranean flora, the well-known invasive alga *Caulerpa taxifolia*.

Introductions for mariculture

The introduction of molluscs as a consequence of mariculture is considered when it is the cultured species which has become established or when the species first became established on sites used for mariculture.

It does not appear that any pre-1950 introductions have resulted in establishing viable populations in the Mediterranean. An Italian company imported live *Meleagrina margaritifera* (the pearl oyster) from the Dahalak Islands, Red Sea around 1860 and kept them in an aquarium, where they grew, reproduced and even produced pearls (Bellet 1899). There were plans to introduce the species on the Calabrian coast between Bova and Torre di Riacci, but there are no ascertained records.

The importation process gained in importance in the 1960s, and reports often appear in unpublished reports (“grey literature”) which makes them difficult to trace. One such record refers to the occurrence of the pearl oyster in Abou-Kir Bay, Alexandria, Egypt (Hasan 1974).

The oyster *Crassostrea gigas* was one of the earliest introductions but it first became established on the Atlantic coast of Europe (see Lambert et al. 1929, for details) and was brought much later to the Mediterranean (Raimbault 1964). Lamarck (1819) described *Gryphaea angulata* as originating from the Tagus estuary, Portugal, and did not relate it to the Japanese species. Populations introduced from Portugal to the Atlantic coast of France in 1869 were long known as “Portuguese” oysters and believed to be a native European species. In the 1970s, when oyster farms were depleted by a disease and Japanese spat of *Crassostrea gigas* was imported to Europe, it was realised that both stocks freely interbred and could be considered conspecific (Menzel 1974). Two pieces of evidence support the introduction hypothesis. First, the early nineteenth century range of the “Portuguese” oyster does not match any pattern observed in native species; molluscs occurring in Portugal are found as a rule elsewhere on the European and/or Moroccan Atlantic coast. Second, such similar gene pools could not have been maintained since the Miocene (supposing a Tethyan relict) without divergence. The history of Lisbon as a cosmopolitan port makes introduction a very likely explanation. Recent evidence from sequences of the mitochondrial genome suggests Taiwan as the likely source for the Portuguese populations (Ó Foighil et al. 1998), and also indicates that sufficient divergence has taken place for both lineages to be traced (Fabioux et al. 2002). Japan is the main source for the recent imports of spat.

Transfers in the context of mariculture may also result in the introduction of native Mediterranean species to parts of the basin where they did not occur naturally. This is veri-

fied for the endemic Adriatic trochid *Gibbula albida*, which has been successfully introduced to the French Mediterranean lagoons (Clanzig 1989) and to the Ebro delta (S. Gofas, pers. obs.). Large amounts of the naticid *Neverita josephina* (Risso 1826), which does not occur in the Alboran Sea, are brought to southern Spain with Adriatic catches of the commercial venerid *Chamelea gallina* (Linné 1758). They are occasionally discarded in harbours, and shells are found, but to date this has not resulted in an introduction of the former species.

An important addition was *Ruditapes philippinarum*. In 1983, 200 000 juvenile individuals originating from an English hatchery and, in 1984, another 500 000 individuals of Atlantic origin were imported in the Venice lagoon for marine farming. The species was subsequently imported in various Italian localities where it was acclimatised, successfully farmed and spread in the wild, locally displacing the native *R. decussatus*. The species has become of high commercial importance. It is now farmed in lagoonal areas where it reaches a density of 1000 ind.m⁻² (Cesari & Pellizzato 1985, Breber 2002). In French lagoons the species was also imported in the 1980s, where it became well established, acclimatised and spread rapidly forming natural populations. A number of accompanying exotic species have been attributed to the import of *R. philippinarum*.

Among oysters, the farming of *Crassostrea gigas* has been successful in the French Mediterranean lagoons and sustains a prosperous commercial activity (Gangnery et al. 2001). Conversely, the introduction of *Saccostrea commercialis* in the Venice area was not, and the species has not been seen in recent years (Mizzan 1999).

Accidental introductions may accompany the voluntary transfers. A typical example of an accidental invader with mariculture is that of *Musculista senhousia*, a fouling organism which is an aggressive invader, with adaptations to a variety of habitats. The species originates from the West Pacific whence it was introduced to northwest America in 1941 (Carlton 1992) and to Australia in 1983 (Willan 1987). In the Mediterranean it is now common in lagoons of the Adriatic and France. On the Pacific coast of America the dramatic increase of the mussel's population is presumably as a result of transfer in the ballast waters of ships. French populations of this species were probably imported with oysters from Japan, around 1978 (Hoenselaar & Hoenselaar 1989). Similarly, the Adriatic populations were possibly introduced with the clam *Ruditapes philippinarum*, which was massively imported for mariculture in 1986 (Lazzari & Rinaldi 1994). Very similar in behaviour, and invasive in character, are the bivalves *Xenostrobus securis* and *Anadara inaequalis* whose massive presence in the Adriatic lagoons is related to intense shellfish farming in the area (Occhipinti-Ambrogi 2000).

