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Isopoda (Crustacea) from the Levantine Sea with comments on the biogeography of Mediterranean isopods

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Abstract

This study focuses on the isopod fauna of the eastern Mediterranean, mainly from the waters of Lebanon. Ninety-five samples containing isopods were obtained by scuba diving (depths from 0 to 44 m) at 32 stations along the coast of Northern Cyprus, Syria, and Lebanon. The most frequently sampled substrates were caves, vertical walls, and calcareous algae crusts or build-ups. A total of 502 individuals were studied, belonging to 28 species and included in 20 genera, nine families, and three suborders. Four new species from this collection (*Atarbolana beirutensis*, *Cirolana bitari*, *Cirolana zibrowiusi*, and *Mesanthura pacoi*) have already been published. Brief diagnoses and illustrations were included. The collection studied here consists mostly of Mediterranean species, some already known in the area. Ten (eleven, when the *cf.* species is confirmed) are new records in the Levantine Sea (*Apanthura addui*, *Cirolana manorae*, *Cymodoce fuscina*, *Cymodoce pilosa*, *Elaphognathia bacescoi*, *Gnathia illepidus*, *Gnathia inopinata*, *Heptanthura cryptobia*, *Kupellonura serritelson*, *Metacirolana rotunda*, and *Pseudocerceis cf. seleneides*). Three of these (four, when the *cf.* species is confirmed) are new records in the Mediterranean Sea (*Apanthura addui*, *Cirolana manorae*, *Metacirolana rotunda*, and *Pseudocerceis cf. seleneides*). Eight species (28.5%) can be considered non-indigenous (*Apanthura addui*, *Cirolana manorae*, *Cymodoce fuscina*, *Metacirolana rotunda*, *Paracerceis sculpta*, *Paradella diana*, *Pseudocerceis cf. seleneides*, and *Sphaeroma walkeri*). This work also provides an inventory of known Mediterranean isopod fauna (excluding Epicaridea, Oniscidea, and brackish water Aselloidea), which total 295 species. The isopod fauna of various subregions of the Mediterranean, the Suez Canal, and the Red Sea/Gulf of Aden are compared, and the transit of species through the Suez Canal is discussed. The list of non-indigenous species in the Mediterranean Sea is updated to 23.

Keywords: Crustacea; Isopoda; taxonomy; biogeography; Levantine Sea; checklist of Mediterranean species; non-indigenous species (NIS); anti-Lessepsian species (Anti_L).

Introduction

In the Mediterranean, the flora and fauna of the Levantine region have been less studied than those of other regions. However, some progress has been made in the last two decades, with the publication of several studies on marine taxa, e.g., fish (Egypt: Akel & Karachle, 2017; Syria: Ali, 2018), bryozoan (Lebanon: Harmelin *et al.*, 2007; Harmelin *et al.*, 2009; Israel: Sokolover *et al.*, 2016), macrophytes (Lebanon: Bitar *et al.*, 2017; Egypt: Shabaka, 2018), mollusca (Lebanon: Crocetta *et al.*, 2020). Extensive surveys carried out in Lebanon resulted in a series of publications (e.g., Zibrowius & Bitar, 2003; Pérez *et al.*, 2004; Harmelin-Vivien *et al.*, 2005; Vacelet *et al.*, 2007; Crocetta *et al.*, 2013a; Crocetta *et al.*, 2013b; Crocetta *et al.*, 2014; Bitar, 2014). Isopods are a group of

peracarid crustaceans with a depressed body and seven pairs of pereopods that are generally similar to each other. Their biological cycle does not include larval stages, except for the Gnathiidae (Cymothoidea), which present hematophagous larvae that are parasitic on fish (Hispano *et al.*, 2013). Isopoda is an order of crustaceans of marine origin that have had great evolutionary success. They display wide morphological diversity and have adapted to all environments (marine, freshwater and terrestrial). It is estimated that there are some 6,250 marine species (Poore & Bruce, 2012), with wide bathymetric distribution, from the surface to abyssal depths (10,000 m). Most marine species live on the bottom and are benthic organisms (e.g., Sphaeromatidea and Valvifera). However, there are groups of Asellota with swimming species that have modified appendages and can be considered pe-

lagic (e.g., Desmosomatidae and Munnopsidae). In terms of habitat, marine isopods have colonized mediolittoral, infralittoral and circalittoral algal substrates up to bathyal and abyssal muddy bottoms. Some species of Sphaeromatidae are euryhaline (e.g., *Lekanesphaera hookeri*). Their diet is diverse. Free-living species range from herbivores to omnivorous scavengers. There are also adaptations to ectoparasitism (e.g., Cymothoidea), whose species feed on the blood and tissues of diverse hosts, mainly fish, and to endoparasitism (Epicaridea), in which species lose their typical form to adapt to live in a variety of hosts, mainly other crustaceans. Isopods make up an important part of the diet of other animals, especially fish. Isopods do not have powerful means of dispersion. Many species are passively spread by marine currents, using drifting objects (e.g., *Idotea*), “hitchhiking” on other organisms such as cephalopods or fish (e.g., Cymothoidea), or ship hulls (e.g., *Limnoria*, and Sphaeromatidea). Despite their abundance, diversity and ecological relevance, there is no complete list of species from the Levantine region even though previous faunistic studies (e.g., Bakir *et al.*, 2014; Kirkim *et al.*, 2009, 2015; Kirkim *et al.*, 2010; Koçatas *et al.*, 2001; Koukouras *et al.*, 2002; Larwood, 1940; Monod, 1931, 1933; Müller, 1989c, 1994; Negoescu, 1980a; Negoescu & Wägele, 1984; Omer-Cooper, 1927; Ramadan *et al.*, 2006; Ramdane & Trilles, 2008; Trilles, 1991; Trilles & Bariche, 2006; Trilles & Paperna, 1980; Ulman *et al.*, 2017; Veuille & Koçatas, 1979; Wägele, 1981a, b) have notably contributed to knowledge of this taxon.

The present paper focuses on a major collection of isopods from Lebanon put together by Ghazi Bitar (GB, Lebanese University, Hadath) and Helmut Zibrowius (HZ, Station Marine d’Endoume, Marseille, at that time) mainly between 1997 and 2003. Additions are from Syria (GB, 2003) and Northern Cyprus (HZ, 1998). This collection has helped to broaden our taxonomic knowledge of the isopod fauna in the area. It also allowed us to carry

out a more comprehensive biogeographical comparison throughout the Mediterranean and assess the level of dispersion of non-indigenous species (NIS).

Materials and Methods

The 95 samples examined (Table 1) were obtained between 1991 and 2003 by scuba diving during various field work projects. The samples correspond to 32 stations in Cyprus, Syria, and Lebanon. Most of the samples (88) are from Lebanon and were obtained between 1997 and 2003, thanks to the French-Lebanese Cooperation Program CEDRE (Ghazi Bitar [GB], Helmut Zibrowius [HZ]). The three samples from Northern Cyprus were obtained by HZ in 1998, although Castelló (2017b) mistakenly mentioned the holotype of *Mesanthura pacoi* with GB as collector. The most frequently sampled stations in Lebanon were Ramkine Island (12 samples), Selaata (10 samples), Batroun (7 samples) and Chak El Hatab (6 samples). Figure 1 (map) indicates the sampled localities.

For biogeographical comparisons (Table 2, Table S2, Table 3, and Table 4), eight Mediterranean subregions (see the respective boundaries in Figure 2, map) and the Suez Canal, Red Sea and Gulf of Aden were considered. These Mediterranean areas broadly coincide with the subregions of the Marine Strategy Framework Directive (MSFD) (Jensen & Panagiotidis, 2015): Western Mediterranean Sea; Adriatic Sea; Ionian Sea and the Central Mediterranean Sea; and Aegean-Levantine Sea. The main differences are the inclusion of an extra subregion (8) corresponding to the southern coasts of the Western and Central Mediterranean, and the subdivisions of the Ionian and the Central Mediterranean (subregions 4 and 8, partly), and the Aegean and Levantine Seas (subregions 5 and 7) because the present collection refers to the latter area. All these subdivisions were considered for comparison purposes.

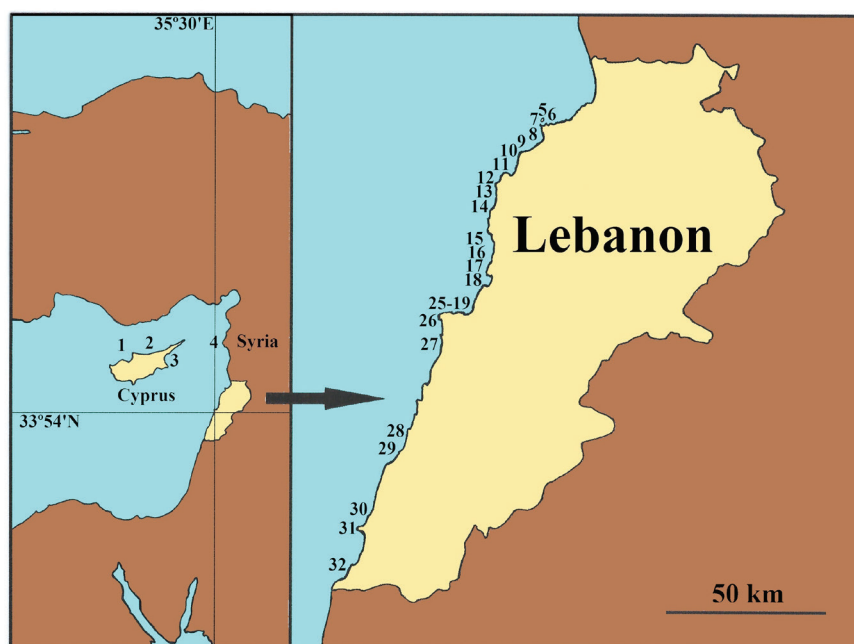


Fig. 1: Map of sampling localities: See Table 1 for number codes.

Table 1. List of sampling sites, with indication of date of collection, geographical coordinates, depth, and additional ecological/geographical data. Stations.- 1 Limnitis, Yesilirmak (Cyprus); 2 Mare Monte (Cyprus); 3 Famagusta (Cyprus); 4 Lattakia, Institut Scientifique des Recherches Marines (Syria); 5 Ramkine Island (Lebanon); 6 Tripoli, Outside Harbor (Lebanon); 7 Tripoli, Inside Harbor (Lebanon); 8 Tripoli, Al Bahsas (Lebanon); 9 Ras El Chakaa (Lebanon); 10 El Heri, Marina Beaulieu, exit East (Lebanon); 11 Chak El Hatab (Lebanon); 12 Selaata (Lebanon); 13 Batroun (Lebanon); 14 Kfar Aabida (Lebanon); 15 Jbail (Lebanon); 16 N Tabarja (Lebanon); 17. S Tabarja (Lebanon); 18 Acquamarina, N Jounieh Bay (Lebanon); 19 Beirut Harbor, inner side of breakwater (Lebanon); 20 Beirut, Inside Harbor (Lebanon); 21 Beirut, Inside Harbor, Quay 60 (Lebanon); 22 Beirut Harbor, outer side of breakwater (Lebanon); 23 Beirut, St.George (Lebanon); 24 Beirut, American University Beirut (Lebanon); 25 Raoucheh (Lebanon); 26 Beirut Airport, pillars (Lebanon); 27 Khaldeh, Marina Villamar (Lebanon); 28 Saida, Harf El Rijmeh (Lebanon); 29 El Zahrani, Harf El Hawieh El Jouani (Lebanon); 30 El Kassmieh (Lebanon); 31 Tyr (Lebanon); 32 Naqoura (Lebanon).

