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Abstract

Six hundred and eighty alien marine multicellular species have been recorded in the Mediterranean Sea, with many establishing viable populations and dispersing along its coastline. A brief history of bioinvasions research in the Mediterranean Sea is presented. Particular attention is paid to gelatinous invasive species: the temporal and spatial spread of four alien scyphozoans and two alien ctenophores is outlined. We highlight few of the discernible, and sometimes dramatic, physical alterations to habitats associated with invasive aliens in the Mediterranean littoral, as well as food web interactions of alien and native fish. The propagule pressure driving the Erythraean invasion is powerful in the establishment and spread of alien species in the eastern and central Mediterranean. The implications of the enlargement of Suez Canal, reflecting patterns in global trade and economy, are briefly discussed.

Keywords

Alien • Vectors • Trends • Propagule pressure • Trophic levels • Jellyfish • Mediterranean Sea

Brief History of Bioinvasion Research in the Mediterranean Sea

The eminent European marine naturalists of the sixteenth century – Belon, Rondelet, Salviani, Gesner and Aldrovandi – recorded solely species native to the Mediterranean Sea, though mercantile horizons have already expanded with geographical discoveries and shipping was no longer confined to European seas.

Recognition that marine species may be introduced into the Mediterranean Sea from other parts of the world

came suddenly with the much publicized plans of the Saint-Simonians for a “Canal de jonction des deux mers” at the Isthmus of Suez. Even before the Suez Canal was fully excavated, the French zoologist Léon Vaillant (1865) argued that the breaching of the isthmus will bring about species migration and mixing of faunas, and advocated what would be considered nowadays a ‘baseline study’. Paul Fischer (1865), who studied molluscs from Port Said, Suez and the Bitter Lakes, was certain that the Canal will modify the faunas at its Mediterranean and Erythraean ends. Yet for the next 50 years the documentation of the changes in the biota in the adjacent marine environments was left to “Forschungsreisender” – a now extinct breed of learned amateurs and natural scientists who styled themselves ‘scientific travelers’. Keller (1883), a professor of Zoology in Zurich, traveled to Egypt in 1882 and 1886 and identified 10 Mediterranean species and 17 Red Sea species from the Canal itself, 5 Mediterranean species in the Red Sea, and 4 Red Sea species in the Mediterranean. Doubts had been raised concerning some of his identifications, as well as his sources,

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however, the importance of his work lies in confirming the role of the canal as a ‘corridor’ for the movement of species and in the transformation of the adjacent marine biotas.

At the same time ship fouling too was recognized as a vector for introduction of marine alien species: in 1873 the tri-masted *Karikal* arrived at the port of Marseille from India carrying on its hull a small forest of “living beings” including three grapsoid crabs species numbering in the hundreds (Catta 1876). Catta, with farsighted acumen, warned of faunal changes stemming from ship-transported organisms. In fact, fouling serpulid polychaetes were already identified as the first alien species in the Mediterranean: *Hydroides dianthus* (Verrill, 1873) was documented in the port of Izmir as early as 1865, and *H. dirampha* Mörch, 1863 and *H. elegans* Haswell, 1883 were recorded in the harbour of Naples in 1870 and 1888, respectively (Carus 1889; Zibrowius 1973).

Fifty-five years after the opening of the Canal, ‘The Cambridge Expedition to the Suez Canal’ embarked on an investigation “...why some forms of life can get through the Canal and others cannot, and ... throw light on marine migrations in general” (Gardiner 1924:521). Indeed, anxieties whether “... such an immigration caused important changes in the fauna of the eastern basin of the Mediterranean?” had already been raised (Steinitz 1919). The investigations of the biota of the southern Levantine continental shelf in the 1940s highlighted the extent the Erythraean taxa have been established along the coast (Ben-Tuvia 1953a, b; Gottlieb 1953, 1960; Holthuis and Gottlieb 1958; Pérès 1958; Tebble 1959). By the 1970s 140 alien species were known to have crossed the Suez Canal into the Mediterranean (Steinitz 1970) and it was perceived that the littoral biota of the Levantine sea has been undergoing a rapid and profound change (Holthuis 1961; George and Athanassiou 1967; Geldiay and Kocatas 1968; Por 1978; Galil and Lewinshon 1981). But as this phenomenon seemed limited to the Levant Por (1990), the scientific community by and large ignored it.

Records of species introduced by shipping and mariculture into the Mediterranean appeared sporadically in the scientific literature (Rioja 1924; Hamel 1926; Berner 1944; Mendez-Domingo 1957; Raimbault 1964; Bascheri 1965), but as their number and impact were considered negligible they “... have not been the subject of inventories as representative as those of lessepsian migrants” (Zibrowius 1992, 1994). This state of affairs changed once the impacts of a pair of invasive chlorophytes have been noted off the Mediterranean coast of France. As Samuel Johnson famously observed “nothing so concentrates the mind as the sight of the gallows”, or “killer algae” (*Caulerpa taxifolia* (Vahl) C. Agardh and *Caulerpa racemosa* var. *cylindracea* (Sonder) Verlaque, Huisman and Boudouresque). Soon, inventories of alien macrophytes were compiled (Verlaque 1994, 1996, 2001; Ribera and Boudouresque 1995; Ribera Siguan 2002).

The European Commission Environmental Programme and the Mediterranean Science Commission (CIESM) organized a workshop on “Introduced species in European coastal waters” (Boudouresque et al. 1994), followed by workshops entitled “Ship-transported alien species in the Mediterranean and Black Sea” and “Impact of mariculture on Mediterranean coastal ecosystems” (www.ciesm.org), and a widely acclaimed illustrated atlas provided information on alien fish, decapod crustaceans, mollusks and macrophytes in the Mediterranean (www.ciesm.org/atlas). Still, research remains Eurocentric and much focused on the *Caulerpa* pair, with a tally of 361 and 150 research articles on *C. taxifolia* and *racemosa* respectively (Klein and Verlaque 2008). Intensive efforts and much funding have been invested in assembling national, regional and EU-wide inventories of marine alien species. More recently, molecular genetic analyses have increasingly been utilized in studying bioinvasions in the Mediterranean: establishing species identity, differentiating among cryptic species, and identifying cryptic invasions, and the history of introduction (Estoup and Guillemaud 2008).

The EU’s ambitious Marine Strategy Framework Directive (MSFD) (2008/56/EC), aiming to achieve good environmental status by 2020 (http://ec.europa.eu/environment/water/marine/directive_en.htm), places great emphasis on the “trends in abundance, temporal occurrence and spatial distribution in the wild of non-indigenous species ... in relation to the main vectors and pathways” (<http://eur-lex.europa.eu/lexUriServ>). Expanding the “state of the art” tools to invasion biology will doubtlessly improve documenting the full extent of the bioinvasion of the Mediterranean Sea and provide information for the development of effective policies and competent management.

‘Alien’ and ‘Invasive’ – Which and Where

Over the past three decades the study of marine bioinvasions has thrived and spawned a profusion of specialized terms, liable to misapplication and error. A computerized search of scientific databases disclosed a surfeit of synonyms, partial synonyms and neologisms that hinder communication (Occhipinti-Ambrogi and Galil 2004). The terminology varies among taxonomic kingdoms, scientific disciplines, and linguistic and national borders. Certain frequently used terms such as adventive, alien, allochthonous, exotic, introduced, invasive, naturalized, non-indigenous and non-native have several commonly established interpretations, leaving us with vague and occasionally overlapping definitions.