Introduction via shipping

The introduction via shipping routes results from transport on ships' hulls or in ballast water. An occurrence first reported in a harbour is, of course, a clue to this pathway of introduction.

Some of the Indo-Pacific species in the eastern Mediterranean have been discussed above and may enter this category. Other records are haphazard and sometimes cannot be clearly demarcated from those resulting from mariculture activities. The occurrence of *Crepidula aculeata* in the harbour of Alicante, Spain, registered in 1980 and still observed in 1997, is a representative example.

In several cases, transport via shipping routes may have occurred in combination with

other pathways of arrival. This situation can apply to exotic species already established in one part of the Mediterranean as, for example, the introduction to Sicily of the lessepsian migrants *Cerithium scabridum* and *Brachidontes pharaonis*. Preliminary results of molecular studies have shown that there are some Red Sea genotypes of the latter species in the Mediterranean Sea, but the non-Red Sea genotypes are fairly common and their frequency increases with distance from the Suez Canal (A. Abelson, pers. comm.). This suggests that ship transport from elsewhere may have occurred for this species rather than natural migration.

Like mariculture, shipping can also affect the range of species originally native in a separate part of the Mediterranean, such as the pulmonate *Siphonaria pectinata*, originally restricted to the Alboran Sea and western Algeria (Morrison 1972) and now thriving in the Saronikos Gulf, Greece (Nicolay 1980, and S. Gofas, pers. obs.).

Figure 3 summarises occurrences of molluscs of other than tropical Indo–Pacific origin in the Mediterranean, in total 21 species (15 established and 6 alien). Among these, 10 originate from temperate areas of the Pacific Ocean, eight from the American Atlantic, and three were native in a distinct part of the Mediterranean. It is noteworthy that among the American species, four (*Crepidula fornicata*, *Mercenaria mercenaria*, *Petricola pholadiformis*, *Mya arenaria*) were well established as introduced species on the Atlantic European coast before proceeding to the Mediterranean.

Are any species entering from the Atlantic?

The current data regarding the Mollusca do not support any hypothesis of dynamic faunal change caused by an influx of subtropical faunal elements through the Straits of Gibraltar. In Table 4, a selection of shelled Mollusca (mainly prosobranchs and bivalves) is listed that have the main part of their range in the tropical or subtropical Atlantic, and which extend northwards at least to southern Morocco. This list is necessarily a choice, because the biotic

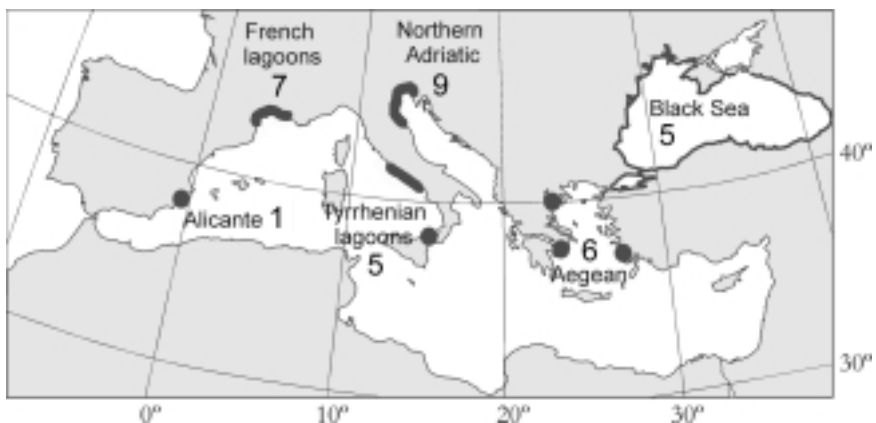


Figure 3 Situation by year 2001 of the introduced species of other than tropical Indo–Pacific origin. The introduced species on the Atlantic coastline, and some isolated occurrences of these in the Mediterranean, are not shown.

units in this area are not straightforward (see Ekman 1953: 81). Many of the species present on the coastline of northwest Africa extend northwards to temperate Europe (including the British Islands and Scandinavia) and the Mediterranean, and belong to the Lusitanian province. The list of Table 4 is based on the data used by Gofas (1999) for latitudinal ranges in northwest Europe and Morocco, from which have been deleted all species with a northern boundary north of 45°N, all species with a southern boundary within Morocco or further north, and some widespread species with teleplanic larvae (e.g. tonnoideans). The remaining taxa represent a pool of tropical/subtropical species which are liable to enter the Mediterranean.