Sample	Date	Latitude N - Longitude E	Depth range (m)	Ecological or/and geographical data
1.1	19.11.98	35.17333° - 32.74500°	4	No data
2.1	18.11.98	35.35583° - 33.20666°	7	No data
3.1	23.11.98	35.13250° - 33.93722°	10	No data
4.1	23.05.03	35.53055° - 35.76694°	10--15	Meadow of <i>Cymodocea nodosa</i> and <i>Penicillus capitatus</i>
5.1	22.10.99	34.49638° - 35.76055°	13	Concretions and corals
5.2	22.10.99	34.49638° - 35.76055°	5	Cave
5.3	22.10.99	34.49638° - 35.76055°	15	Cave
5.4	22.10.99	34.49638° - 35.76055°	13-14	Concretions
5.5	22.10.99	34.49638° - 35.76055°	5	Cave
5.6	31.05.00	34.49638° - 35.76055°	5	Shaded wall
5.7	31.05.00	34.49638° - 35.76055°	5-7	Cave with corals
5.8	01.06.00	34.49638° - 35.76055°	3-5	Under boulders
5.9	01.06.00	34.49638° - 35.76055°	0,5	<i>Dyctyopterus polypodioides</i> and <i>Sargassum</i>
5.10	05.04.01	34.49638° - 35.76055°	1	Fouling of a tourist boat
5.11	14.07.03	34.49638° - 35.76055°	15	Cave
5.12	14.07.03	34.49638° - 35.76055°	15	Cave
6.1	20.09.02	34.45722° - 35.81444°	5	Outer side of the breakwater
7.1	19.09.02	34.45583° - 35.81527°	0	Crust of <i>Spirobranchus kraussii</i>
7.2	19.09.02	34.45583° - 35.81527°	2-5	Dock with oysters and ascidians
7.3	08.07.03	34.45583° - 35.81527°	0	Crust of <i>Spirobranchus kraussii</i>
7.4	08.07.03	34.45583° - 35.81527°	2-5	Oysters, ascidians and <i>Niphates toxifera</i>
8.1	26.11.91	34.41972° - 35.82027°	1	<i>Dyctyopterus polypodioides</i> association
9.1	19.10.99	34.31305° - 35.68305°	5-8	Concretions on vertical wall
9.2	19.10.99	34.31305° - 35.68305°	10	Cave
9.3	04.06.00	34.31305° - 35.68305°	10	Cave
9.4	21.09.02	34.31305° - 35.68305°	10	Photophilous algae
10.1	03.06.00	34.31027° - 35.69750°	2-3	Photophilous algae
10.2	03.06.00	34.31027° - 35.69750°	1	<i>Ellisolandia elongata</i> association
11.1	04.06.00	34.29333° - 35.67138°	6	Cave

continued

Table 1 continued

Sample	Date	Latitude N - Longitude E	Depth range (m)	Ecological or/and geographical data
11.2	04.06.00	34.29333° - 35.67138°	5	Cave
11.3	05.07.03	34.29333° - 35.67138°	9	Concretions
11.4	05.07.03	34.29333° - 35.67138°	14	Cave
11.5	13.07.03	34.29333° - 35.67138°	12-14	Cave
11.6	13.07.03	34.29333° - 35.67138°	12-14	Cave
12.1	18.10.99	34.28416° - 35.65861°	3-8	Small caves and concretions
12.2	18.10.99	34.28416° - 35.65861°	3-8	Small caves
12.3	23.10.99	34.28416° - 35.65861°	7	Concretions
12.4	23.10.99	34.28416° - 35.65861°	0,5-1	<i>Ellisolandia elongata</i> association
12.5	23.10.99	34.28416° - 35.65861°	1	<i>Ellisolandia elongata</i>
12.6	06.07.03	34.28416° - 35.65861°	6-7	Concretions
12.7	06.07.03	34.28416° - 35.65861°	20	Cave
12.8	06.07.03	34.28416° - 35.65861°	35	Concretions
12.9	06.07.03	34.28416° - 35.65861°	20	Cave
12.10	06.07.03	34.28416° - 35.65861°	35	Concretions
13.1	25.09.93	34.25361° - 35.65527°	3	Photophilous algae
13.2	26.06.97	34.25361° - 35.65527°	1	<i>Dyctiopteris polypodioides</i> association
13.3	16.10.99	34.25361° - 35.65527°	9	Concretion on vertical wall
13.4	16.10.99	34.25361° - 35.65527°	9	Concretions on "Phenician wall"
13.5	26.09.02	34.25361° - 35.65527°	6	Calcareous algae
13.6	15.07.03	34.25361° - 35.65527°	5	Calcareous algae
13.7	15.07.03	34.25361° - 35.65527°	5	Calcareous algae
14.1	30.05.00	34.23388° - 35.65416°	7-8	Small cave, concretions
14.2	30.05.00	34.23388° - 35.65416°	5-12	Photophilous algae
15.1	17.10.99	34.12166° - 35.64111°	15	Concretions, Tableh Shoal
16.1	10.07.03	34.03555° - 35.62472°	10	<i>Galaxaura rugosa</i> and <i>Halopteris scoparia</i>
17.1	11.07.03	34.02527° - 35.62222°	6	Photophilous algae
17.2	11.07.03	34.02527° - 35.62222°	8-18	<i>Peyssonnelia</i> and <i>Eudendrium</i>
18.1	10.07.03	34.01416° - 35.63250°	10-25	Rocky boulders
18.2	11.07.03	34.01416° - 35.63250°	14-23	<i>Peyssonnelia</i>
19.1	15.09.02	33.90722° - 35.52111°	21	Hard bottom
19.2	09.07.03	33.90722° - 35.52111°	14	Boulders covered by <i>Chama pacifica</i> , <i>Niphates toxifera</i> and <i>Eudendrium</i>
20.1	02.06.00	33.90194° - 35.50861°	1-2	Under stones
20.2	02.06.00	33.90194° - 35.50861°	3-8	Muddy boulders covered by <i>Chama pacifica</i> and <i>Spondylus spinosus</i>

continued

Table 1 continued

Sample	Date	Latitude N - Longitude E	Depth range (m)	Ecological or/and geographical data
20.3	02.06.00	33.90194° - 35.50861°	1-2	<i>Chama pacifica</i> and <i>Spondylus spinosus</i> (covered with mud)
20.4	02.06.00	33.90194° - 35.50861°	2--5	Muddy boulders covered by <i>Chama pacifica</i> and <i>Spondylus spinosus</i>
20.5	15.09.02	33.90194° - 35.50861°	0	Crust of <i>Spirobranchus kraussii</i>
21.1	16.09.02	33.90249° - 35.51638°	0	<i>Spirobranchus kraussii</i> facies
21.2	16.09.02	33.90249° - 35.51638°	5-7	<i>Chama</i> and <i>Spondylus</i>
21.3	16.09.02	33.90249° - 35.51638°	6-8	<i>Chama</i> and <i>Balanus</i>
21.4	16.09.02	33.90249° - 35.51638°	0	Crust of <i>Spirobranchus kraussii</i>
22.1	16.09.02	33.90777° - 35.52083°	5-15	<i>Galaxaura rugosa</i>
22.2	16.09.02	33.90777° - 35.52083°	10	<i>Galaxaura rugosa</i> association and <i>Balanus</i>
22.3	09.07.03	33.90777° - 35.52083°	5-8	<i>Chama pacifica</i> and <i>Balanus</i>
22.4	09.07.03	33.90777° - 35.52083°	15	Concretions
23.1	07.07.03	33.90305° - 35.49527°	10	Dike covered by <i>Ellisolandia elongata</i> and <i>Galaxaura rugosa</i>
23.2	07.07.03	33.90305° - 35.49527°	10	Gastropods epifauna
24.1	09.05.92	33.90333° - 35.48250°	1-2	<i>Pterocliadiella capillacea</i> and <i>Ellisolandia elongata</i> association
24.2	17.04.01	33.90333° - 35.48250°	0,5	Photophilous algae
25.1	17.09.02	33.88833° - 35.46694°	0-1	Cave
25.2	17.09.02	33.88833° - 35.46694°	1-3	Cave
25.3	17.09.02	33.88833° - 35.46694°	7-9	Rock
25.4	16.07.03	33.88833° - 35.46694°	5	Cave
26.1	25.09.02	33.84222° - 35.48000°	3-10	Pillar
26.2	16.07.03	33.84222° - 35.48000°	0	Pillar, crust of <i>Spirobranchus kraussii</i>
26.3	16.07.03	33.84222° - 35.48000°	3-11	Pillar
27.1	07.06.00	33.77888° - 35.46944°	1	Photophilous algae
27.2	07.06.00	33.77888° - 35.46944°	3	<i>Styopodium schimperi</i> association
27.3	07.06.00	33.77888° - 35.46944°	3	Photophilous algae
28.1	05.06.00	33.56666° - 35.36944°	11	<i>Styopodium schimperi</i> , <i>Colpomenia sinuosa</i> and <i>Spondylus spinosus</i>
29.1	06.06.00	33.49611° - 35.33361°	10	Corallinaceae
29.2	06.06.00	33.49611° - 35.33361°	14	Corallinaceae
29.3	06.06.00	33.49611° - 35.33361°	14	Flat rocky bottom
30.1	25.10.99	33.33944° - 35.23861°	44	Coralligenous bottom and freshwater sources
31.1	25.10.99	33.26555° - 35.19000°	12	High bottom, on a boulder
32.1	01.05.01	33.11583° - 35.11972°	8	<i>Cystoseira</i> sp. and <i>Halopteris scoparia</i> association

Table 2. Mediterranean distribution of isopod species, excluding Epicaridea, Oniscidea, and brackish water Aselloidea, by subregions (species present in the Suez Canal and the Red Sea are also indicated); see Figure 2 for number codes. *not in WoRMS (last accessed: 20 November 2019); ** doubtful record; ***uncertain validity; ****uncertain taxonomic significance; abbreviations: A, absent; P, previously cited; S, found in the present study; RS, Red Sea; SC, Suez Canal; NIS, non-indigenous species in the Mediterranean; New NIS, non-indigenous species in the Mediterranean considered in the present study and not recorded before.