We follow the definitions set out by the International Council for the Exploration of the Sea (ICES) (as “Introduced species”) and the International Union for Conservation of Nature (IUCN) (as “Alien species”), though recognizing that ‘population’ rather than ‘species’ is “transported intentionally

or accidentally by a human-mediated vector into aquatic habitats outside its native range” and “... could not occupy without direct or indirect introduction or care by humans” respectively (<http://www.ices.dk/reports/general/2003/codemarineintroductions2003.pdf>; http://iucn.org/about/union/secretariat/offices/iucnmed/iucn_med_programme/species/invasive_species/). We use the term ‘invasive’ to denote an alien population which maintains itself without human assistance and spreads beyond its point of introduction, without assumption as to adverse environmental or economic impact.

Populations with naturally shifting distributions (e.g. due to climate change) are not to be considered alien, but a founder alien population spreading beyond its initial range in the recipient region, even if unmediated by humans, is still considered an alien population.

Six hundred eighty multicellular species are recognized as aliens in the Mediterranean Sea, and a great many are invasive – 118 alien species were recorded in 5 or more countries, and some 19 hyper-invasive species were recorded in 10 or more countries. As noted in previous analyses (Galil 2012), molluscs (31 %), crustaceans (17 %) and bony fish (16 %) make the largest contributions to the number of documented alien species in the Mediterranean and comprise 63 % of total alien species richness in the sea. Macrophytes (14 %), annelid polychaetes (9 %), bryozoans and cnidarians (each 3 %), and all other taxa (7 %) complete the number. The great majority of these are littoral benthic or demersal species. The data is presumably most accurate for large conspicuous species, yet on closer examination some dissolved into “species complexes” (Bucciarelli et al. 2002; Holland et al. 2004; Tsoi et al. 2007; Terranova et al. 2007; Golani and Bernardi 2012). The record grossly underestimates the total number of alien species. The magnitude of the gap is difficult to assess and differs among taxa, locations and habitats as research efforts vary greatly along the coasts of the Mediterranean. Data is entirely absent for many of the small-sized invertebrate phyla because of limited search effort and erosion of taxonomic expertise. The alien unicellular biota is nearly entirely invisible though it is well established that anthropic dispersal and redistribution of propagules in ballast water and sediments and shellfish transplantation facilitate range expansions not only of harmful algal blooms (HABs) causatives and other microalgae, but of other microbial loop components as well, including viruses, algicidal bacteria, and microbial loop grazers such as protoperidinians, ciliates and other protists (Hallegraeff and Bolch 1992; Pierce et al. 1997; Galil and Hülsmann 1997; Smayda 2007).

There are considerable differences among the peri Mediterranean countries in the number of alien species recorded (Galil 2012). Far more alien species have been

documented in the Levantine Basin than the entire western Mediterranean: 346 multicellular alien species were reported along the 180 km long coast of Israel, whereas only 56 alien species were reported off the 1,660 km long Mediterranean coast of peninsular Spain. And whereas most of the alien species in the eastern Mediterranean have presumably entered through the Suez Canal, shipping and massive shellfish farming are the drivers in the western Mediterranean (Fig. 27.1).

Food Web Interactions of Alien and Native Fish

An analysis of the trophic level of alien species is essential for estimating their impact on native species through competition and predation. To date, little information is available regarding the diet of most native and alien species in the Mediterranean, nor do we have solid information on their biomass. This gap is especially significant in the Levant, where aliens have been gradually replacing native species. Fish are the only taxa for which sufficient and reliable information on the trophic level is available. A comparison of alien and native species in the Mediterranean based on data extracted from FISHBASE (Froese and Pauly 2012a, b) revealed that the average trophic levels of native and alien fish species are similar (3.509 ± 0.496 (S.D.) and 3.456 ± 0.531 respectively), though the distribution of the trophic levels differs (Fig. 27.2, Table 27.1). Herbivorous species comprise 5 % of aliens but only 2 % of native fish. Moreover, the native herbivores are either small sized (e.g. *Scartella cristata* (Linnaeus, 1758), *Parablennius sanguinolentus* (Pallas, 1811) and *Parablennius gattorugine* (Brünnich, 1768)) of negligible biomass (Goren and Galil 2001) or relatively rare (e.g. *Sarpa salpa* (Linnaeus 1758)), while the two alien herbivores, *Siganus rivulatus* Forsskal, 1775 and *S. luridus* (Rüppell, 1829) comprise about one third of the fish biomass in shallow rocky habitats, impacting the local macrophytes and food web (Goren and Galil 2001; Lundberg et al. 2004). Sala et al. (2011) who studied the impact of the two siganids on the Mediterranean coast of Turkey, where they comprise 46–57 % of the total fish biomass in rocky habitats, found they outcompeted native sea urchins, denuded rocky ledges from their algal cover and formed extensive “barrens”. Also among the carnivorous fish (trophic levels 3.4–4.5; Fig. 27.2) in rocky habitats the proportion of aliens is slightly higher than natives (64 % and 59 % respectively). However, on soft-bottom habitats the trophic status of the alien fish differs greatly. The biomass of herbivorous fish, both alien and native is negligible, and the distribution of the native and alien species among the higher trophic guilds differs. A study of fish collected off the southern Israeli coast revealed that the weighted trophic level of the alien species is much higher (and statistically significant) than that of the