Most tropical/subtropical species which occur in Atlantic Morocco, north of Agadir have had a limited range within the Mediterranean for a long time (Fig. 4), occurring on the coasts of Morocco (Pallary 1920), Algeria (Pallary 1900) and southern Spain (Hidalgo 1917). There are only a few exceptions to this: two (*Osilinus sauciatus* and *Nassarius pfeifferi*) are intertidal, have a sharp boundary at the Strait of Gibraltar and are barred from the Mediterranean by the lack of a suitable habitat, and a few more species (e.g. *Solatia piscatoria* or *Marginella glabella*) are established in Atlantic Morocco but do not enter the Mediterranean.

The eastern boundary of the species which penetrate into the Alboran Sea may yet experience some variations. One example is *Patella nigra*, a large, prevalently West African limpet which also lives along the coasts of North Africa and southern Spain. On European shores, prior to 1998, this species was found only to the west of the city of Málaga, whereas it now thrives at Rincón de la Victoria, some 20km further east. This is, however, an anthropophilous species, which rapidly builds up populations in perturbed sites, especially where new artificial rock piers are built. Another possible “natural” change in Mediterranean distributions regards the small prosobranch *Tricolia miniata*, originally described from the North

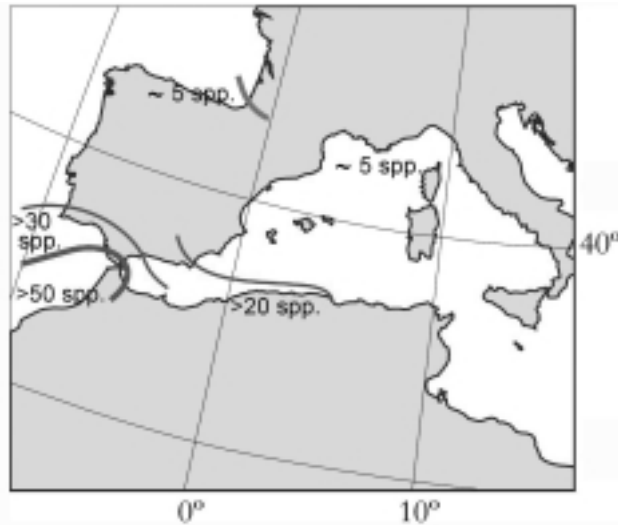


Figure 4 The occurrence, inside and near the Mediterranean, of Mollusca with a main range in tropical or subtropical West Africa. Most of the species reach a natural, stable limit near Gibraltar.

Table 4 Distribution of tropical or subtropical species of Mollusca, occurring on the Moroccan coast and liable to occur in the Mediterranean Sea.

	Sahara	Morocco	Algarve	N. Spain	Alboran	Algeria	Other W Med.
Class GASTROPODA, subclass Prosobranchia							
<i>Patella nigra</i> da Costa, 1771	*	*			*	*	
<i>Fissurella nubecula</i> (Linné, 1758)	*	*			*	*	*
<i>Clanculus kraussi</i> (Philippi, 1846)	*						
<i>Osilinus sauciatus</i> (Koch, 1845)	*	*	*				
<i>Tricolia miniata</i> (Monterosato, 1884)	*	*			*	*	*
<i>Littorina punctata</i> (Gmelin, 1791)	*	*			*	*	
<i>Mesalita brevalis</i> (Lamarck, 1822)	*	*	*		*	*	
<i>Dendropoma petraeum</i> (Monterosato, 1884)	*	*			*	*	
<i>Natica fanel</i> Récluz, 1844	*						
<i>Natica vittata</i> (Gmelin, 1791)	*	*	*		*	*	
<i>Tectonatica filosa</i> (Philippi, 1845)	*	*			*	*	*
<i>Sinum bifasciatum</i> (Récluz, 1851)	*	*			*	*	
<i>Zonaria pyrum</i> (Gmelin, 1791)	*	*	*		*	*	*
<i>Erosaria spurca</i> (Linné, 1758)	*	*			*	*	
<i>Trivia bitou</i> Pallary, 1912	*	*			*	*	
<i>Epitonium jolyi</i> (Monterosato, 1878)	*	*	*		*	*	
<i>Opalia crenata</i> (Linné, 1758)	*	*	*	*	*	*	
<i>Stramonita haemastoma</i> (Linné, 1766)	*	*	*	*	*	*	*
<i>Orania fusulus</i> (Brocchi, 1814)	*	*	*	*	*	*	
<i>Nassarius goreensis</i> (von Maltzan, 1884)	*	*			*	*	
<i>Nassarius elatus</i> (Gould, 1845)	*	*	*		*	*	
<i>Nassarius heynemanni</i> (von Maltzan, 1884)	*	*	*		*	*	
<i>Nassarius denticulatus</i> (Adams A., 1851)	*	*			*	*	
<i>Nassarius pfeifferi</i> (Philippi, 1844)	*	*	*		*	*	
<i>Nassarius vaucheri</i> (Pallary, 1906)	*	*	*		*	*	
<i>Bullia miran</i> (Bruguère, 1792)	*	*					
<i>Demoulia obtusata</i> (Link, 1807)	*						
<i>Mitrella bruggeni</i> van Aartsen, Menkhorst & Gittenberger, 1984	*	*	*		*	*	
<i>Mitrella broderipi</i> (Sowerby G.B. I, 1844)	*	*	*		*	*	
<i>Marginella glabella</i> (Linné, 1758)	*						
<i>Gibberula oryza</i> (Lamarck, 1822)	*	*					
<i>Gibberula secreta</i> Monterosato, 1889	*	*					