SPECIES	MEDITERRANEAN SUBREGIONS								SUEZ CANAL/ RED SEA
	1	2	3	4	5	6	7	8	9
ASELLOTA									
GNATHOSTENETROIDOIDEA									
Gnathostenetroididae									
<i>Caecostenetroides ischitanum</i> Fresi & Schiecke, 1968		P							A
<i>Gnathostenetroides laodicense</i> Amar, 1957		P					P, S		A
JANIROIDEA									
Desmosomatidae									
<i>Chelator chelatus</i> (Stephensen, 1915)	P	P		P (cf.)	P		P	P	A
<i>Chelator insignis</i> (Hansen, 1916)	P								A
<i>Desmosoma affine</i> Fresi & Schiecke, 1969		P							A
<i>Desmosoma atypicum</i> Schiecke & Fresi, 1969		P							A
<i>Desmosoma elegans</i> Fresi & Schiecke, 1969		P							A
<i>Desmosoma latipes</i> Hansen, 1916		P							A
<i>Desmosoma lineare</i> Sars, 1864	P								A
<i>Desmosoma puritanum</i> Fresi & Schiecke, 1969		P							A
<i>Desmosoma serratum</i> Fresi & Schiecke, 1969		P							A
<i>Desmosoma thoracicum</i> Fresi & Schiecke, 1969		P							A
<i>Desmosoma tyrrhenicum</i> Fresi & Schiecke, 1969		P							A
<i>Echinopleura aculeata</i> (Sars, 1864)	P		P	P					A
<i>Eugerdia filipes</i> (Hult, 1936)	P	P							A
<i>Pseudomesus bispinosus</i> Chardy, 1974								P	A
<i>Mirabilicoxa curticoxalis</i> Pasternak, 1982	P								A
<i>Whoia angusta</i> (Sars, 1899)		P							A
Ischnomesidae									
<i>Gracilimesus tropicalis</i> (Menzies, 1962)								P	A
<i>Ischnomesus bispinosus</i> (Sars, 1868)		P		P					A
Janirellidae									
<i>Janirella bonnieri</i> Stephensen, 1915	P	P							A
<i>Janirella nanseni</i> Bonnier, 1896	P								A
Janiridae									
<i>Austrofilius majoricensis</i> Castelló, 2008*	P								A
<i>Austrofilius mediterraneus</i> Castelló, 2002	P								A
[New NIS] <i>Carpas crosslandi</i> (Stebbing, 1910)								P	RS
<i>Carpas galloprovincialis</i> (Amar, 1950)		P							A
<i>Carpas stebbingi</i> (Monod, 1933)	P	P	P		P		P, S		A
<i>Ianiropsis breviremis</i> (Sars, 1883)	P				P		P		A
[NIS] <i>Ianiropsis serricaudis</i> Gurjanova, 1936		P	P						A
<i>Jaera (Jaera) albifrons</i> Leach, 1814								P	A
<i>Jaera (Jaera) bocqueti</i> Veuille & Koçatas, 1979					P				A
<i>Jaera (Jaera) hopeana</i> Costa, 1853	P	P	P	P	P	P	P		A
<i>Jaera (Jaera) italica</i> Kesselyak, 1938		P	P	P	P	P	P		A
<i>Jaera (Jaera) nordica</i> Lemercier, 1958		P							A
<i>Jaera (Jaera) nordmanni</i> (Rathke, 1837)	P	P	P		P	P	P	P	A
<i>Jaera (Jaera) petiti</i> Schulz, 1953		P							A
<i>Jaera (Jaera) sarsi</i> Valkanov, 1936					P	P			A
<i>Jaera (Jaera) schellenbergi</i> Kesselyak, 1938			P						A
<i>Jaera (Jaera) sorrentina</i> Verhoeff, 1943		P							A

continued

Table 2 continued

SPECIES	MEDITERRANEAN SUBREGIONS								SUEZ CANAL/ RED SEA
	1	2	3	4	5	6	7	8	9
<i>Janira alta</i> (Stimpson, 1853)	P								A
<i>Janira denticulata</i> Gourret, 1891		P							A
<i>Janira maculosa</i> Leach, 1814	P	P	P		P	P	P		A
<i>Microjaera anisopoda</i> Bocquet & Lévi, 1955	P	P							A
<i>Microjanira dentifrons</i> Schiecke & Fresi, 1970		P	P						A
Joeropsididae									
<i>Joeropsis brevicornis</i> Koehler, 1885 [subsp. <i>littoralis</i> Amar, 1949]	P	P		P	P		P	P	A
<i>Joeropsis dollfusi</i> Norman, 1899		P						P	A
<i>Joeropsis legrandi</i> Juchault, 1962	P						P, S		A
<i>Joeropsis mediterranea</i> Amar, 1961*		P							A
<i>Joeropsis montalentii</i> Fresi, 1968*		P							A
[New NIS] <i>Joeropsis rathbunae</i> Richardson, 1902							P		SC
Microparasellidae									
<i>Angeliara phreaticola</i> Chappuis & Delamare-Deboutteville, 1952		P							A
<i>Microcharon marinus</i> Chappuis & Delamare-Deboutteville, 1954	P	P							A
<i>Microcharon motasi</i> Serban, 1964						P			A
<i>Microcharon oltenicus</i> Serban, 1964						P			A
<i>Microcharon orghidani</i> Serban, 1964						P			A
<i>Microcharon ullae</i> Pesce, 1981					P				A
Munnidae									
<i>Munna fabricii</i> Kröyer, 1846	P								A
<i>Munna limicola</i> Sars, 1866	P								A
<i>Munna wolffi</i> Fresi & Mazzella, 1974		P							A
<i>Uromunna mediterranea</i> (Pierantoni, 1916)		P							A
<i>Uromunna petiti</i> (Amar, 1948)	P	P	P		P		P	P	A
<i>Uromunna similis</i> (Fresi & Mazzella, 1971)		P							A
Munnopsidae									
<i>Aspidarachna sekhari</i> (George & Menzies, 1968)	P								A
<i>Belonectes parvus</i> (Bonnier, 1896)	P			P					A
<i>Disconectes cf. furcatus</i> (Sars, 1870)				P					A
<i>Disconectes cf. phalangium</i> (Sars, 1864)				P					A
<i>Disconectes picardi</i> (Amar, 1957)		P							A
<i>Eurycope laticuneata</i> Pasternak, 1982		P							A
<i>Munnopsurus atlanticus</i> (Bonnier, 1896)	P			P					A
<i>Ilyarachna calidus</i> George & Menzies, 1968*	P	P		P				P	A
<i>Ilyarachna calva</i> Pasternak, 1982	P	P							A
<i>Ilyarachna longicornis</i> (Sars, 1864)	P			P	P				A
<i>Ilyarachna medorientalis</i> Chardy, 1974					P			P	A
Nannoniscidae									
<i>Austroniscus coronatus</i> Schiecke & Modigh-Tota, 1976		P							A
Paramunnidae									
<i>Boreosignum maltinii</i> (Schiecke & Fresi, 1972)	P	P							A
<i>Tethygonium variabile</i> (Schiecke & Modigh-Tota, 1976)	P	P							A
Pleurocopidae									
<i>Pleurocope dasyura</i> Walker, 1901		P							A
STENETRIOIDEA									
Stenetriidae									
<i>Stenetrium mediterraneum</i> Hansen, 1905	P	P	P	P					A

continued

Table 2 continued

SPECIES	MEDITERRANEAN SUBREGIONS								SUEZ CANAL/ RED SEA	
	1	2	3	4	5	6	7	8	9	
<i>Tristenium longicorne</i> (Lucas, 1849)			P					P	P	A
CYMOTHOIDA										
<i>CYMOTHOIDEA</i>										
Aegidae										
<i>Aega affinis</i> Milne-Edwards, 1840	P									A
<i>Aega bicarinata</i> Leach, 1818			P	P				P		A
<i>Aega hirsuta</i> Schiödte & Meinert, 1879		P								A
<i>Aega psora</i> (Linnaeus, 1758)	P									A
<i>Aega rosacea</i> (Risso, 1816)****	P	P	P					P		A
<i>Aegapheles deshaysiana</i> (Milne-Edwards, 1840)	P	P	P					P		A
<i>Aegiochus incisa</i> (Schiödte & Meinert, 1879)		P		P						A
<i>Rocinela danmoniensis</i> Leach, 1818	P									A
<i>Rocinela dumerilii</i> (Lucas, 1849)		P	P		P			P	P	A
<i>Rocinela ophthalmica</i> Milne-Edwards, 1840	P	P	P		P			P		A
<i>Syscenus infelix</i> Harger, 1880	P	P	P		P			P		A
Cymothoidae										
<i>Anilocra frontalis</i> Milne-Edwards, 1840	P	P	P	P		P	P	P		A
[New NIS] <i>Anilocra leptosoma</i> Bleeker, 1857								P		RS
<i>Anilocra physodes</i> (Linnaeus, 1758)	P	P	P	P	P	P	P	P		A
[NIS] <i>Anilocra pilchardi</i> Bariche & Trilles, 2006								P		A
<i>Ceratothoa capri</i> (Trilles, 1964)	P	P	P	P	P		P	P		A
<i>Ceratothoa collaris</i> Schiödte & Meinert, 1883		P	P	P	P		P	P		A
<i>Ceratothoa gaudichaudii</i> Milne-Edwards, 1840***					P					A
<i>Ceratothoa gobii</i> Schiödte & Meinert, 1883		P								A
[New NIS] <i>Ceratothoa imbricata</i> (Fabricius, 1775)					P					RS
<i>Ceratothoa italica</i> Schiödte & Meinert, 1883	P	P	P	P	P		P	P		A
<i>Ceratothoa oestroides</i> (Risso, 1816)	P	P	P	P	P		P	P		A
<i>Ceratothoa oxyrrhynchaena</i> Koelbel, 1878		P	P	P	P		P	P		RS
<i>Ceratothoa parallela</i> (Otto, 1828)	P	P	P	P	P		P	P		A
<i>Ceratothoa steindachneri</i> Koelbel, 1879	P	P	P	P			P	P		A
<i>Cymothoa gibbosa</i> Gourret, 1892		P								A
[NIS] <i>Cymothoa indica</i> Schiödte & Meinert, 1884								P		A
<i>Cymothoa nigropunctata</i> Risso, 1816		P								A
[New NIS] <i>Elthusia nanooides</i> (Stebbing, 1905)								P		RS
<i>Elthusia sinuata</i> (Koelbel, 1879)		P	P	P	P			P		A
<i>Emetha adriatica</i> Bovallius, 1885			P							A
<i>Emetha audouini</i> (Milne-Edwards, 1840)	P	P	P	P	P		P	P		A
<i>Idusa dieuzeidei</i> Dollfus, 1950	P		P					P		A
<i>Livoneca pomatomi</i> Gaillat Airoldi, 1940 ****		P			P			P		A
<i>Livoneca punctata</i> (Uljanin, 1872)*		P			P	P		P		A
[New NIS] <i>Livoneca redmanii</i> Leach, 1818								P		A
<i>Mothocya belonae</i> Bruce, 1986		P				P				A
<i>Mothocya contracta</i> Costa, 1851****		P								A
<i>Mothocya epimerica</i> Costa, 1851	P	P	P		P	P		P		A
<i>Mothocya nana</i> (Schiödte & Meinert, 1884)			P					P		A
<i>Mothocya taurica</i> (Czerniavsky, 1868)						P				A
<i>Nerocila bivittata</i> (Risso, 1816)	P	P	P	P	P	P	P	P		SC
<i>Nerocila cuspidata</i> Costa, 1851****		P								A
<i>Nerocila orbignyi</i> (Guérin-Méneville, 1832)	P	P	P	P	P	P	P	P		A
<i>Nerocila rhabdota</i> Koelbel, 1879*			P					P		A