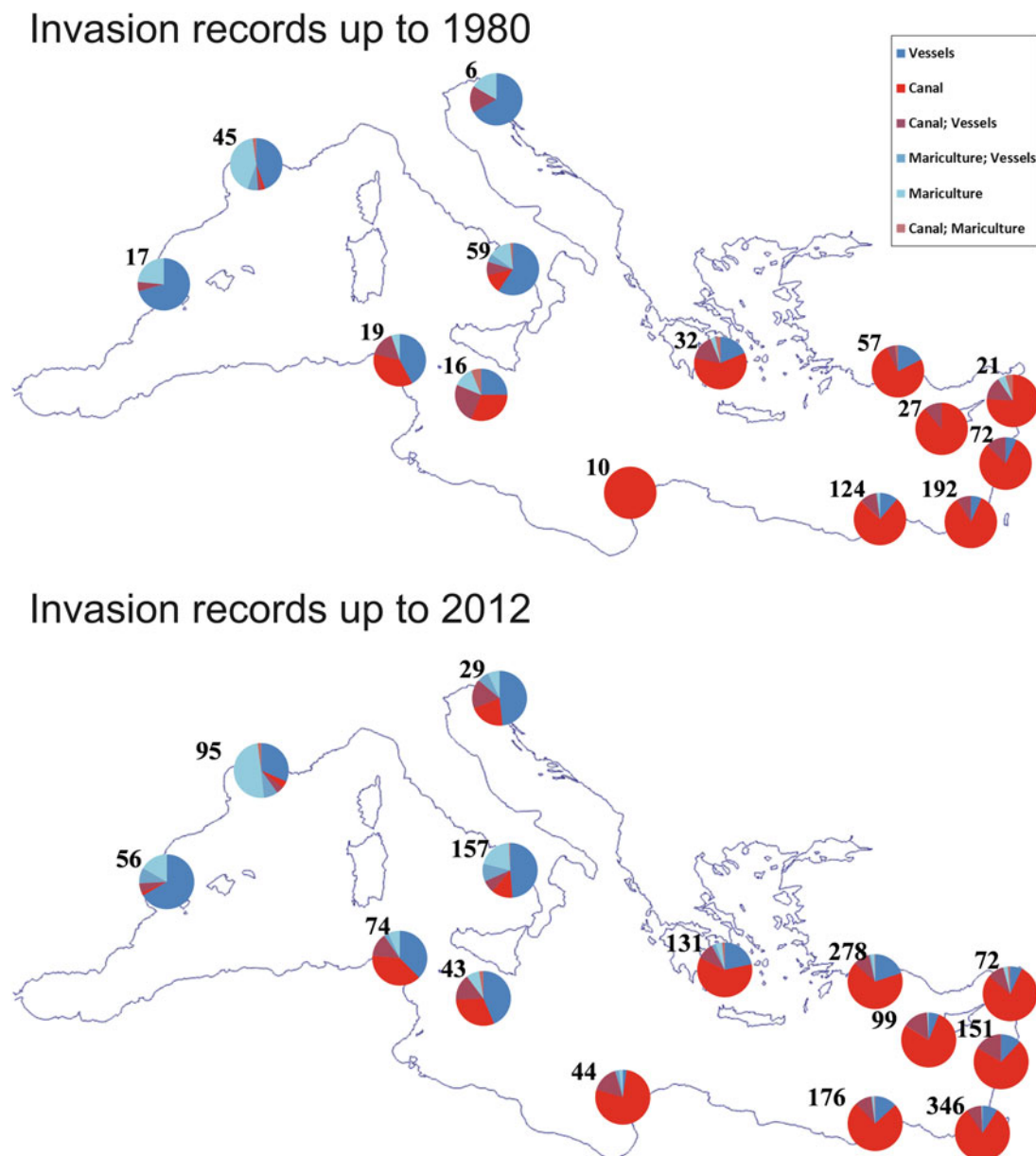


Fig. 27.1 Number of multicellular marine alien species in peri-Mediterranean countries, and their means of introduction (After Galil 2012)

natives (Levit 2012). At trophic level of 3.7 and higher, aliens comprise 38.5 % of the total catch while natives comprise 15.7 % (data extracted and calculated from Levit 2012). Trophic interactions affect ecosystem processes by altering fluxes of energy and material, or by impacting the abundance of populations that control those fluxes. The sharp increase in the weighted trophic level due to the expansion of the alien fish populations may explain in part the decline in local fishery catch (Shapiro 2007). The alien species in this trophic guild (abundance > 1 % of total catch) are of high commercial value: *Scomberomorus commerson* (Lacepède, 1800), *Decapterus russelli* (Rüppell, 1830), *Saurida macrolepis* Tanaka, 1917, *Nemipterus randalli* Russell, 198 and *Upeneus*

moluccensis (Bleeker, 1855), whereas the native species at this trophic level, *Raja clavata* Linnaeus, 1758 and *R. miraletus* Linnaeus, 1758, lack commercial value.

Alien Jellyfish and Comb Jellies in the Mediterranean

Periodic outbreaks of indigenous scyphozoan jellyfish have long been noted in the Mediterranean (UNEP 1991; CIESM 2001). Various anthropogenic perturbations including eutrophication, overfishing, global warming and the increase of littoral man-made hard substrates have been

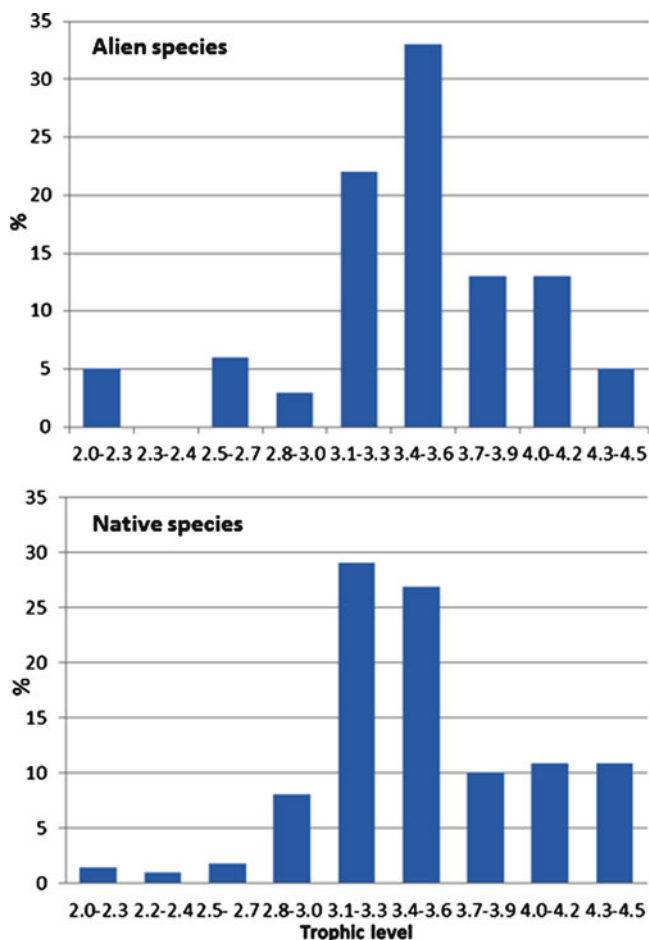


Fig. 27.2 Comparison of the trophic levels of native and alien fish species in the Mediterranean Sea (Data on trophic levels extracted from Froese and Pauly (2012a))

suggested as contributing to the proliferation of jellyfish populations in recent decades (CIESM 2001; Daskalov et al. 2007; Purcell 2007, 2012; Richardson et al. 2009; Riisgard et al. 2012). Boero et al. (2008) proposed that the removal of top predators and the formation of oligotrophic temperature-stable water masses may cause the suppression of the high energy fish and mammal-dominated food web and the re-emergence of medusozoan-dominated food web. But whereas most jellyfish outbreaks in the western and central Mediterranean consist of native species, alien species have taken over in the eastern part of the sea. The SE Levant is unique in hosting four alien scyphozoan jellyfish concurrently, in addition to two alien ctenophores (Fig. 27.3).