Table 4 continued

	Sahara	Morocco	Algarve	N. Spain	Alboran	Algeria	Other W Med.
<i>Gibberula caelata</i> (Monterosato, 1877)		*	*		*	*	
<i>Cymbium olla</i> (Linné, 1758)		*	*		*		
<i>Cymbium tritonis</i> (Broderip, 1830)	*						
<i>Cymbium cucumis</i> Röding, 1798	*						
<i>Cancellaria cancellata</i> (Linné, 1767)	*	*			*	*	
<i>Solatia piscatoria</i> (Gmelin, 1791)	*	*					
<i>Fusiturris similis</i> (Bivona And., 1838)	*	*	*		*	*	
Class GASTROPODA, subclass Pulmonata							
<i>Siphonaria pectinata</i> (Linné, 1758)	*	*	*		*	*	
Class BIVALVIA							
<i>Nuculana bicuspidata</i> (Gould, 1845)	*						
<i>Anadara corbuloides</i> (Monterosato, 1878)	*	*	*		*	*	
<i>Perna perna</i> (Linné, 1758)	*	*	*		*	*	
<i>Myoforceps aristatus</i> (Dillwyn, 1817)	*	*	*		*	*	
<i>Modiolus stultorum</i> Jousseaume, 1891	*						
<i>Modiolus lulat</i> Dautzenberg, 1891	*	*			*		
<i>Amygdalum agglutinans</i> (Cantraine, 1835)	*	*	*		*	*	
<i>Pinna rudis</i> Linné, 1758	*	*			*	*	
<i>Ungulina cuneata</i> (Spengler, 1782)	*	*	*		*	*	
<i>Diplodonta brocchii</i> (Deshayes, 1852)	*	*	*		*	*	
<i>Scacchia zorni</i> van Aartsen & Fehr de Wal, 1985	*	*	*		*	*	
<i>Digitaria digitaria</i> (Linné, 1758)	*	*	*	*	*		
<i>Cuna gambiensis</i> Nicklès, 1955	*						
<i>Sinupharus combieri</i> (Ficher-Piette & Nicklès, 1946)	*	*	*	*	*	*	
<i>Tellina compressa</i> Brocchi, 1814	*	*	*		*	*	
<i>Gari intermedia</i> (Deshayes, 1855)	*	*	*		*		
<i>Gari pseudoweinkauffi</i> Cosel, 1989	*	*	*		*		
<i>Eastonia rugosa</i> (Heibling, 1779)	*	*	*		*	*	
<i>Panopea glycymeris</i> (von Born, 1778)	*	*	*		*	*	
<i>Clavagella aperta</i> Sowerby G.B. I, 1823	*	*	*		*	*	
Totals	56	47	30	6	38	26	5

African coast, but never mentioned from France in the nineteenth century literature. In 1988, the authors recorded large numbers of this species in Les Embiez, southern France.

These isolated case histories can be balanced by others in the opposite direction. There are nineteenth century records regarding tropical Atlantic species which are nowadays established in the southern Iberian Peninsula but are not found further inside the Mediterranean. Examples are *Cancellaria cancellata* and *Siphonaria pectinata*, reported for the coast of France by Locard (1886). The prosobranch *Sinum bifasciatum* is well established on the coast of Málaga, but there are scanty nineteenth century records from the Balearics and southern Italy (see Rueda & Gofas 2000, and references therein).