continued

Table 2 continued

SPECIES	MEDITERRANEAN SUBREGIONS								SUEZ CANAL/ RED SEA
	1	2	3	4	5	6	7	8	9
<i>Nerocila swainsoni</i> Leach, 1818		P**		P**					A
<i>Olencira lamarckii</i> Leach, 1818	P								A
Gnathiidae									
<i>Elaphognathia bacescoi</i> (Kussakin, 1969)						P	S		A
<i>Gnathia dentata</i> (Sars, 1872)	P						P, S	P	A
<i>Gnathia fallax</i> Monod, 1926	P								A
<i>Gnathia illepidus</i> (Wagner, 1869)	P	P	P	P	P		S		A
<i>Gnathia inopinata</i> Monod, 1925	P	P			P		S		A
<i>Gnathia maxillaris</i> (Montagu, 1804)	P	P		P	P	P	P	P	A
<i>Gnathia oxyuraea</i> (Lilljeborg, 1855)	P	P	P	P	P	P	P		A
<i>Gnathia phallonajopsis</i> Monod, 1925	P	P	P		P			P	A
<i>Gnathia venusta</i> Monod, 1925	P		P						A
<i>Gnathia vorax</i> (Lucas, 1849)	P	P	P	P	P	P	P, S	P	A
<i>Paragnathia formica</i> (Hesse, 1864)		P			P	P	P		A
ANTHUROIDEA									
Antheluridae									
<i>Ananthura ovalis</i> Barnard, 1925				P			P	P	A
<i>Anthelura elongata</i> Norman & Stebbing, 1886		P							A
Anthuridae									
<i>Amakusanthura libyana</i> (Negoescu, 1980)								P	A
<i>Anthura filiformis</i> Lucas, 1846****							P	P	A
<i>Anthura gracilis</i> (Montagu, 1808)	P	P	P	P	P		P	P	A
[New NIS] <i>Apanthura addui</i> Wägele, 1981							S		A
<i>Apanthura corsica</i> Amar, 1953		P		P	P		P		A
[NIS] <i>Apanthura sandalensis</i> Stebbing, 1900							P	P	RS
<i>Apanthura tyrrhenica</i> Wägele, 1980		P							A
<i>Apanthuroides mediterranea</i> (Negoescu, 1981)								P	A
<i>Apanthuroides spathulicauda</i> (Wägele, 1981)	P	P					P	P	A
<i>Cyathura carinata</i> (Kröyer, 1847)	P		P		P	P	P	P	A
<i>Haliophasma alaticauda</i> Amar, 1966	P	P							A
<i>Haliophasma caprii</i> Wägele, 1981		P							A
<i>Indanthura larwoodi</i> (Wägele, 1981)	P						P		A
<i>Mesanthura pacoii</i> Castelló, 2017*							S		A
[NIS] <i>Mesanthura cf. romulea</i> Poore & Lew-Ton, 1986	P	P		P			P	P	A
<i>Notanthura maroccana</i> (Wägele & Platvoet, 1982)	P								A
<i>Pilosanthura fresii</i> (Wägele, 1980)		P			P		P		A
Expanthuridae									
<i>Eisothistos macrurus</i> Wägele, 1979		P					P, S		A
<i>Eisothistos pumilus</i> Wägele, 1979		P							A
<i>Heptanthura cryptobia</i> (Wägele, 1979)	P	P					S		A
Hyssuridae									
<i>Hyssura ligurica</i> Wägele, 1981		P							A
<i>Hyssura profunda</i> Barnard, 1925		P							A
<i>Kupellonura flexibilis</i> (Pasternak, 1982)	P							P	A
<i>Kupellonura mediterranea</i> Barnard, 1925	P	P		P					A
<i>Kupellonura serratelson</i> Wägele, 1981		P					S		A
<i>Neohyssura spinicauda</i> (Walker, 1901)	P	P						P	A
Leptanthuridae									
<i>Leptanthura apalpata</i> Wägele, 1981		P			P			P	A
<i>Leptanthura muelleri</i> Negoescu, 1980								P	A
<i>Leptanthura sculpta</i> Pasternak, 1982		P							A

continued

Table 2 continued

SPECIES	MEDITERRANEAN SUBREGIONS								SUEZ CANAL/ RED SEA
	1	2	3	4	5	6	7	8	9
Paranthuridae									
<i>Paranthura costana</i> Bate & Westwood, 1866	P	P			P		P	P	A
[NIS] <i>Paranthura japonica</i> Richardson, 1909	P	P	P	P	P			P	A
<i>Paranthura nigropunctata</i> (Lucas, 1846)	P	P	P	P	P		P	P	A
CIROLANOIDEA									
Cirolanidae									
<i>Atarbolana beirutensis</i> Castelló, 2017							S		A
<i>Cirolana bitari</i> Castelló, 2017							S		A
<i>Cirolana bovina</i> Barnard, 1940							P		SC, RS
<i>Cirolana cranchii</i> Leach, 1818	P	P			P		P, S	P	A
<i>Cirolana ferruginosa</i> Risso, 1826		P							A
[New NIS] <i>Cirolana manorae</i> Bruce & Javed, 1987							S		SC
<i>Cirolana parva</i> Hansen, 1890								P**	SC**, RS**
<i>Cirolana zibrowiusi</i> Castelló, 2017							S		A
<i>Conilera cylindracea</i> (Montagu, 1804)	P	P	P						A
<i>Eurydice affinis</i> Hansen, 1905	P	P	P	P	P		P	P	A
<i>Eurydice czerniavsky</i> Bacescu, 1948		P			P				A
<i>Eurydice dollfusi</i> Monod, 1930		P	P		P	P		P	A
<i>Eurydice grimaldii</i> Dollfus, 1888		P		P (cf.)					A
<i>Eurydice inermis</i> Hansen, 1890	P	P		P	P				RS
<i>Eurydice longispina</i> Jones, 1969					P				A
<i>Eurydice pontica</i> (Czerniavsky, 1868)		P			P	P			A
<i>Eurydice pulchra</i> Leach, 1815					P	P	P	P	SC, RS
<i>Eurydice racovitzae</i> Bacescu, 1949						P			A
<i>Eurydice rotundicauda</i> Norman, 1906					P				A
<i>Eurydice spinigera</i> Hansen, 1890	P	P	P	P	P	P	P	P	A
<i>Eurydice truncata</i> (Norman, 1868)	P	P		P	P		P	P	A
<i>Eurydice valkanovi</i> Bacescu, 1949						P			A
[New NIS] <i>Metacirolana rotunda</i> (Bruce & Jones, 1978)							S		RS
<i>Natanolana borealis</i> (Lilljeborg, 1851)	P	P	P	P			P		A
<i>Natanolana caeca</i> (Dollfus, 1903)		P							A
<i>Natanolana gallica</i> (Hansen, 1905)	P								A
<i>Natanolana hirtipes</i> (Milne-Edwards, 1840)					P				A
<i>Natanolana neglecta</i> (Hansen, 1890)	P	P	P	P	P		P		A
<i>Saharolana seurati</i> Monod, 1930								P	A
LIMNORIOIDEA									
LIMNORIOIDEA									
Limnoriidae									
<i>Limnoria carinata</i> Menzies & Becker, 1957		P							A
<i>Limnoria lignorum</i> (Rathke, 1799)	P**	P**	P**	P**	P**		P**	P**	SC
<i>Limnoria mazzellae</i> Cookson & Lorenti, 2001	P	P	P		P			P	A
<i>Limnoria quadripunctata</i> Holthuis, 1949			P					P	A
<i>Limnoria tripunctata</i> Menzies, 1951	P	P			P		P	P	A
<i>Limnoria tuberculata</i> Sowinsky, 1884		P			P	P			A
<i>Limnoria turae</i> Castelló, 2011*	P								A
MICROCERBERIDEA									
Microcerberidae									
<i>Coxicerberus adriaticus</i> (Karaman, 1955)			P						A
<i>Coxicerberus arenicola</i> (Chappuis & Delamare-Deboutteville, 1952)		P							A

continued

Table 2 continued

SPECIES	MEDITERRANEAN SUBREGIONS								SUEZ CANAL/ RED SEA
	1	2	3	4	5	6	7	8	9
<i>Coxicerberus remanei</i> (Chappuis & Delamare-Deboutteville, 1952)	P	P	P				P	P	A
<i>Microcerberus remyi</i> Chappuis, 1953	P	P							A
SPHAEROMATIDEA									
SPHAEROMATOIDEA									
Sphaeromatidae									
<i>Campecopea hanseni</i> (Racovitza, 1908)		P							A
<i>Campecopea hirsuta</i> (Montagu, 1804)	P	P					P		A
<i>Campecopea ischiana</i> (Verhoeff, 1943)		P							A
<i>Cymodoce emarginata</i> Leach, 1818	P	P			P		P		A
[New NIS] <i>Cymodoce erythraea</i> Nobili, 1906		P			P	P			RS
[NIS] <i>Cymodoce fuscina</i> Schotte & Kensley, 2005					P (aff.)		S		A
<i>Cymodoce hanseni</i> Dumay, 1972	P	P			P		P		A
<i>Cymodoce pilosa</i> Milne-Edwards, 1840	P	P	P		P		S	P	RS
<i>Cymodoce rubropunctata</i> (Grube, 1864)	P	P	P					P	A
<i>Cymodoce spinosa</i> (Risso, 1816)	P	P	P	P	P		P		SC, RS
<i>Cymodoce tattersalli</i> Torelli, 1929	P	P	P		P	P			A
<i>Cymodoce truncata</i> Leach, 1814	P	P	P	P	P		P	P	SC, RS
<i>Cymodoce tuberculata</i> Costa, 1851	P	P			P		P		A
<i>Dynamene bicolor</i> (Rathke, 1837)	P	P	P	P	P	P	P, S	P	A
<i>Dynamene bidentata</i> (Adams, 1800)	P**	P**			P**	P**	P**	P**	SC, RS
<i>Dynamene bifida</i> Torelli, 1930	P	P		P	P		P		A
<i>Dynamene edwardsi</i> (Lucas, 1849)	P	P	P		P		P	P	SC, RS
<i>Dynamene magnitorata</i> Holdich, 1968	P	P			P		P, S	P	A
<i>Dynamene tubicauda</i> Holdich, 1968		P		P				P	A
[New NIS] <i>Dynamenella savignii</i> (Milne-Edwards, 1840)							P		RS
<i>Ischyromene bicarinata</i> Harrison, 1981							P, S		A
<i>Ischyromene lacazei</i> Racovitza, 1908	P	P			P		P		A
<i>Lekanesphaera ephippium</i> (Costa, 1882)		P							A
<i>Lekanesphaera hookeri</i> (Leach, 1814)	P	P	P	P	P	P	P	P	A
<i>Lekanesphaera levii</i> (Argano & Ponticelli, 1981)	P	P							A
<i>Lekanesphaera marginata</i> (Milne-Edwards, 1840)		P	P						A
<i>Lekanesphaera monodi</i> (Arcangeli, 1934)	P	P	P		P	P	P	P	A
<i>Lekanesphaera rugicauda</i> (Leach, 1814)	P						P		A
<i>Lekanesphaera weilli</i> (Elkaïm, 1967)	P	P							A
[NIS] <i>Paracerceis sculpta</i> (Holmes, 1904)	P	P	P	P	P		P, S	P	SC
[NIS] <i>Paradella diana</i> (Menzies, 1962)	P	P			P		P, S	P	A
[New NIS] <i>Pseudocerceis cf. seleneides</i> Messana, 1988							S		A
<i>Sphaeroma boryi</i> Guérin-Méneville, 1832								P	A
<i>Sphaeroma emarginatum</i> Grube, 1864			P						A
<i>Sphaeroma serratum</i> (Fabricius, 1787)	P	P	P	P	P	P	P	P	SC, RS
<i>Sphaeroma venustissimum</i> Monod, 1931		P							A
[NIS] <i>Sphaeroma walkeri</i> Stebbing, 1905	P	P			P	P	P, S	P	SC, RS
VALVIFERA									
Arcturidae									
<i>Arcturina rhomboidalis</i> Koehler, 1911	P								A
<i>Arcturinella banyulensis</i> Poisson & Maury, 1931	P								A
<i>Arcturinella deltensis</i> Castelló, Molina, Constenla & Soler, 2016*	P								A
<i>Arcturoopsis giardi</i> (Bonnier, 1896)		P							A