Already in 1886 *Cassiopea andromeda* (Forskål, 1775) occurred in the Suez Canal (Keller 1888), and a short time later was recorded off Cyprus (Maas 1903). It established populations along the Levantine coastline (Spanier 1989; Bilecenoglu 2002), but was recently reported from further afield – Malta (Schembri et al. 2010). *Phyllorhiza punctata*

Lendenfeld, 1884 was first sighted in the Mediterranean off the Israeli coast in 1965; where, since 2005, it established a regularly recorded resident population (Galil et al. 1990, 2009). Also off Lefkada Island, Greece, where it was recorded in 2005 and 2006, the population has apparently occurred for a number of years (Abed-Navandi and Kikinger 2007). Recently, a single specimen was collected in Iskenderun Bay, Turkey, and another photographed off Tavolaro Island, Sardinia, Italy (Boero et al. 2009; Çevik et al. 2011). The recently described *Marivagia stellata* (Galil et al. 2010), established a small population off Israel and the adjacent Lebanese coast. It is unclear whence *M. stellata* has arrived; but as the native range of nine out of ten alien species recorded off the SE Levant is the Indo-Pacific Ocean, the Indian Ocean or the Red Sea (Galil 2007), and the Indo-Pacific is a hot-spot for cepheid jellyfish, it may have originated there. Though found occasionally in small aggregations, the Mediterranean populations of these alien scyphozoans have remained small. In contrast, the Erythraean *Rhopilema nomadica* Galil, 1990, first recorded in the Mediterranean in the early 1970s, is notorious for the swarms it has formed each summer since the early 1980s along the SE Levantine coast (Galil et al. 1990). *Rhopilema* swarms adversely affect tourism, fisheries and coastal installations. The annual swarming results each year in envenomation victims suffering adverse effects that may last weeks and even months after the event (Benmeir et al. 1990; Silfen et al. 2003; Yoffe and Baruchin 2004; Sendovski et al. 2005). Coastal trawling and purse-seine fishing are disrupted for the duration of the swarming due to net clogging and inability to sort yield. Jellyfish-blocked water intake pipes pose a threat to desalination plants and seawater cooling systems of coastal power plants: in the summer of 2011 Israel Electric removed tons of jellyfish from its seawater intake pipes at its largest power plants (www.bbc.co.uk/news/world-middle-east-14038729) (Fig. 27.4).

The comb jelly *Mnemiopsis leidyi* A. Agassiz, 1865, indigenous in western Atlantic coastal waters (40°N to 46°S), has spread in the past three decades to the Black, Caspian, Baltic and North seas (Mianzan 1999; Shiganova et al. 2001a, b; Javidpour et al. 2006; Faasse et al. 2006). The introduction of the zooplanktivorous *M. leidyi* to the Black Sea in the 1980s set in motion a dramatic chain of events that culminated in a crash of the sea's major fishery and massive economic losses that garnered the species a slot on the International Union for Conservation of Nature (IUCN) list of 100 'World's Worst' invaders (http://www.issg.org/worst100_species.html). Given the severe ecological and economical harm elsewhere, the introduction of *M. leidyi* into the Mediterranean is of major concern. It was first recorded in the Mediterranean Sea in 1990 in the western Aegean Sea presumably swept with the outflow of the Black Sea water masses (Shiganova et al. 2001b), shortly thereafter

Table 27.1 List of alien fish species in the Mediterranean Sea, October 2012

Species	Introduction	Trophic level
<i>Abudefduf vaigiensis</i> (Quoy & Gaimard, 1825)	Suez Canal; Aquaculture	2.6
<i>Alepes djedaba</i> (Forsskål, 1775)	Suez Canal	3.3
<i>Aphanius dispar</i> (Rüppell, 1829)	Suez Canal	2.2
<i>Apogonichthyoides pharaonis</i> Bellotti, 1874	Suez Canal	3.5
<i>Apogon queketti</i> Gilchrist, 1903	Suez Canal	3.5
<i>Apogon smithi</i> (Kotthaus, 1970)	Suez Canal	3.5
<i>Atherinomorus forskalii</i> (Rüppell, 1838)	Suez Canal	3.3
<i>Bregmaceros atlanticus</i> Goode & Bean, 1886	Suez Canal; Vessels	3.1
<i>Callionymus filamentosus</i> Valenciennes, 1837	Suez Canal	3.3
<i>Chaetodon austriacus</i> Rüppell, 1836	Suez Canal	3.3
<i>Chaetodon larvatus</i> Cuvier, 1831	Suez Canal	3.4
<i>Champsodon nudivittis</i> (Ogilby, 1895)	Suez Canal	4.2
<i>Chanos chanos</i> (Forsskål, 1775)	Aquaculture	2
<i>Cheilodipterus novemstriatus</i> Rüppell, 1836	Suez Canal	3.6
<i>Coryogalops ochetica</i> (Norman, 1927)	Suez Canal	3.2
<i>Crenidens crenidens</i> (Forsskål, 1775)	Suez Canal	2.8
<i>Cyclichthys spilostylus</i> (Leis & Randall, 1982)	Suez Canal	3.5
<i>Cynoglossus sinuorabici</i> (Chabanaud, 1913)	Suez Canal	3.3
<i>Decapterus russelli</i> (Rüppell, 1830)	Suez Canal	3.7
<i>Dussumieria elopsoides</i> Bleeker, 1849	Suez Canal	3.4
<i>Elates ransonetti</i> (Steindachner, 1876)	Vessels	4.1
<i>Epinephelus coioides</i> (Hamilton, 1822)	Suez Canal	3.9
<i>Epinephelus fasciatus</i> (Forsskål, 1775)	Suez Canal	3.7
<i>Epinephelus malabaricus</i> (Bloch & Schneider, 1804)	Suez Canal	3.8
<i>Equulites elongatus</i> (Günther, 1874)	Suez Canal	3.5
<i>Equulites klunzingeri</i> (Steindachner, 1898)	Suez Canal	3.5
<i>Etrumeus golanii</i> DiBattista, Randall & Bowen, 2012	Suez Canal	3.5
<i>Fistularia commersonii</i> (Rüppell, 1835)	Suez Canal	4.3
<i>Glaucostegus halavi</i> (Forsskål, 1775)	Suez Canal	4.1
<i>Hemiramphus far</i> (Forsskål, 1775)	Suez Canal	2.9
<i>Heniochus intermedius</i> Steindachner, 1893	Suez Canal	3.5
<i>Herklotsichthys punctatus</i> (Rüppell, 1837)	Suez Canal	3.2
<i>Hippocampus fuscus</i> Rüppell, 1838	Suez Canal	3.4
<i>Hyporhamphus affinis</i> (Günther, 1866)	Suez Canal	3.5
<i>Iniistius pavo</i> Valenciennes, 1840	Suez Canal	3.5
<i>Lagocephalus sceleratus</i> (Gmelin, 1788)	Suez Canal	3.6
<i>Lagocephalus spadiceus</i> (Richardson, 1844)	Suez Canal	3.5
<i>Lagocephalus suezensis</i> Clark & Gohar, 1953	Suez Canal	3.5
<i>Liza carinata</i> (Valenciennes, 1836)	Suez Canal	2.6
<i>Liza haematocheilus</i> (Temminck & Schlegel, 1845)	Aquaculture	2.5
<i>Lutjanus argentimaculatus</i> Forsskål, 1775)	Suez Canal	3.6
<i>Monotaxis grandoculis</i> (Forsskål, 1775)	Suez Canal	3.2
<i>Muraenesox cinereus</i> (Forsskål, 1775)	Suez Canal	4.1
<i>Mycteroperca fusca</i> (Lowe, 1838)	Aquaculture	4.4
<i>Nemipterus randalli</i> Russell, 1986	Suez Canal	3.7
<i>Omobranchius punctatus</i> (Valenciennes, 1836)	Suez Canal; Vessels	2.5
<i>Oplegnathus fasciatus</i> (Temminck & Schlegel, 1944)	Vessels	3.6
<i>Ostorhinchus fasciatus</i> (White, 1790)	Suez Canal	3.5
<i>Ostracion cubicus</i> Linnaeus, 1758	Suez Canal	3.4
<i>Oxyurichthys petersi</i> (Klunzinger, 1871)	Suez Canal	3.5
<i>Pagrus major</i> (Temminck & Schlegel, 1843)	Aquaculture	3.7
<i>Pampus argenteus</i> (Euphrasen, 1788)	Vessels	3.1
<i>Papilloculiceps longiceps</i> (Cuvier, 1829)	Suez Canal	4.1