Several recent records of tropical West African species in Mediterranean localities have been disregarded since they were based on discards from fishing boats. Examples are the records of West African *Mesalia opalina* in the Ionian Sea (Garavelli & Melone 1967) and of *Cymbium cucumis* in Sardinia (Giuseppetti et al. 1991).

To summarise, the authors do not know of any tropical or subtropical Atlantic molluscan species recently found in the Mediterranean that could be suspected of being a newcomer, which has arrived from the Atlantic in a dynamic process comparable with lessepsian immigration. The possible variation in boundaries of the species listed in Table 4 should be the focus of ongoing studies, because some may expand their range inside the Mediterranean and this may be in response to long-term climatic change.

Summary of invasion pathways

The processes inferred for the arrival of exotic species (without considering the questionable species) in the Mediterranean are summarised in Figure 5. The main process, termed “Erythrean invasion” by Galil & Zenetos (2002), is clearly the influx from the Red Sea. These are not “introduced” species in the strict sense (i.e. man is responsible for the construction of the new waterway, but not the transport of the molluscs themselves).

Shipping is the next most important vector and is extremely unpredictable. Among the 137 established or alien exotic molluscs of the Mediterranean, only 17 appear to have arrived or have been transported within the Mediterranean via shipping.

Transport of live molluscs for mariculture was a vector for 12 species, of which six are deliberate introductions (two rock oysters: *Crassostrea gigas* and *Saccostrea commercialis*; two pearl oysters: *Pinctada margaritifera* and *Pinctada radiata*; and two clams: *Mercenaria mercenaria* and *Ruditapes philippinarum*); the others have been accidental introductions.

Possible reasons for success

Much has already been written on invasive species, both plant and animal. Investigations have focused on the genetic background of the successful invaders, the breadth of trophic niche and the life-history strategy (Golani 1998). The molluscan data in the Mediterranean suggest that some important factors are associated with the characteristics of the recipient environment, and with the intensity and time of exposure to the immigrants.

In the Mediterranean, 10 species are locally invasive. These are the gastropods *Cerithium scabridum*, *Rhinoclavis kochi*, *Strombus persicus* and *Bursatella leachi*, and the bivalves

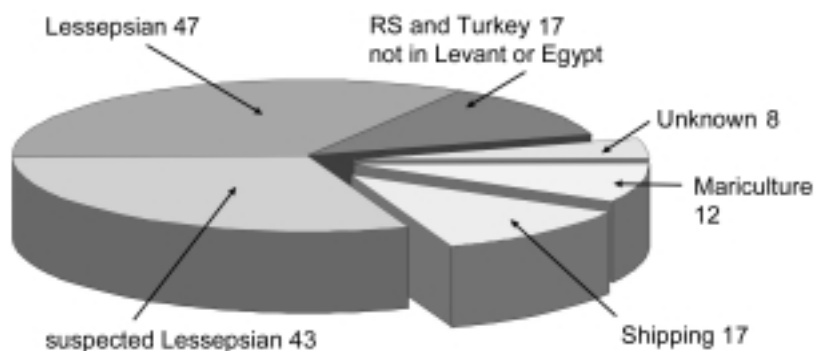


Figure 5 The inferred pathways for exotic molluscan species in the Mediterranean basin. Seven species (see Table 2) are considered twice because two different modes of introduction are assumed. The questionable and cryptogenic species are not considered.

Pinctada radiata and *Brachidontes pharaonis* in the eastern Mediterranean, the gastropod *Rapana venosa*, and the bivalves *Anadara inaequalis*, *Musculista senhousia* and *Xenostrobus securis* in the northern Adriatic and/or the western Mediterranean lagoons. There is a rule-of-thumb that for every 100 species brought alive to an exotic locality, 10 will settle and one may become invasive (Williamson & Fitter 1996). If this is applicable in the Mediterranean, some 1000 species may have had an opportunity to settle.

Ecological characters related to successful establishment

There has been much debate on the life-history characteristics that make a successful invader (review in Morton 1996). Regarding Mediterranean exotics, Ritte & Pashtan (1982) and Lavie & Nevo (1986) tried to investigate a possible relationship between the profile of successful colonisers and the amount of genetic variation evidenced by allozyme polymorphism but a clear picture did not emerge.