continued

Table 2 continued

SPECIES	MEDITERRANEAN SUBREGIONS								SUEZ CANAL/ RED SEA
	1	2	3	4	5	6	7	8	9
<i>Astacilla axeli</i> Castelló, 1992	P								A
<i>Astacilla bonnierii</i> Stephensen, 1915	P								A
<i>Astacilla carlosoteroi</i> (Reboreda, Wägele & Garmendia, 1994)	P								A
<i>Astacilla cingulata</i> Castelló & Carballo, 2000	P							P	A
<i>Astacilla damnoniensis</i> (Stebbing, 1874)	P								A
<i>Astacilla depressa</i> Castelló & Poore, 1998	P							P	A
<i>Astacilla dilatata</i> Sars, 1882	P	P						P	A
<i>Astacilla gorgonophila</i> Monod, 1925	P	P						P	A
<i>Astacilla laevis</i> Castelló & Poore, 1998	P								A
<i>Astacilla longicornis</i> (Sowerby, 1806)	P		P		P		P	P	A
<i>Astacilla mediterranea</i> Koehler, 1911	P	P					P		A
<i>Astacilla monodi</i> Tattersall, 1925								P	A
<i>Astacilla paucisaetosa</i> Castelló & Carballo, 2000	P								A
Chaetiliidae									
<i>Parachiridotea mediterranea</i> Roman, 1991	P								A
<i>Proidotea haughi</i> Racovitza & Sevastos, 1910*****						P			A
<i>Saduria entomon</i> (Linnaeus, 1758)						P			A
Holognathidae									
<i>Cleantis prismatica</i> (Risso, 1826)	P	P	P	P	P		P	P	A
Idoteidae									
<i>Idotea balthica</i> (Pallas, 1772)	P	P	P		P	P	P	P	RS
<i>Idotea chelipes</i> (Pallas, 1766)	P	P	P					P	A
<i>Idotea emarginata</i> (Fabricius, 1793)	P							P	A
<i>Idotea granulosa</i> Rathke, 1843		P						P	A
<i>Idotea linearis</i> (Linnaeus, 1766)	P	P						P	A
<i>Idotea metallica</i> Bosc, 1802	P	P	P	P	P	P	P	P	RS
<i>Idotea neglecta</i> Sars, 1897	P								A
<i>Idotea ostroumovi</i> Sowinsky, 1895						P			A
<i>Idotea pelagica</i> Leach, 1815	P					P			A
<i>Stenosoma aaseni</i> Artüz & Kubanç, 2015					P				A
<i>Stenosoma acuminatum</i> Leach, 1814	P	P	P	P				P	A
<i>Stenosoma albertoi</i> (Castellanos & Junoy, 2005)	P								A
<i>Stenosoma appendiculatum</i> (Risso, 1826)	P	P	P	P	P			P	A
<i>Stenosoma bellonae</i> (Daguerre de Hureaux, 1968)	P								A
<i>Stenosoma capito</i> (Rathke, 1837)	P	P	P	P	P	P	P	P	A
<i>Stenosoma carinata</i> (Lucas, 1814)								P	A
<i>Stenosoma inonuei</i> Artüz & Kubanç, 2015					P				A
<i>Stenosoma lancifer</i> Miers, 1881	P**	P	P		P			P	A
<i>Stenosoma mediterranea</i> (Rezig, 1989)	P							P	A
<i>Stenosoma nadejda</i> (Rezig, 1989)	P							P	A
<i>Stenosoma raquelae</i> (Hedo & Junoy, 1999)	P								A
<i>Stenosoma spinosum</i> (Amar, 1957)		P	P					P	A
<i>Stenosoma stephensei</i> Santos & Xavier, 2011	P							P	A
<i>Stenosoma teissieri</i> (Prunus & Pantoustier, 1976)								P	A
[New NIS] <i>Synidotea variegata</i> Collinge, 1917							P		SC, RS
<i>Synischia hectica</i> (Pallas, 1772)	P	P	P		P	P	P	P	A

Table 3. Species shared among the areas considered (Epicaridea, Oniscidea, and brackish water Aselloidea excluded). *doubtful record; **not in WoRMS (last accessed: 20 November 2019).

	Mediterranean Sea [MS]	Suez Canal [SC]	Red Sea [RS]	Gulf of Aden [GA]	Indian Ocean [IO]
Number of species in the region	295	25	72	16	860
Number of shared species	34: 15SC, 23RS, 1GA, 19IO	22: 15MS, 17RS, 1GA, 9IO	48: 23MS, 17SC, 6GA, 30IO	9: 1MS, 1SC, 6RS, 6IO	41: 19MS, 9SC, 30RS, 6GA
	<i>Angeliera phreaticola</i> [IO] <i>Anilocera leptosoma</i> [RS] <i>Apanthura addui</i> [IO] <i>Apanthura sandalensis</i> [RS, GA, IO] <i>Carpas crosslandi</i> [RS, IO] <i>Ceratohoa imbricata</i> [RS, IO] <i>Ceratohoa oxyrrynchaena</i> [RS] <i>Cirolana bovina</i> [SC, RS, IO] <i>Cirolana cranchii</i> [IO] <i>Cirolana manorae</i> [SC, IO] <i>Cirolana parva*</i> [SC, RS] <i>Cymodoce erythraea</i> [RS] <i>Cymodoce fuscina</i> [IO] <i>Cymodoce pilosa</i> [RS] <i>Cymodoce spinosa</i> [SC, RS] <i>Cymodoce truncata</i> [SC, RS] <i>Dynamene bidentata*</i> [SC, RS] <i>Dynamene edwardsi</i> [SC, RS] <i>Dynamene savignii</i> [RS, IO] <i>Elthusa nanoides</i> [RS, IO] <i>Eurydice pulchra</i> [SC, RS, IO] <i>Idotea balthica</i> [RS] <i>Joeropsis rathbunae</i> [MS] <i>Limnoria lignorum*</i> [MS] <i>Nerocila bivittata</i> [MS] <i>Paracercis sculpta</i> [MS, IO] <i>Paradella heptaphymata</i> [RS] <i>Rocinela orientalis</i> [RS, GA, IO] <i>Sphaeroma serratum</i> [MS, RS, IO] <i>Eurydice inermis</i> [RS] <i>Eurydice pulchra</i> [SC, RS, IO] <i>Idotea balthica</i> [RS] <i>Joeropsis rathbunae</i> [SC, IO] <i>Limnoria lignorum*</i> [SC] <i>Metacirrolana rotunda</i> [RS, IO] <i>Nerocila bivittata</i> [SC] <i>Paracercis sculpta</i> [SC, IO] <i>Pleurocope dasyura</i> [IO] <i>Pseudocercis cf. seleneides</i> [IO] <i>Sphaeroma serratum</i> [SC, RS, IO] <i>Sphaeroma walkeri</i> [SC, RS, IO] <i>Syndotea variegata</i> [SC, RS]	<i>Carpas stylodactylus</i> [RS] <i>Cirolana anadema**</i> [RS] <i>Cirolana bovina</i> [MS, RS, IO] <i>Cirolana manorae</i> [MS, IO] <i>Cirolana parva*</i> [MS, RS] <i>Cirolana theleceps</i> [RS, IO] <i>Cymodoce spinosa</i> [MS, RS] <i>Cymodoce truncata</i> [MS, RS] <i>Cymothoa exigua</i> [RS] <i>Dynamene bidentata*</i> [MS, RS] <i>Dynamene edwardsi</i> [MS, RS] <i>Eurydice pulchra</i> [MS, RS, IO] <i>Gnathia rhinobatis**</i> [RS] <i>Joeropsis rathbunae</i> [MS] <i>Limnoria lignorum*</i> [MS] <i>Nerocila bivittata</i> [MS] <i>Paracercis sculpta</i> [MS, IO] <i>Paradella heptaphymata</i> [RS] <i>Rocinela orientalis</i> [RS, GA, IO] <i>Sphaeroma walkeri</i> [MS, RS, IO] <i>Syndotea variegata</i> [MS, RS, IO]	<i>Aegiochus dollfusii</i> [IO] <i>Amakusanthura motasi</i> [GA] <i>Anilocera leptosoma</i> [MS, IO] <i>Apanthura sandalensis</i> [MS, GA, IO] <i>Argathona macronema</i> [IO] <i>Carpas algicola</i> [IO] <i>Carpas crosslandi</i> [MS, IO] <i>Carpas stylodactylus</i> [SC] <i>Ceratohoa guttata</i> [IO] <i>Ceratohoa imbricata</i> [MS, IO] <i>Ceratohoa oxyrrynchaena</i> [MS] <i>Cilicaca latreillei</i> [IO] <i>Cirolana anadema**</i> [SC] <i>Cirolana bovina</i> [MS, SC, IO] <i>Cirolana corrugis</i> [IO] <i>Cirolana parva*</i> [MS, SC] <i>Cirolana theleceps</i> [SC, IO] <i>Cymodoce erythraea</i> [MS] <i>Cymodoce pilosa</i> [MS] <i>Cymodoce spinosa</i> [MS, SC] <i>Cymodoce truncata</i> [MS, SC] <i>Cymothoa eremita</i> [GA, IO] <i>Cymothoa exigua</i> [SC] <i>Dynamene bidentata*</i> [MS, SC] <i>Dynamene edwardsi</i> [MS, SC] <i>Dynamenella savignii</i> [MS, IO] <i>Elthusa nanoides</i> [MS, IO] <i>Eurydice inermis</i> [MS] <i>Eurydice pulchra</i> [MS, SC, IO] <i>Excirrolana orientalis</i> [IO] <i>Gnathia rhinobatis**</i> [SC] <i>Hansenium chiltoni</i> [IO] <i>Idotea balthica</i> [MS] <i>Idotea metallica</i> [MS, IO]	<i>Amakusanthura motasi</i> [RS] <i>Apanthura sandalensis</i> [MS, RS, IO] <i>Arcturinoidea gibbosus</i> [IO] <i>Caenanthura indica</i> [IO] <i>Cymothoa eremita</i> [RS, IO] <i>Haliophasma adinae</i> [IO] <i>Leptanthura thalassae</i> [RS] <i>Rocinela orientalis</i> [SC, RS, IO] <i>Sphaeroma granti</i> [RS]	<i>Aegiochus dollfusii</i> [RS] <i>Angeliera phreaticola</i> [MS] <i>Anilocera leptosoma</i> [RS] <i>Apanthura addui</i> [MS] <i>Apanthura sandalensis</i> [MS, RS, GA] <i>Arcturinoidea gibbosus</i> [GA] <i>Argathona macronema</i> [RS] <i>Carpas cf. algicola</i> [RS] <i>Carpas crosslandi</i> [MS, RS] <i>Caenanthura indica</i> [GA] <i>Ceratohoa guttata</i> [RS] <i>Ceratohoa imbricata</i> [MS, RS] <i>Cilicaca latreillei</i> [RS] <i>Cirolana bovina</i> [MS, SC, RS] <i>Cirolana corrugis</i> [RS] <i>Cirolana cranchii</i> [MS] <i>Cirolana manorae</i> [MS, SC] <i>Cirolana theleceps</i> [SC, RS] <i>Cymodoce fuscina</i> [MS] <i>Cymothoa eremita</i> [RS, GA] <i>Dynamenella savignii</i> [MS, RS] <i>Elthusa nanoides</i> [MS, RS] <i>Eurydice pulchra</i> [MS, SC, RS] <i>Excirrolana orientalis</i> [RS] <i>Haliophasma adinae</i> [GA] <i>Hansenium chiltoni</i> [RS] <i>Idotea metallica</i> [MS, RS] <i>Lanocira latifrons</i> [RS] <i>Lanocira zeylanica</i> [RS] <i>Machatrium monodi</i> [RS] <i>Metacirrolana rotunda</i> [MS, RS] <i>Mothocya melanosticta</i> [RS] <i>Nerocila sigani</i> [RS] <i>Paracercis sculpta</i> [MS, SC]