(continued)

Table 27.1 (continued)

Species	Introduction	Trophic level
<i>Papillogobius melanobranchus</i> (Fowler, 1934)	Suez Canal	3.3
<i>Parexocoetus mento</i> (Valenciennes, 1846)	Suez Canal	3.3
<i>Parupeneus forsskali</i> (Fourmanoir & Guézé, 1976)	Suez Canal	3.3
<i>Pelates quadrilineatus</i> (Bloch, 1790)	Suez Canal	3.5
<i>Pempheris rhomboidea</i> Kossmann & Räuber 1877	Suez Canal	3.4
<i>Petroscirtes ancylodon</i> Rüppell, 1838	Suez Canal	2.1
<i>Pinguipes brasilianus</i> Cuvier, 1829	Vessels	3.8
<i>Platax teira</i> (Forsskål, 1775)	Suez Canal	4
<i>Platycephalus indicus</i> (Linnaeus, 1758)	Suez Canal	3.6
<i>Plotosus lineatus</i> (Thunberg, 1787)	Suez Canal	3.5
<i>Pomacanthus imperator</i> (Bloch, 1787)	Suez Canal	2.7
<i>Pomacanthus maculosus</i> (Forsskål, 1775)	Suez Canal	2.7
<i>Pomadasystris stridens</i> (Forsskål, 1775)	Suez Canal	4
<i>Priacanthus sagittarius</i> Starnes, 1988	Suez Canal	4.1
<i>Pteragogus pelycus</i> Randall, 1981	Suez Canal	3.5
<i>Pterois miles</i> (Bennet, 1803)	Suez Canal	3.7
<i>Rachycentron canadum</i> (Linnaeus, 1766)	Suez Canal	4
<i>Rastrelliger kanagurta</i> (Cuvier, 1816)	Suez Canal	3.2
<i>Rhabdosargus haffara</i> (Forsskål, 1775)	Suez Canal	3.5
<i>Rhynchoconger trewavasae</i> Ben-Tuvia, 1993	Suez Canal	3.9
<i>Sargocentron rubrum</i> (Forsskål, 1775)	Suez Canal	3.5
<i>Saurida macrolepis</i> Shindo & Yamada, 1972	Suez Canal	4.2
<i>Scarus ghobban</i> Forsskål, 1775	Suez Canal	2
<i>Sciaenops ocellatus</i> (Linnaeus, 1766)	Aquaculture	4.1
<i>Scomberomorus commerson</i> Lacepède, 1800	Suez Canal	4.5
<i>Siganus luridus</i> (Rüppell, 1829)	Suez Canal	2
<i>Siganus rivulatus</i> Forsskål, 1775	Suez Canal	2
<i>Silhouettea aegyptia</i> (Chabanaud, 1933)	Suez Canal	3.3
<i>Sillago sihama</i> (Forsskål, 1775)	Suez Canal	3.4
<i>Sorsogona prionota</i> (Sauvage, 1873)	Suez Canal	3.7
<i>Sphyaena chrysotaenia</i> Klunzinger, 1884	Suez Canal	4
<i>Sphyaena flavicauda</i> Rüppell, 1838	Suez Canal	3.8
<i>Spratelloides delicatulus</i> (Bennett, 1831)	Suez Canal	3.1
<i>Stephanolepis diaspros</i> Fraser-Brunner, 1940	Suez Canal	2.8
<i>Stolephorus insularis</i> Hardenberg, 1933	Suez Canal	3.2
<i>Synagrops japonicus</i> (Doderlein, 1884)	Vessels	3.5
<i>Synanceia verrucosa</i> Bloch & Schneider, 1801	Suez Canal	4.2
<i>Terapon jarbua</i> (Forsskål, 1775)	Suez Canal	3.9
<i>Terapon puta</i> (Cuvier, 1929)	Suez Canal	3.1
<i>Terapon theraps</i> Cuvier, 1829	Suez Canal	3.5
<i>Tetrosomus gibbosus</i> (Linnaeus, 1758)	Suez Canal	3.5
<i>Torquigener flavimaculosus</i> Hardy & Randall, 1983	Suez Canal	3.2
<i>Trachurus indicus</i> Necrasov, 1966	Suez Canal	3.8
<i>Tridentiger trigonocephalus</i> (Gill, 1859)	Vessels	3.3
<i>Trypauchen vagina</i> (Bloch & Scheider, 1801)	Suez Canal	3.5
<i>Tylerius spinosissimus</i> (Regan, 1908)	Suez Canal	3.2
<i>Tylosurus chorum</i> (Rüppell, 1837)	Suez Canal	4.4
<i>Tylosurus crocodilus</i> (Péron & Lesueur, 1821)	Suez Canal	4.5
<i>Upeneus moluccensis</i> (Bleeker, 1855)	Suez Canal	3.6
<i>Upeneus pori</i> Ben-Tuvia & Golani, 1989	Suez Canal	3.3
<i>Vanderhorstia mertensi</i> Klauswitz, 1974	Suez Canal	3.3
<i>Himantura uarnak</i> (Gmelin, 1789)	Suez Canal	3.6
<i>Torpedo sinuspersici</i> Olfers, 1831	Suez Canal	4.5

Data on trophic levels extracted from Froese and Pauly (2012a)