Species which have been introduced or have invaded tend to occur in a similar manner elsewhere in the world. Among the species introduced in the Mediterranean, examples are *Rapana venosa* (see Mann et al. 2002), *Musculista senhousia* (see Willan 1987). Table 5 lists the Mediterranean exotic or cryptogenic species which are known to have been introduced (or are regarded as cryptogenic) in other areas, namely the Black Sea (Zaitsev & Ozturk 2001), North Sea (Reise et al. 1999), European Atlantic coast (Gouletquer et al. 2002), North American Atlantic coast (Carlton 1992, Mann et al. 2002), Pacific coast of North America (Carlton 1992), and Australasia (Willan 1987).

Some studies find that exotics are “typical” opportunistic species, while others state that there are as many exceptions to this generalisation as there are examples supporting it. A good example of an opportunist that fits the classical concept is that of *Musculista senhousia*. It is a short-lived mussel that suffers high mortality, can experience very high, but often variable, population size, is small in body size, grows quickly and has a long planktonic dispersal stage (Crooks 1996). It is depicted as an “opportunist which is likely to pre-empt food and space” (Willan 1987). *Brachidontes pharaonis*, another very successful mytilid, is described as an euryhaline species by Morton (1988). *Pinctada radiata*, a very

Table 5 Records of introduction of some non-lessepsian immigrants worldwide.

	Origin	Medit.	Black Sea	NE Atlantic	North Sea	NW Atlantic	NE Pacific	Australia N.Z.
<i>Crepidula fornicata</i>	NW Atlantic	1957		1949	1887		1937	
<i>Rapana venosa</i>	NW Pacific	1974	1946	1998		1998		
<i>Anadara inaequivalvis</i>	NW Pacific	1969	1982					
<i>Musculista senhousia</i>	SE Asia	1964					1941	1980s
<i>Mytilus galloprovincialis</i>	Mediterranean	native	native	native			1880?	
<i>Crassostrea gigas</i>	NW Pacific	1964	1900s	1819	1964		1932	
<i>Mercenaria mercenaria</i>	NW Atlantic	1965		1861	1864	native	1967	
<i>Ruditapes philippinarum</i>	NW Pacific	1981		1973-4			1936	
<i>Perricola pholadiformis</i>	NW Atlantic	1994			1890	native		
<i>Mya arenaria</i>	NW Atlantic	1976	1966	<1800	<1800	native	1946	
<i>Teredo navalis</i>	SE Asia	<1800	<1800	<1800	1730	<1800	1913	

successful and early settler in the Mediterranean, is described as a sturdy, euryhaline and eurythermal species, which can stay alive after several days out of the water (Seurat 1929). The superfamily Cerithioidea, which includes many euryoecious shallow marine species, is also illustrative of the success of opportunistic species.

Nevertheless, the family with the highest number of recorded immigrant species is the Pyramidellidae (Fig. 6), which are specialised animals, obligate ectoparasites of other invertebrates, mainly polychaetes and molluscs. There is a loose specificity of the parasite species to the host species, but a pyramidellid species will parasitise hosts only within a given phylum. The success of the pyramidellids as immigrants relies on their ability to adapt to new host species of the appropriate higher taxon. The pyramidellid *Adalactaeon amoenus* has been observed (Oliverio 1994) on *Acanthocardia tuberculata*, a native Mediterranean species which cannot be its original host in the Red Sea. Nevertheless, another factor in this case may be the high number of species present in the Red Sea (47 species according to Dekker & Orlin 2000, certainly underestimated).

The exotic species experience changes in their niche. The newcomers may find some companion species but will usually find drastic changes in their biotic environment compared with their place of origin. The small columbellid *Anachis selasphora* certainly was not an inhabitant of *Posidonia* meadows, but now thrives in the cavities of the rhizomes of *Posidonia* in southern Turkey (Tringali & Villa 1995). In the long run, such shifts may lead to evolutionary change and this will make the Mediterranean an extraordinary natural laboratory for the study of adaptive evolution.