continued

Table 3 continued

	Mediterranean Sea [MS]	Suez Canal [SC]	Red Sea [RS]	Gulf of Aden [GA]	Indian Ocean [IO]
Species shared among the areas considered (species in alphabetical order)			<i>Lanocira latifrons</i> [IO] <i>Lanocira zeylanica</i> [IO] <i>Leptanthura thalassae</i> [GA] <i>Machatrium monodi</i> [IO] <i>Metacirrolana rotunda</i> [MS, IO] <i>Mothocya melanosticta</i> [IO] <i>Nerocila sigani</i> [IO] <i>Paracilicæa mossambica</i> [IO] <i>Paradella heptaphymata</i> [SC] <i>Rocinela orientalis</i> [SC, GA, IO] <i>Sphaeroma granti</i> [GA] <i>Sphaeroma serratum</i> [MS, SC, IO] <i>Sphaeroma walkeri</i> [MS, SC, IO] <i>Synidotea variegata</i> [MS, SC, IO]		<i>Paracilicæa mossambica</i> [RS] <i>Pleurocope dasyura</i> [MS] <i>Pseudocercis cf. selenides</i> [MS] <i>Rocinela orientalis</i> [SC, RS, GA] <i>Sphaeroma serratum</i> [MS, SC, RS] <i>Sphaeroma walkeri</i> [MS, SC, RS] <i>Synidotea variegata</i> [SC, RS]

Table 4. Autoecology and global distribution of the species present in the Suez Canal and nearby areas (the species recorded in the Suez Canal not extended to other areas [*Amilocra meridionalis*, *Cyathura francispori*, and *Nerocila thresherorum*] are not included). Anti_L: anti-Lessepsian, NIS: non-indigenous species, *doubtful record; **not in WoRMS (last accessed: 20 November 2019). Sources consulted: Borja *et al.*, 2000; Castelló, 2011; Cookson, 1991; El-Komi *et al.*, 1998; Geldiay & Kocatas, 1972; Holdich, 1970; Jacobs, 1987; Martínez-Laiz *et al.*, 2018; Müller, 1993; Vieira *et al.*, 2016; WoRMS Editorial Board, 2019.

Species (in alphabetical order)	Habitat / Feeding type	Means of dispersion	Bathymetric and ecological characteristics	Westernmost distribution	Easternmost distribution (SC considered more eastern than the Mediterranean [subr. 7] for analysis purposes)	Considered as (Anti_L, NIS)
SPECIES REPORTED FROM BOTH THE MEDITERRANEAN SEA AND THE SUEZ CANAL						
<i>Cirolana manorae</i> <i>Joeropsis rathbunae</i>	Scavenger, predator Intertidal	Natural spread, vessel hulls Vessel hulls	Shallow 0-36 m	Mediterranean [7] North West Atlantic	Indian Ocean (Pakistan) Suez Canal	NIS NIS
<i>Limnoria lignorum</i> *	Mainly untreated timbers, xylophagous	Vessel hulls, rafting on wood debris	0-20 m	Northern hemisphere (*doubtful Mediterranean records)	Northern hemisphere (*doubtful Mediterranean records)	Not predictable due to the probable invalidity of Mediterranean records (Castelló, 2011; Cookson, 1991)
<i>Nerocila bivittata</i>	Fish host, parasitic	By host	Depth range according to host	North East Atlantic	Suez Canal	Anti_L

continued

Table 4 continued

Species (in alphabetical order)	Habitat / Feeding type	Means of dispersion	Bathymetric and ecological characteristics	Westernmost distribution	Easternmost distribution (SC considered more eastern than the Mediterranean [subr. 7] for analysis purposes)	Considered as (Anti_L, NIS)
<i>Paracerceis sculpta</i>	Algae; fouling substrates; floating structures (Martínez- Láiz <i>et al.</i> , 2018)	Natural spread, vessel hulls	Shallow. Tolerant to disturbance (Borja <i>et al.</i> , 2000)	North West Atlantic	North East Pacific	NIS
SPECIES REPORTED FROM BOTH THE MEDITERRANEAN SEA, THE SUEZ CANAL, AND THE RED SEA / GULF OF ADEN						
<i>Cirolana bovina</i>	Scavenger, predator	Natural spread, vessel hulls	Intertidal	South East Atlantic	Indian Ocean (India)	NIS
<i>Cirolana parva</i> *	Scavenger, predator	Natural spread, vessel hulls	Shallow	Gulf of Mexico, Caribbean Sea	Red Sea (*doubtful records)	Not predictable due to the probable invalidity of Mediterranean, Suez Canal, and Red Sea records (Bruce, in WoRMS Editorial Board, 2019)
<i>Cymodoce spinosa</i>	Algae; sponge (Geldiay & Kocataş, 1972)	Natural spread, vessel hulls	Shallow (0-1 m). Very sensitive to disturbance (Borja <i>et al.</i> , 2000)	North East Atlantic	Red Sea	Anti_L
<i>Cymodoce truncata</i>	Photophile and sciaphile algae, and <i>Posidonia</i>	Natural spread, vessel hulls	0-25 m. Very sensitive to disturbance (Borja <i>et al.</i> , 2000)	North East Atlantic	Red Sea	Anti_L
<i>Dynamene bidentata</i> *	Mid- to lower littoral algae, and also in rock pools in the upper littoral zone; also in barnacles (Vieira <i>et al.</i> , 2016)	Natural spread, vessel hulls	Shallow. Indifferent to disturbance (Borja <i>et al.</i> , 2000)	North East Atlantic (*doubtful Mediterranean records)	Red Sea	Not predictable due to the probable invalidity of Mediterranean records (Holdich, 1970; Vieira <i>et al.</i> , 2016)
<i>Dynamene edwardsi</i>	Algae; amongst mussels and tube worm colonies and barnacle tests; associated with encrusting matter on solid surfaces in some harbors and canals; in empty <i>Chthamalus</i> (Vieira <i>et al.</i> , 2016)	Natural spread, vessel hulls	0-10 m. Indifferent to disturbance (Borja <i>et al.</i> , 2000)	North East Atlantic	Red Sea	Anti_L
<i>Eurydice pulchra</i>	Intertidal	Natural spread, vessel hulls	Estuarine	North East Atlantic	Red Sea	Anti_L

continued

Table 4 continued

Species (in alphabetical order)	Habitat / Feeding type	Means of dispersion	Bathymetric and ecological characteristics	Westernmost distribution	Easternmost distribution (SC considered more eastern than the Mediterranean [subr. 7] for analysis purposes)	Considered as (Anti_L, NIS)
<i>Sphaeroma serratum</i>	Intertidal; under stones	Natural spread, vessel hulls	0-1 m. Eurihaline. Tolerant to disturbance (Borja <i>et al.</i> , 2000)	North East Atlantic	W Australia	Anti_L
<i>Sphaeroma walkeri</i>	Intertidal; crevices of rock and wood or in empty shells; outside wall of ships (Jacobs, 1987)	Natural spread, vessel hulls	Estuarine	Worldwide	Worldwide	NIS
<i>Synidotea variegata</i>	Shallow, infratidal	Natural spread, vessel hulls, rafting on floating objects	1-20 m	South Africa	Indochina	NIS
SPECIES REPORTED FROM BOTH THE SUEZ CANAL AND THE RED SEA / GULF OF ADEN						
<i>Carpas sylvodactylus</i>	Intertidal and shallow rockpools; algae; dead corals; under stones (Müller, 1993)	Natural spread, vessel hulls	Shallow	North West Atlantic	South East Pacific	Candidate for future possible introduction in the Mediterranean
<i>Cirolana anadema</i> **	Algae	Natural spread, vessel hulls	2-3 m	Suez Canal	Red Sea	Candidate for future possible introduction in the Mediterranean
<i>Cirolana theleceps</i>	Scavenger, predator	Natural spread, vessel hulls	Intertidal	South Africa	Red Sea	Candidate for future possible introduction in the Mediterranean
<i>Cymothoa exigua</i>	Fish host, parasitic	By host	Depth range according to host	Galapagos Islands, Eastern Pacific	Red Sea (origin: alien [WoRMS Editorial Board, 2019])	Candidate for future possible introduction in the Mediterranean
<i>Gnathia rhinobatis</i> **	Praniza on fish host, parasitic	By host	Depth range according to host	Suez Canal	Red Sea	Candidate for future possible introduction in the Mediterranean
<i>Paradella heptaphymata</i>	Bulk community of fouling (EI- Komi <i>et al.</i> , 1998)	Natural spread, vessel hulls	Shallow (on buoys (EI- Komi <i>et al.</i> , 1998))	Suez Canal	Red Sea	Candidate for future possible introduction in the Mediterranean
<i>Rocinela orientalis</i>	Fish host, parasitic	By host	Depth range according to host (22-500 m)	South Africa	Eastern Australia	Candidate for future possible introduction in the Mediterranean

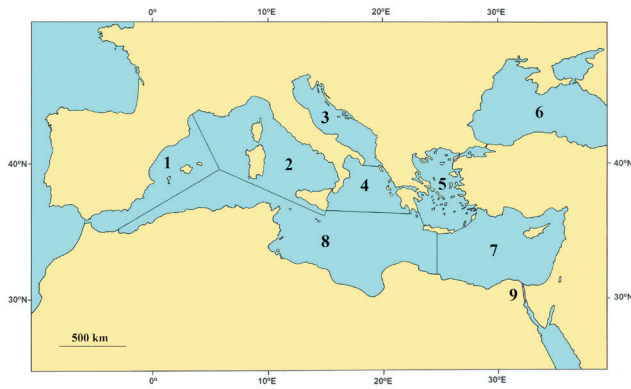


Fig. 2: Biogeographical subregions distinguished here for comparison purposes: Subregion 1. Western Mediterranean: Iberian Peninsula (Strait of Gibraltar, Alboran Sea, and Mediterranean Sea), eastern archipelagos of the Iberian Peninsula, and Roussillon (France); Subregion 2. Western coasts of Italy and French Provence: Ligurian and Tyrrhenian Seas; Subregion 3. Eastern coasts of Italy: Adriatic Sea; Subregion 4. Eastern coasts of Italy: Ionian Sea; Subregion 5. Aegean and Marmara Seas; Subregion 6. Black Sea; Subregion 7. Levant Sea: Southern Turkey, Cyprus, Syria, Lebanon, Israel, and Egypt; Subregion 8. Algeria, Tunisia, Libya, and Malta; Subregion 9. Suez Canal/Red Sea.