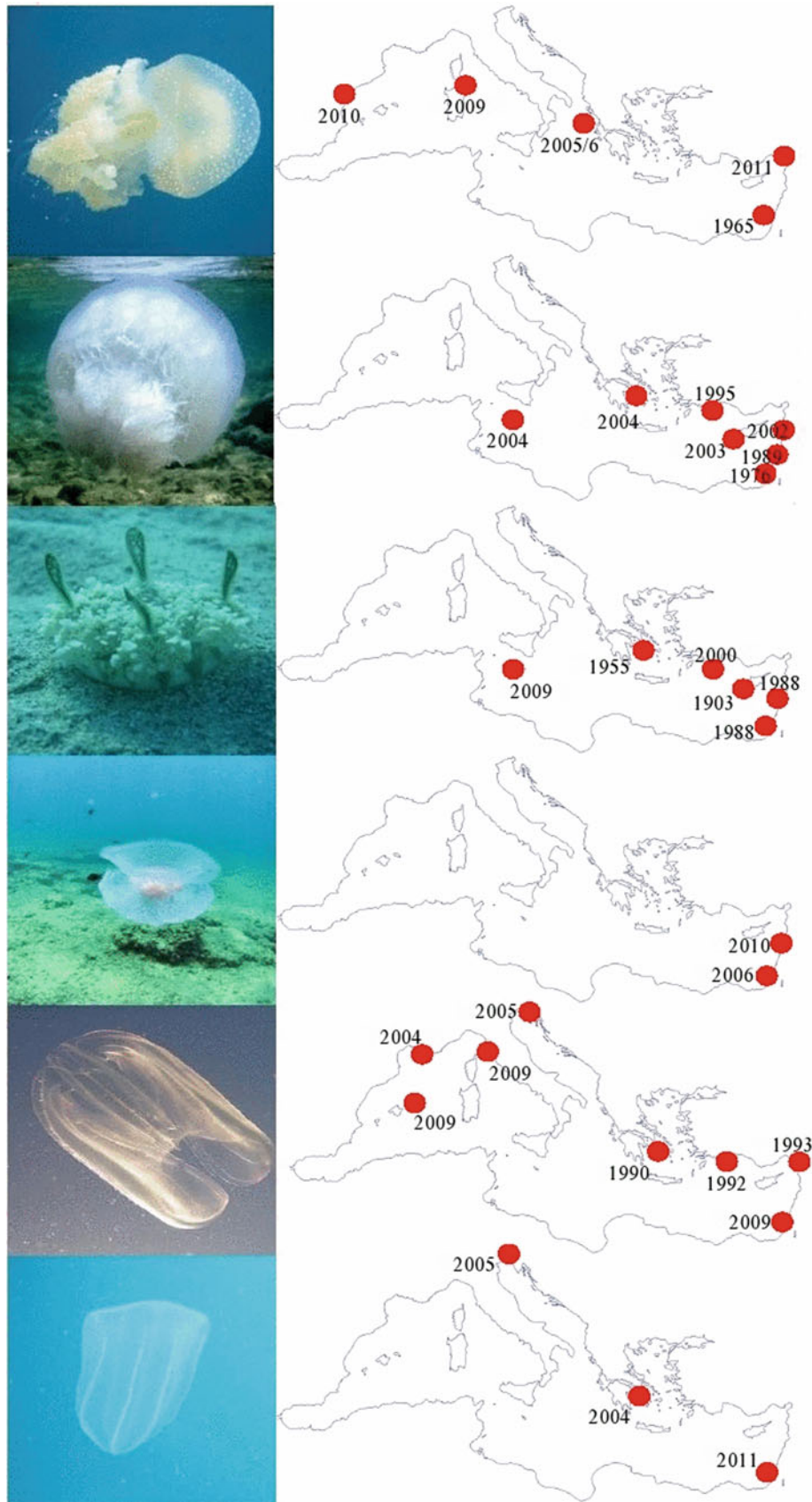


Fig. 27.3 Gelatinous alien species in the Mediterranean Sea, with distribution maps and date of first record per country. From top: *Phyllorhiza punctata* Lendenfeld, 1884, *Rhopilema nomadica* Galil, 1990, *Cassiopea*

andromeda (Forsskål, 1775), *Marivagia stellata* Galil & Gershwin, 2010, *Mnemiopsis leidyi* A. Agassiz, 1865, *Beroe ovata* Bruguière, 1789 (Photos by IOLR, R. Gevili, G. Paz, G. Rilov, S. Shafir) (After Galil 2012)



Fig. 27.4 *Rhophilema nomadica* Galil, 1990. Jellyfish removed from blocked seawater cooling systems of a coastal power plant, Israel, summer 2011

off Turkey's Aegean and Mediterranean coasts (Uysal and Mutlu 1993; Kideys and Niermann 1994) and off the Syrian coast (Shiganova 1997). As all those locales are in the vicinity of ports, and no population persisted long, it was suggested that it had been introduced with ballast water (Shiganova et al. 2001b). Its presence in the Bay of Piran, northern Adriatic Sea (Shiganova and Malej 2009) too was presumably caused by "... ballast water originating from the Black Sea, as there is direct connection between the Port of Koper and various Black Sea ports" (Shiganova and Malej 2009: 64). Suddenly, in 2009, large swarms appeared along the Ligurian, Tyrrhenian, and Ionian shores of Italy, the Mediterranean coast of Spain including the Balearic Islands and the SE Levant (Boero et al. 2009; Fuentes et al. 2009; Galil et al. 2009). Since January 2009 swarms of *M. leidyi* have been intermittently observed along the Israeli coast, where summer SST tops 30 °C. *Mnemiopsis*-fouled fishing gear poses a hardship to local artisanal fisheries. *Mnemiopsis* blocked water intake pipes threaten desalination plants and force plant engineers to modify their operation by increasing the frequency of backwash cycles in the pretreatment stage and consequently raising the discharge of coagulants such as ferric sulfate into the sea, and ultimately reducing output. The ctenophore *Beroe ovata* Bruguière, 1789, a specialized predator of *M. leidyi*, was first noted in the Mediterranean in Greece, in 2004 (Shiganova et al. 2007), a year later in the northern Adriatic Sea (Shiganova and Malej 2009), and recently (2011–2013), it was recorded near the Port of Ashdod, Israel (Galil et al. 2011).

Invasive alien scyphozoan and ctenophorans may impact the ecosystem in ways we neither expect nor understand, and which are more significant than their obvious impacts in economic and human health terms. As gelatinous plankton plays a pivotal role in marine food webs and elemental fluxes, invasive alien populations may affect production cycles in

plankton and benthos. Exploiting their high feeding and growth rate potentials, their massive consumption of plankton, including eggs and larvae of fish and invertebrates, may directly impact recruitment, to the point it may be impossible for the pre-invasion ecosystem to recover.

Metamorphoses: The Changing of the Mediterranean Littoral

Alien macrophytes, invertebrates and fish – all of 680 species that have been recorded in the Mediterranean Sea (Galil 2012) – are found in most littoral habitats, forming some prominent micro-communities and biological facies (*sensu* Last et al. 2010). With few exceptions, the role invasive alien species play *vis a vis* the native biota is poorly known, though it is believed that engineering and keystone invasive aliens cause major changes in community composition and structure and alter ecosystem processes over spatial and temporal scales and a wide range of impacts (Ehrenfeld 2011). A large minority (as much as 30 %) of established invasive aliens are highly disruptive and affect ecosystem functions substantially (Strayer 2010; Simberloff 2011).

Physical alteration is the most frequently recorded pathways of ecosystem change, either through substantial change in species population size and density, or through structural conversion of the physical character of the habitat (Crooks 2002; Simberloff 2011; Strayer and Hillebrand 2012). Such transformations are often accompanied by changes in local species composition and relative abundances, inducing further changes in ecosystem processes and pathways.

We highlight a few of the discernible and sometimes dramatic physical alterations to habitats associated with invasive aliens in the Mediterranean Sea (Fig. 27.5).