Pattern of larval development

The pattern of larval dispersal should have some bearing on colonisation success. Marine invertebrates, including molluscs, can be roughly divided into species with a pelagic larval

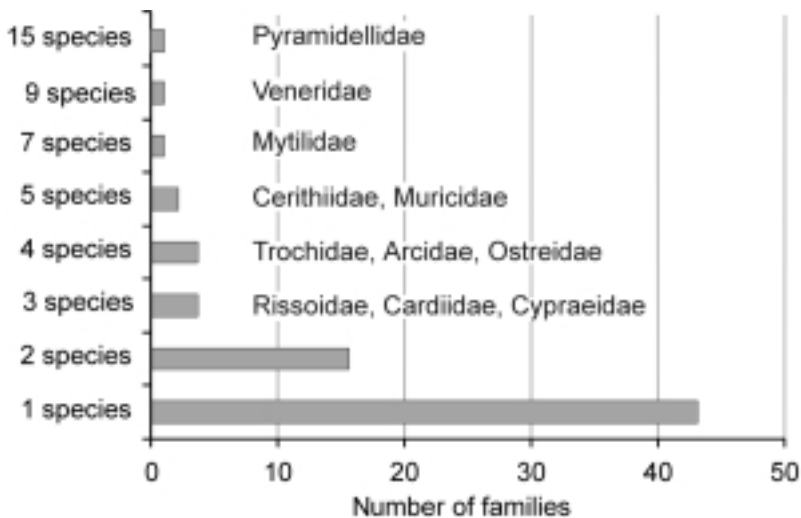


Figure 6 Ranking of molluscan families according to the number of immigrant species registered in the Mediterranean.

Table 6 Numbers of species, among the prosobranchs listed in Table 2, according to their type of larval development and their establishment status.

Total	Planktotrophic		Total	Non-planktotrophic	
	Established	Invasive		Established	Invasive
25	17	4	17	11	–

stage, and those with so-called direct development. The former remain several days to several weeks in the plankton, on which they feed before they settle down for adult life, and this makes them prone to a broad dispersal. The direct developers hatch directly as small benthic organisms and normally settle at the same place as their progenitors. However, there is no straightforward picture as to which are the more aggressive invaders.

Among prosobranchs (Table 6), where the type of larval development is best assessed because it can be deduced from the morphology of the protoconch, more than half of the recorded species are planktotrophic, and this pattern holds true even when only the established species are considered. This figure is similar to the natural occurrence of planktotrophic species in temperate latitudes (Thorson 1950) and does not indicate that larval planktotrophy is a key factor for the success of immigration. It is nevertheless noteworthy that the invasive gastropods *Cerithium scabridum*, *Rhinoclavis kochi*, *Strombus decorus*, *Rapana venosa* and also the invasive bivalve *Musculista senhousia* have a planktotrophic development.

Factors related to the recipient sites

Vermeij (1996) posed the question of how the assemblages rich in immigrants could differ from those in which few or no foreign species have become established. The data collected in the Mediterranean show that the occurrence of an immigrant component in the fauna is significant in the eastern Mediterranean as a whole, in the Adriatic and in the western Mediterranean lagoons.

In the eastern Mediterranean, the present day fauna is possibly not as diverse as its environment could support, because the area is not readily accessible to tropical Atlantic species and thus the niche for tropical/subtropical elements may be only partly occupied.

In the western Mediterranean, there are only two reported lessepsians, and they did not arrive before the 1990s. These are the bivalve *Fulvia fragilis* found at Cullera, Valencia, Spain (collected 1991 by J. Trigo; original observation communicated by E. Rolán, Vigo) and the opisthobranch *Bursatella leachi*, reported in various points of the Tyrrhenian Sea and in Cagliari, Sardinia (original observation, communicated by A. Olita). The finding of the Indo-Pacific nudibranch *Chromodoris quadricolor* in 1982 was an isolated occurrence. The occurrence of the other introduced species is limited to lagoons, to the coastal northern Adriatic, which is a secluded area and in this respect is comparable to lagoons, and to harbours. Any randomly taken sample in the open sea is currently free of exotic molluscs.

The authors speculate that the rarity of exotic species in the western Mediterranean can be explained because that area has a higher species richness and is closer to the potential source in the Atlantic. According to this view, the western Mediterranean open-sea is saturated for the sustainable species richness compatible with the heterogeneity and the

resources of the environment. Thus, it is a difficult place for the penetration of alien species. The same conclusion was reached by Carlton (1992: 500) regarding the open-sea communities of the American Pacific coast.

Conversely, lagoons and other marginal marine sites have low species richness compared with the surrounding open sea. Their environment is constrained by demanding physical factors, which make them unsuitable for most of the locally available open-sea species. Thus, lagoons are oligospecific because they have a limited pool of eligible species locally available. In this context, any species belonging to marginal marine biota from a remote area makes a very likely successful coloniser. Success in the new environments may be enhanced by the lack of natural competitors and enemies. The native species in general do not have means to compete with the aliens because they had not co-evolved with them.