The list of 165 species for the entire Mediterranean (no subdivisions) by Van der Land (2001) was considered as the starting point for constructing Table 2. The systematic criteria of Martin & Davis (2001) and Brandt & Poore (2003) were used for the assignment to supra-generic categories. The World Register of Marine Species (WoRMS Editorial Board, 2019) was used to update data from the literature that was consulted. The species considered *taxa inquirenda* (uncertain validity) and *nomina dubia* (uncertain taxonomic significance) were included in Table 2 and Table S2 (indicated with three [***] and four [****] asterisks respectively). The subspecies were not considered. For example, for *Jaera nordmanni*, data on its distribution at species level were compiled using data from different subspecies. A single exception can be seen in Table 2: the Mediterranean distribution of *Joeropsis brevicornis* refers only to the subspecies *littoralis*, while the subspecies *brevicornis* is restricted to the North Atlantic. The Oniscidea are not included in Table 2 because they are considered terrestrial in the WoRMS database (WoRMS Editorial Board, 2019), although many species of several genera (e.g., *Ligia*, *Halophiloscia*, and *Tylos*) are common in the supralittoral zone or interstitial in sandy beaches. Species that have not been cited since their original description, of which the holotype is not known to exist, are included in Table 2 if their status in the WoRMS database is “accepted” (e.g., *Arcturinaella banyulensis*, *Cirolana ferruginosa*). Table S2 provides a list of species reported from the Indian Ocean, Gulf of Aden, Red Sea, and Suez Canal, with an indication of the Mediterranean subregions in which they also occur. For each subregion, the sources concerning the species included in Table 2 and Table S2 are given in Table S3, and the publications that are referred to are mainly

those with the most inclusive lists. The term “Lessepsian” (L) is applied, according to Por (1978), to species that crossed the Suez Canal by their own means and reached the Mediterranean Sea. As “non-indigenous species” (NIS), all authors refer to species introduced into the Mediterranean, regardless of the route and means of entry. Therefore, all Lessepsian species can be considered non-indigenous but not *vice versa*. Por (1978) also used the term “anti-Lessepsian” (Anti_L) to refer to species that follow a path opposite to Lessepsians. From a biogeographical point of view, “pre-Lessepsian” (PL) species are those that shared the Mediterranean Sea and the Red Sea before the opening of the Suez Canal, and relict species (R) are those that existed in the Tethys before the separation of the Mediterranean Sea and the Indian Ocean. For biogeographic considerations, the area of analysis that is considered is the Mediterranean Sea. Therefore, non-exclusive terms such as NIS refer to this area. Furthermore, terms such as Anti_L may be equivalent to NIS for the Red Sea.

Results

Taxonomy

A total of 28 species were found, included in 20 genera, 9 families, and 3 suborders. Taxonomic descriptions of four new species from this collection (*Mesanthura pacoi*, *Atarbolana beirutensis*, *Cirolana bitari*, and *Cirolana zibrowiusi*) have already been published by Castelló (2017b). Here, brief diagnoses and illustrations (Figs. 3-6) with useful morphological details for identification are included.

The origin, collecting data and material examined are detailed in Table 1 and Table S1.

Order Isopoda Latreille, 1817

Suborder Asellota Latreille, 1802

Superfamily Gnathostenetroidoidea Kussakin, 1967

Family Gnathostenetroididae Kussakin, 1967

Gnathostenetroides laodicense Amar, 1957

Distribution in this study: Stations 5, 11, 12, 13, 17, 30.

General distribution: Mediterranean Sea (subregions 2 and 7).

Remarks: The male of sample 30.1 has no mandibular process; this absence is interpreted as a juvenile feature. Other differences with regards to the adult male in sample 12.9 are: Antenna 1 has fewer articles and Pleopod 1 has 8 + 8 setae (13 + 13 in male 12.9). *Gnathostenetroides laodicense* is the only species of this genus in the Mediterranean Sea.

Superfamily Janirooidea Sars, 1897

Family Janiridae Sars, 1897

Carpas stebbingi (Monod, 1933)

Distribution in this study: Stations 7, 11, 12, 13, 14, 17, 23.

General distribution: Mediterranean Sea (subregions 1, 2, 3, 5 and 7).

Remarks: Three species of this genus have been reported from the Mediterranean Sea: *C. crosslandi* (Steb-

bing, 1910), *C. galloprovincialis* (Amar, 1950), and *C. stebbingi* (Monod, 1933).

Family Joeropsididae Nordenstam, 1933

Joeropsis legrandi Juchault, 1962

Distribution in this study: Stations 5, 12, 25.

General distribution: Mediterranean Sea (subregions 1 and 7).

Remarks: Six Mediterranean species of this genus (*J. brevicornis* Koehler, 1885 [subsp. *littoralis* Amar, 1949], *J. dollfusi* Norman, 1899, *J. legrandi* Juchault, 1962, *J. mediterranea* Amar, 1961, *J. montalentii* Fresi, 1968, and *J. rathbunae* Richardson, 1902).

Suborden Cymothoidea Leach, 1814

Superfamily Anthuroidea Leach, 1814

Family Anthuridae Leach, 1814

Apanthura addui Wägele, 1981

Distribution in this study: Stations 3, 13, 14, 17, 19, 20, 22, 25.

General distribution: Maldives Islands (Indian Ocean). The present records are the first in the Mediterranean Sea (Lebanon and Cyprus; see Table 2 and Figure 1 for details). This disjunct distribution could be a symptom of human-mediated introduction, and it may be considered a non-indigenous species (NIS), although it could also be a relict species (R).

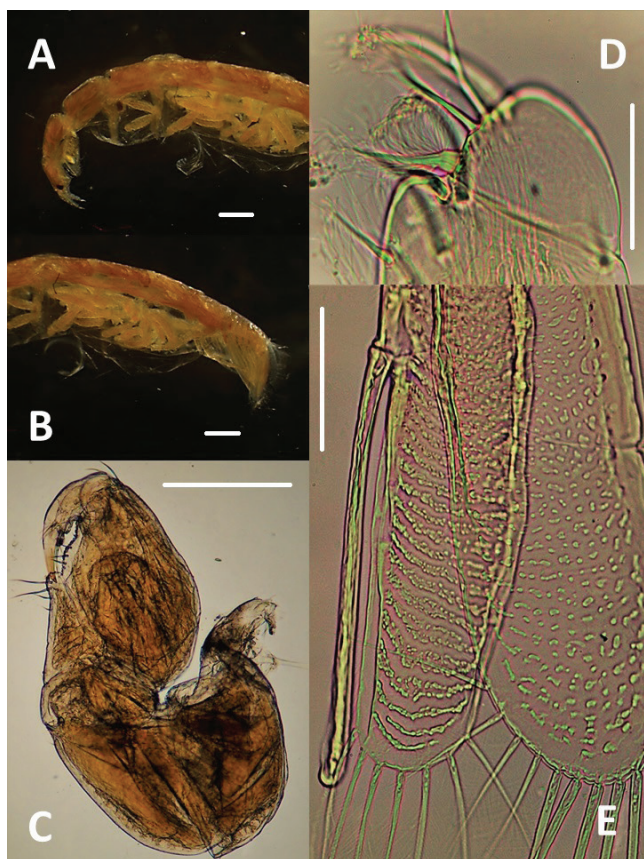


Fig. 3: *Mesanthura pacoi* Castelló, 2017. Useful morphological details for its identification. Ovigerous female, sample 7.4: A, Body, anterior section, lateral view; B, Body, posterior section, lateral view; C, Pereopod 1; Female, sample 3.1: D, Maxilliped, detail of palp apical segment: note the stout plumose seta; Male, sample 7.4: E, Pleopod 2, detail of appendix masculina. Scale bars: A, B, 1 mm; C, 0.5 mm; D, 0.035 mm; E, 0.12 mm.

Remarks: There are four species of this genus in the Mediterranean Sea (*A. addui* Wägele, 1981, *A. corsica* Amar, 1953, *A. sandalensis* Stebbing, 1900, and *A. tyrhenica* Wägele, 1980).

Mesanthura pacoi Castelló, 2017 (Fig. 3)

Distribution in this study: Stations 3, 5, 7, 10, 11, 12, 20, 21, 22, 25, 26, 27.

Brief diagnosis: Yellowish color, without chromatophores; dorsal coloring only present in the largest adults (Figs. 3A, B). Maxillipedal palp article 1 with outer margin slightly excavated, apical article with plumose seta and 3 simple setae mediolaterally and robust plumose seta basally (Fig. 3D). Pereopod 1 (Fig. 3C) palm with shallow crenulated basal step; dactylus with toothed boss at the base of the unguis. Male pleopod 2 (Fig. 3E) with appendix masculina inserted at a third of the length of the endopod, reaching beyond its end.

Remarks: The genus *Mesanthura* was cited in the Mediterranean by Lorenti *et al.* (2009) for specimens from Italy considered *Mesanthura sp.* and subsequently identified by Ulman *et al.* (2017) as *M. cf. romulea* Poore & Lew-Ton, 1986 with additional new records from the Levant area. Thus, *Mesanthura pacoi* is the second species of *Mesanthura* found in the Mediterranean Sea.

Family Expanathuridae Poore, 2001

Eisothistos macrurus Wägele, 1979

Distribution in this study: Stations 11, 12.

General distribution: Mediterranean Sea (subregions 2 and 7).

Remarks: Two species of this genus in the Mediterranean Sea (*E. macrurus* Wägele, 1979, and *E. pumilus* Wägele, 1979).

Heptanthura cryptobia (Wägele, 1979)

Distribution in this study: Station 11.

General distribution: Mediterranean Sea (subregions 1, 2 and 7).

Remarks: The specimen examined is a damaged juvenile (without cephalon and pereonite 1). All features of pereopods 2-7, pleopods, and pleotelson match the description and figures of Wägele's (1979) immature adult. Although the individual had initially been identified as *cf.* (compared favorably), there is no reason to leave the identification open. *Heptanthura cryptobia* is the only species of this genus in the Mediterranean Sea.

Family Hyssuridae Wägele, 1981

Kupellonura serritelson Wägele, 1981

Distribution in this study: Station 7.

General distribution: Bermuda Islands (North Atlantic Ocean) and Mediterranean Sea (subregions 2 and 7).

Remarks: Three species of this genus in the Mediterranean Sea (*K. flexibilis* (Pasternak, 1982), *K. mediterranea* Barnard, 1925, and *K. serritelson* Wägele, 1981).

Superfamily Cymothoidea Leach, 1814

Family Cirolanidae Dana, 1852

Atarbolana beirutensis Castelló, 2017 (Fig. 4)

Distribution in this study: Station 25.