An invasive Australian strain of the tropical alga *C. taxifolia*, unintentionally introduced into the Mediterranean in 1984 with aquaria outflow (Jousson et al. 1998), has since spread to Spain, France, Italy, Croatia and Tunisia. Its propensity to form dense meadows (up to 14,000 blades per m²) on various infralittoral bottom types, especially in areas of elevated nutrient loads, led to formation of homogenized microhabitats and replacement of native *Cymodocea nodosa* and *Posidonia oceanica*. The alga's dense clumps of rhizomes and stolons and the defensive secondary metabolites alter total species richness, density and biomass of resident biota, from epiphytic Foraminifera and invertebrates to fish assemblages. It is considered "a real threat for the balance of the marine coastal biodiversity". (Boudouresque et al. 1994; Verlaque and Fritayre 1994; Francour et al. 1995; Villele and Verlaque 1995; Ceccherelli and Cinelli 1999; Harmelin-Vivien et al. 1999; Levi and Francour 2004; Longpierre et al. 2005; Francour et al. 2009; Guillem et al. 2010). The extremely invasive *C. racemosa* var. *cylindracea*, was

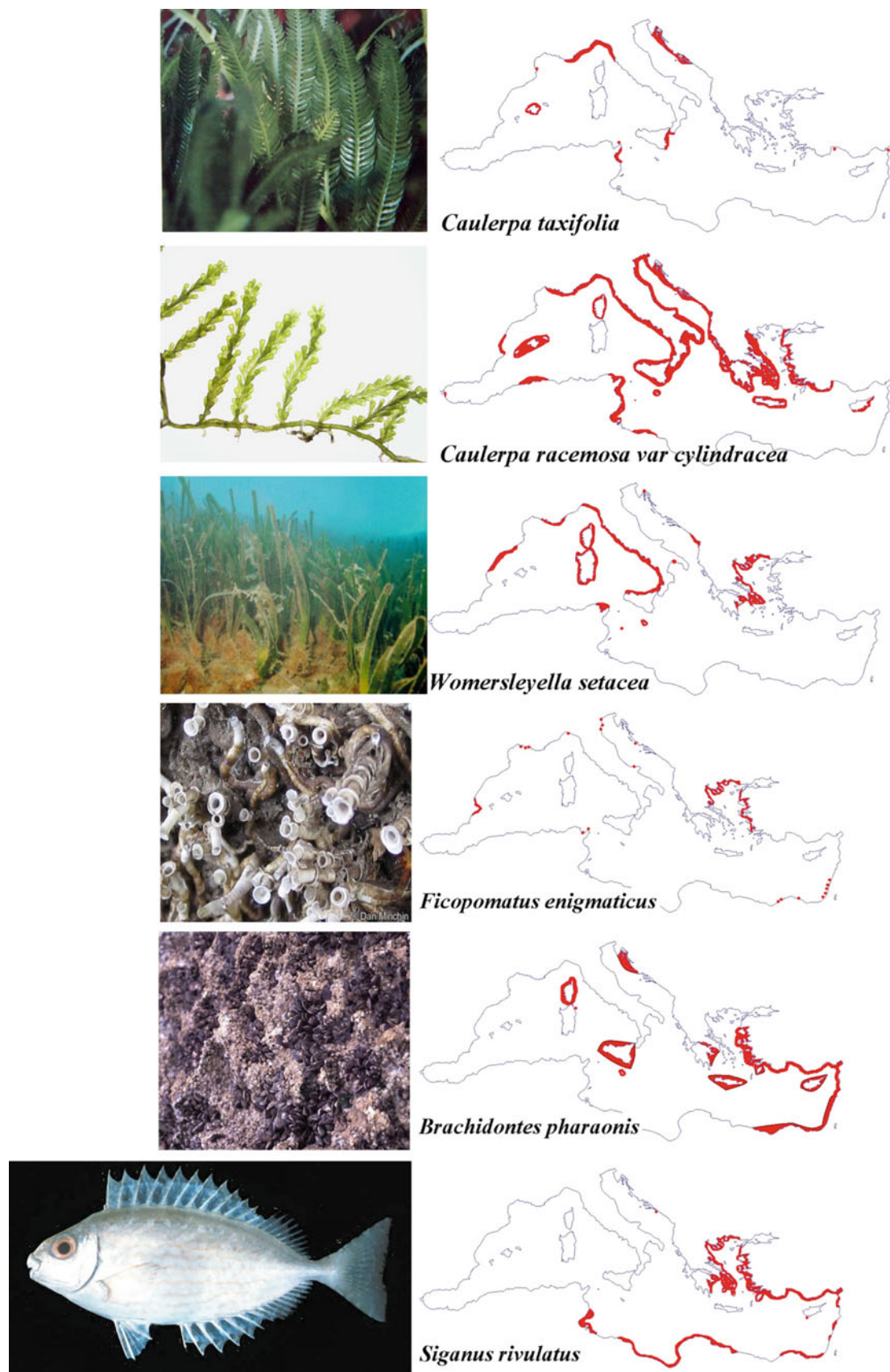


Fig. 27.5 Invasive alien species in the Mediterranean Sea, with distribution maps. From top: *Caulerpa taxifolia* (Vahl) C. Agardh, *Caulerpa racemosa* var. *cylindracea* (Sonder) Verlaque, Huisman and Boudouresque,

Womersleyella setacea (Hollenberg) R.E.Norris 1992, *Ficopomatus enigmaticus* (Fauvel, 1923), *Brachidontes pharaonis* (Fischer P., 1870), *Siganus rivulatus* Forsskål, 1775

discovered in the Mediterranean in 1990, and has since spread from Cyprus to Spain. Its fast growing stolons allow it to overgrow other macroalgae, mainly turf and encrusting species, and to curtail species number, percent cover and diversity of the macroalgal community, even in highly diverse, native macroalgal assemblages with dense coverage. The drastic change in the composition of the phytobenthos brought about a modification of the macrobenthos and consequent trophic guild, niche breadth shift and ecosystem functioning. A study of the meiofauna revealed an increase in average density but a significant decrease of diversity, and profound change in the crustacean assemblage, where harpacticoid copepods proliferate at the expense of ostracods, cumaceans, isopods, amphipods and tanaidaceans (Argyrou et al. 1999; Carriglio et al. 2003; Verlaque et al. 2003; Piazzì et al. 2001, 2003; Klein and Verlaque 2008; Piazzì and Balata 2008; Baldacconi and Corriero 2009; Vazquez-Luis et al. 2009; Box et al. 2010; Deudero et al. 2011; Lorenti et al. 2011; Zuljevic et al. 2011). The invasive rhodophyte *Womersleyella setacea* was discovered in Italy in 1986, presumably introduced with vessel fouling. It forms thick, persistent carpets in deep sublittoral rocky substrata, substantial negative effects on native communities, modifies benthic assemblages and outcompetes gorgonians. Lower values of diversity and significant differences in species composition and abundance. Changes in assemblage structure and reduced species richness were noted in coralligenous communities, reducing diversity and abundance of other turf algae; avoided by herbivorous fishes (Benedetti-Cecchi and Cinelli 1989; Verlaque 1994; Piazzì and Cinelli 2000; Piazzì et al. 2007; Antoniadou and Chintiroglou 2007; Tomas et al. 2011; Cebrian and Rodriguez-Prieto 2012). The reef building serpulid worm *Ficopomatus enigmaticus* is found in brackish to hypersaline sheltered coasts, estuaries and lagoons. An engineering species, it forms extensive reefs - large, complex structures where no hard substrate had existed before. The structural conversion from flat soft-bottom to dimensionally complex dense tube colonies provide refuge for invertebrates (Bianchi and Morri 1996, 2001; Fornos et al. 1997; Ben Eliahu and Ten Hove 2011).