Impact on the native fauna and prospects

In those areas with high impact of immigrants, and where the native fauna was formerly species poor, the newcomers imply a major reorganisation of the faunal assemblages. The impact of the Indo-Pacific fauna is restricted to the eastern basin of the Mediterranean, but there it is of major significance. A comparison of the results of Tom & Galil (1991) with those of Gilat-Gottlieb (1959) revealed massive penetration of four Indo-Pacific species, among which are the gastropods *Rhinoclavis kochi* and *Minolia nedyma*. *Rhinoclavis kochi* was first reported from Haifa Bay in 1963, and in the 1970s large numbers were collected (Barash & Danin 1973). In a benthic sample collected off Haifa (leg. B. Galil, 9.1997), 15 species out of 119 (i.e. 12%) were lessepsian, and these comprised 270 individuals out of 894 (i.e. 30%). The most abundant species was *Rhinoclavis kochi*, and the second most abundant was also an immigrant, *Finella pupoides*. The Israeli coast holds 90 exotic species of Erythrean origin (25%) in a total of 372 species cited by Barash & Danin (1992).

At some 300km away from the Levantine coast, in a sample from Kyrenia, northern Cyprus (leg. Zibrowius 11.1998), six species out of 76 (7.9%) were lessepsian but they represent only 13 specimens out of 527 (2.5%) of the specimens. More globally, 32 out of 627 (5%) of the species of molluscs cited from Cyprus (Cecalupo & Quadri 1996, Buzzurro & Greppi 1997) are exotics. In Greece figures are still lower, with only 23 exotic species (2.3%) out of a total of 1095 (Delamotte & Vardala-Theodorou 2001).

Data illustrated in Figures 1 and 2 (pp.257, 259) indicate that the rate of influx for migrants from the Red Sea remains steady with no sign of saturation. Both the total number of Red Sea species and the extension of the area colonised by at least one Red Sea species are increasing. There is still a pool of about 90 species (see Table 3, p.255) reported from the Suez Canal which are likely to be found in the Mediterranean in the near future but none of these has been seen there yet. The total number of Red Sea species, amounting to a conservative figure of 1765, cited by Dekker & Orlin (2000), shows that the source area has as least as many species as the Mediterranean itself.

Only two lessepsian immigrants have settled in the western Mediterranean, and they did not arrive before the 1990s. The number of such immigrants is likely to increase in the future.

The non-lessepsian introductions, and especially those connected with mariculture, seem to have reached a peak in the 1960s (*Crassostrea gigas* and *Mercenaria mercenaria*,

introduced deliberately; *Rapana venosa*, *Polycerella emertoni*, *Anadara inaequalis*, and *Musculista senhousia*, introduced inadvertently). Their later movements have been mainly inside the basin, namely, from the Black Sea to the Adriatic and thence to the western Mediterranean coastal lagoons. Nothing remains of the nineteenth century attempts to introduce certain molluscs for farming (the American oyster *Crassostrea virginica* shipped to Sicily, see di Monterosato (1915), and the pearl oyster *Pinctada margaritifera*, which was not mentioned by Seurat (1929)).

In the 1980s, there were several non-lessepsian newcomers (*Polycera hedgpethi*, *Chromodoris quadricolor*, *Melibe fimbriata*, *Chlamys lischkei*, *Saccostrea commercialis*, *Ruditapes philippinarum*) but only the last two are related to mariculture and only *Melibe fimbriata* and *Ruditapes philippinarum* have become established. Displacements may occur, as can be observed on the Adriatic coast for *R. decussatus* driven out by *R. philippinarum*. In the 1990s, apart from the Red Sea migrants, *Haminaea callidegenita* and *Xenostrobus securis* were added to the Mediterranean fauna. The slow-down is real, and can be explained because the commercial routes for circulation of spat repeatedly carry the same species. Thus, those species from the current donor areas which were brought to the Mediterranean, and were likely to settle, became established exotics, whereas others that are regularly presented but cannot survive (e.g. *Littorina littorea*, several species of *Gibbula* from the European Atlantic coast) remain barred. A new wave of immigrants is to be expected only if new sources of species are made available.

The most unpredictable source of non-native species remains transportation by ships, both through ballast waters, on hulls, and as discards from fishing operations. For these introductions, the limiting factors (i.e. space where physical factors and/or the native fauna will not bar the immigrants) are the same as for mariculture but the potential source areas are virtually unlimited. However alarming this may look, the situation is still such that there is no recorded extinction of a marine species in the Mediterranean by anthropogenic means. Furthermore, among the factors of extinction in the marine realm (see Carlton et al. 1999, Roberts & Hawkins 1999), the impact of introduced species comes far behind those of over-exploitation and of urban development.

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