Macrophytes and reef-building invertebrates such as corals, molluscs or polychaetes, are obvious examples of species able to modify their physical environment and create habitats for other species. Planktonic ecosystem engineering seems at first oxymoronic, yet jellyfish clearly alter their physical environment by trophic interactions that control abundances of other species (predator-mediated landscape structure *sensu* Breitburg et al. 2010). Swarms of the Erythraean scyphozoan *R. nomadica*, some over 100 km long, must play havoc with resources in the oligotrophic Levant. It had replaced the native *Rhizostoma pulmo* (Galil 2007).

Changes in food web architecture provide another mechanism by which ecosystem processes are altered. The

gregarious intertidal Erythraean mytilid bivalve *Brachidontes pharaonis* (Fischer P., 1870) is one of the earliest invasive aliens recorded in the Mediterranean. Where suitable conditions are present it forms extremely dense aggregations (1,000/m²) on natural and man-made hard substrates. It locally displaced the smaller-sized and thinner shelled native mytilid *Mytilaster minimus*, possibly affecting trophic guilds. (Fuchs 1878; Safriel et al. 1980; Safriel and Sasson-Frostig 1988; Rilov et al. 2002; Mienis 2003; Sara et al. 2006; Crocetta et al. 2009; Cilia and Deidun 2012). Similarly, the schooling herbivorous Erythraean rabbitfish *Siganus rivulatus*, first recorded in the Mediterranean in 1924, replaced native herbivorous fish along the Levant. It formed “barrens” in the rocky infralittoral- dramatically reducing habitat complexity, altered the community structure and the native food web along the Levantine rocky infralittoral, accelerated transfer of energy from the producer to the consumer levels and has served as major prey item for larger predators (Steinitz 1927; Goren and Galil 2001, 2005; Aronov 2002; Sala et al. 2011).

The biology and ecology of the great majority of invasive alien species in the Mediterranean have never been studied, so it is impossible to say to what degree they impacted the ecosystem.

Invasiveness, Invasibility and Propagule Pressure

It was a truth universally acknowledged that species and ecosystems traits, “invasiveness” and “invasibility” respectively, determined in large part invasion success (Ehrlich 1989; Catford et al. 2012). Researchers were determined to elucidate the biological characteristics of a “successful invader” and thus identify potential invasive species into the Mediterranean Sea, or characterize an habitat vulnerable to invasion (Safriel et al. 1980; Safriel and Ritte 1980). They puzzled over the “universal correlates of colonizing ability” of Erythraean aliens that “distinguishes these species from the many hundreds of Red Sea species that have not (yet?) used the opportunity to colonize the Mediterranean” (Safriel and Ritte 1983, p. 231). Safriel and Ritte (1986) set out to examine these correlates in a pair of closely related mollusks, *Cerithium caeruleum* G.B. Sowerby II, 1855 and *C. scabridum* Philippi, 1848. Though both species occur in the Suez Canal and the life history traits of the former are such that it “should have migrated through the Suez Canal with much greater ease than the colonizer [*C. scabridum*, BG]” (there, p. 572), only the latter invaded the Mediterranean. Following studies of a small Erythraean mytilid mussel, *B. pharaonis*, that in the early 1970s was “c. 250 times rarer” than the native mytilid *Mytilaster minimus* (Poli, 1795), it was predicted the Erythraean alien would neither establish dense populations nor displace the native from the intertidal rocky

ledges along the southern Levant (Safriel et al. 1980, p. 39). How disappointing then that their sincere and ardent efforts to relate species traits to “invasiveness” have failed to alight on the “universal correlates”: these very ledges are to date covered with dense clumps of the alien mytilid “.. while *M. minimus* is only rarely encountered.” (Mienis 2003, p. 15).

Since the Levant Sea was recognized early as pregnable (Steinitz 1927), it was *ipso facto* an “undersaturated niche” (Diamant et al. 1986), “biologically underexploited by marine life ... a sort of ecological vacuum where many ecological niches are available” (Oliverio and Taviani 2003, p. 314), where “The Lessepsian migrants may be considered, in a figurative sense “welcome guests” in the impoverished, subtropical cul-de-sac” (Por 1978, p. 123), even, to have “biologically enriched” the sea (Tortonese 1973, p. 327). Lately however, such heavily invaded “Godot basins” (Oliverio and Taviani 2003) as the Levant and coastal lagoons, are considered impacted by ‘propagule pressure’ (Verlaque 2001; Galil 2007, 2009; Boudouresque and Verlaque 2012). A composite measure of the number of viable alien individuals, genotypes and taxa, the number of discrete introduction events, their frequency and duration, ‘propagule pressure’ is recognized as the primary determinant of invasion success even to overwhelming disturbance and biodiversity (Wonham et al. 2001; Verling et al. 2005; Von Holle and Simberloff 2005; Simberloff 2009). Indeed, a meta-analysis of invasiveness and invasibility studies found it was a significant predictor of both (Colautti et al. 2006). It stands to reason that, when controlling for donor and recipient regions, large inocula are more likely to lead to establishment and that the establishment chance increases with introduction frequency. Large and recurring introductions enable nascent alien populations to overcome limitations associated with small population sizes, including deleterious genetic effects, and weather adverse environmental or demographic events. Recurring introductions of individuals from the same donor location into the same recipient location sustain nascent populations even if initial transfers were of insufficient size or badly timed (Lockwood et al. 2005; Roman and Darling 2007). Indeed, the genetic diversity of the Mediterranean populations of Erythraean aliens proved to be high, and no evidence of founder effect or bottleneck was found. Instead, high levels of gene flow were found between the Red Sea and the Mediterranean populations (Safriel and Ritte 1986; Golani and Ritte 1999; Bucciarelli et al. 2002; Bonhomme et al. 2003; Hassan et al. 2003; Hassan and Bonhomme 2005; Azzurro et al. 2006; Terranova et al. 2006; Golani et al. 2007; Bariche and Bernardi 2009; Sanna et al. 2011; Rius et al. 2012; Rius and Shenkar 2012). A likely explanation is that the propagule pressure driving the Erythraean invasion is large enough to overcome the loss of genetic diversity. Of the three high propagule conveyances – shipping, mariculture, Suez Canal – the latter supplies the largest number of successfully established aliens in the eastern

and central Mediterranean Sea by virtue of the magnitude, frequency, and duration of the trans-isthmian corridor invasion and the common evolutionary history of its components. Such high propagule pressure of co-evolved invaders greatly increases the risk of further invasions (Ricciardi et al. 2011).

The sea level lockless Suez Canal that opened in 1869 was 8 m deep, its cross section 304 m². Repeatedly deepened and widened, the present canal is 24 m deep and its cross section 5,200 m². Already the Suez Canal Authority (SCA) is evaluating the feasibility of further increasing the Canal’s depth and doubling its width to increase its capacity and reduce transit time (www.suezcanal.gov.eg). The implications of a deeper Canal combined with higher through-current velocities on propagule pressure of Erythraean aliens are all too clear- increasing the delivery of multiple invaders, increasing the supply of deeper living taxa, thus accounting for the observed long term changes in the Erythraean invasion. The influx of thermophilic Erythraean aliens has not abated, quite the opposite (Galil 2012), and recently they have been recorded in deeper waters (Goren et al. 2011; Kalogirou and Corsini-Foka 2012), increasing the spatial extent of the recipient ecosystem in the Mediterranean Sea and establishing an ever larger invasion bridgehead in the Mediterranean Sea.

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