Brief diagnosis: Body 2.4 times longer than wide (Fig. 4A, B). Apex of pleotelson truncated, with 10 robust setae (Fig. 4D). Uropodal exopod like an elongated spoon, with a concave section (Fig. 4C).



Fig. 4: *Atarbolana beirutensis* Castelló, 2017. Useful morphological details for its identification. Ovigerous female, sample 25.1: A, Body, dorsolateral view; B, Body distal section, dorsal view; C, Uropod; D, Telson, apex. Scale bars: A, 1 mm; B, 0.5 mm; C,D, 0.25 mm.

Remarks: The genus *Atarbolana* Bruce & Javed, 1987 comprises 5 species (*A. beirutensis* Castelló, 2017, *A. exoconta* Bruce & Javed, 1987, *A. setosa* Javed & Yasmeen, 1989, *A. dasycolus* Yasmeen, 2004, and *A. makranensis* Khalaji-Pirbalouty, Naderloo & Keikhosravi, 2015). *A. beirutensis* significantly expands the known distribution of the genus *Atarbolana*, the other species known from Pakistan and Iran (the Gulf of Oman).

Cirolana bitari Castelló, 2017 (Fig. 5)

Distribution in this study: Stations 7, 19, 22, 26.

Brief diagnosis: Body flat, depressed, about 3.0 times as long as wide (Figs. 5A, B). Dorsal surface of body without tubercles. Posterior margin of pereonites and pleonites without denticles or nodules (Fig. 5E). Stiff setae on pleonite 5 and pleotelson (Fig. 5F). Penes flat, well-developed (Fig. 5C). Male pleopod 2 (Fig. 5D) with appendix masculina robust, curved, surpassing length of endopod, with thin and winding apex.

Remarks: Seven species of this genus are known from the Mediterranean Sea (*C. bitari* Castelló, 2017, *C. bovina* Barnard, 1940, *C. cranchii* Leach, 1818, *C. ferruginosa* Risso, 1826, *C. manorae* Bruce & Javed, 1987, *C. parva* Hansen, 1890, and *C. zibrowiusi* Castelló, 2017). However, according to Bruce (in WoRMS Editorial Board, 2019), the Mediterranean record (Ayari & Afli, 2003; Ayari, 2004) of the species *C. parva* is a misidentification, as its distribution is restricted to the Caribbean



Fig. 5: *Cirolana bitari* Castelló, 2017. Useful morphological details for its identification. Male, sample 19.2: A, Body, lateral view; B, Body, ventrolateral view; C, Penes: note a pair, flat, well-developed; D, Pleopod 2, with appendix masculina; Female, sample 19.2: E, Pleonites 4-7; F, Pleotelson, stiff setae. Scale bars: A, B, E, 1 mm; C, D, F, 0.5 mm.

region and the Pacific coast of Panama.

Cirolana cranchii Leach, 1818

Distribution in this study: Station 1.

General distribution: North East Atlantic Ocean, South Africa, and Mediterranean Sea (subregions 1, 2, 5, 7 and 8).

Remarks: The specimen studied is an 11mm male from Cyprus. Appendix masculina of P12 slightly exceeding the endopodite, slightly curved at its distal part, and smooth, without spines on its surface.

Cirolana manorae Bruce & Javed, 1987

Distribution in this study: Station 26.

General distribution: Pakistan (Indian Ocean).

Remarks: None of the males studied had penes. There are two nodes on pleonite 5 and four nodes on the pleotelson, no dorsal setae on the pleotelson, and few lateral setae on the uropods (only in the distal half of the exopod). These characters point to *C. manorae*. However, antenna 2 reaches the end of pereonite 3, which is a character of *C. bovina*. In our opinion, *C. bovina* needs to be described again to specify whether penes are present, and antenna 2 needs to be compared with that of *C. manorae*. The present record from Lebanon is the first in the Mediterranean Sea. It can be considered a non-indigenous species (NIS), introduced by ship transport.

Cirolana zibrowiusi Castelló, 2017 (Fig. 6)

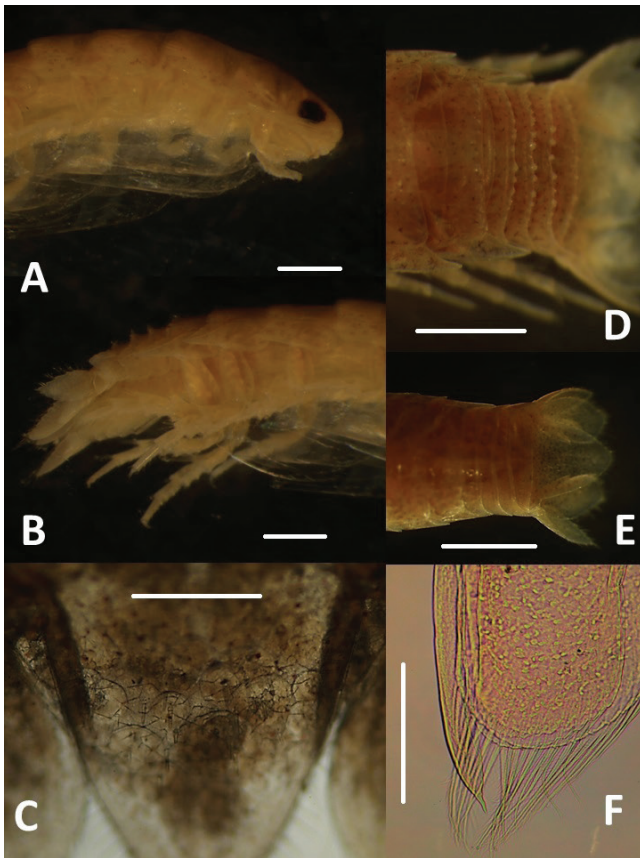


Fig. 6: *Cirolana zibrowiusi* Castelló, 2017. Useful morphological details for its identification. Ovigerous female, sample 26.3: A, Body, anterior section, lateral view; B, Body, posterior section, lateral view; Ovigerous female, sample 26.1: C, Pleotelson: note the conspicuous stiff setae; D, Pleonites 4-7; Male, sample 26.1: E, Body distal section, dorsal view; F, Pleopod 2, detail of appendix masculina. Scale bars: A, B, D, E, 1 mm; C, F, 0.5 mm.

Distribution in this study: Stations 21, 26.

Brief diagnosis: Body rounded, slightly depressed, about 3.7 times as long as wide (Figs. 6A, B). Posterior margin of pereonites 5–7 and pleonites 2–5 with denticles or nodules present (Fig. 6D) or absent (Fig. 6E). Stiff setae on pereonite 7, pleonites 2–5 and pleotelson (Figs. 6C, E). Penes flat, well-developed. Male pleopod 2 with appendix masculina robust, curved, surpassing the length of the endopod (Fig. 6F).

Metacirolana rotunda (Bruce & Jones, 1978)

Distribution in this study: Stations 3, 5, 9, 10, 12, 13, 15, 16, 17, 18, 19, 20, 22.

General distribution: East Africa (Indian Ocean) to Northern Red Sea.

Remarks: In the Cirolanidae the sex can commonly be distinguished when the appendix masculina is already present (for example, from 20 mm long in *Natatolana borealis* (Lilljeborg 1851), see Wong & Moore (1996), and from 6 mm in *Baharilana richmondi*, see Bruce & Svavarsson (2003)). Adult males and females of *Metacirolana* are morphologically similar, except for “swimming” males. These are characterized by a more elongate pleon, larger eyes, and longer antennulae and antennae (see Bruce (1986) for *M. serrata* (Bruce, 1980), with a

swimming male illustration). They also differ because males have penial processes and appendix masculina in pleopod 2, whereas females have oostegites or oostegites buds. In the case of *M. rotunda*, no specimens with appendix masculina or penial processes or vas deferens have been observed. Thus, the sex of many specimens that are considered immature remains uncertain. Juveniles (mancas) do not have pereopod 7 yet. The examination of a large series suggests that adult males are rare. Bruce & Jones (1978) and Bruce (1981) did not mention any adult males. *Metacirolana rotunda* was originally described as *Cirolana rotunda* from the gulfs of Suez and Aqaba. Other previous records were from the island of Mbudya in Tanzania. The present records from Lebanon and Cyprus are the first from the Mediterranean Sea. It can be considered a non-indigenous species (NIS), introduced by ship transport.

Family Gnathiidae Leach, 1814

Elaphognathia bacescoi (Kussakin, 1969)

Distribution in this study: Stations 5, 10, 12, 13, 14, 27, 30.

General distribution: Mediterranean Sea (subregions 6 and 7).

Remarks: The genus *Elaphognathia* currently includes 23 species, of which *E. bacescoi* is the only one occurring in the Mediterranean Sea. Here it was found for the first time outside the Black Sea.

Gnathia dentata (Sars, 1872)

Distribution in this study: Stations 3, 12.

General distribution: North East Atlantic and Mediterranean Sea (subregions 1, 7 and 8).

Remarks: Nine species of this genus occur in the Mediterranean Sea (*G. dentata* (Sars, 1872), *G. fallax* Monod, 1926, *G. illepidus* (Wagner, 1869), *G. inopinata* (Monod, 1925), *G. maxillaris* (Montagu, 1804), *G. oxyuraea* (Lilljeborg, 1855), *G. phallonajopsis* Monod, 1925, *G. venusta* Monod, 1925, and *G. vorax* (Lucas, 1849)).

Gnathia illepidus (Wagner, 1869)

Distribution in this study: Station 26.

General distribution: Mediterranean Sea (subregions 1, 2, 3, 4, 5 and 7).

Gnathia inopinata (Monod, 1925)

Distribution in this study: Station 13.

General distribution: Mediterranean Sea (subregions 1, 2, 5 and 7).

Gnathia vorax (Lucas, 1849)

Distribution in this study: Station 12.

General distribution: North East Atlantic and Mediterranean Sea (subregions 1, 2, 3, 4, 5, 6, 7 and 8).

Gnathiidae sp.

Material examined: Sample 13.4: 1 damaged female, Sample 18.2: 1 praniza, Sample 27.3: 1 praniza, Sample 31.1: 2 praniza.

Remarks: Identification impossible, possibly *Elaphognathia* or *Gnathia*. *Elaphognathia bacescoi* and *Gnathia inopinata* were found in station 13 and *Elaphognathia bacescoi*, in station 27.

Suborder Sphaeromatidea Wägele, 1989

Superfamily Sphaeromatoidea Latreille, 1825

Family Sphaeromatidae Latreille, 1825

Cymodoce fuscina Schotte & Kensley, 2005

Distribution in this study: Stations 4, 26.

General distribution: Persian Gulf (Indian Ocean) and Mediterranean Sea (subregions 5 and 7).

Remarks: Collected in Syria and Lebanon, thereby confirming its presence in the Mediterranean. Previously recorded in Greece by Ulman *et al.* (2017) as *Cymodoce aff. fuscina*. Considered a non-indigenous species (NIS). Ten species of this genus in the Mediterranean Sea (*C. emarginata* Leach, 1818, *C. erythraea* Nobili, 1906, *C. fuscina* Schotte & Kensley, 2005, *C. hanseni* Dumay, 1972, *C. pilosa* Milne-Edwards, 1840, *C. rubropunctata* (Grube, 1864), *C. spinosa* (Risso, 1816), *C. tattersalli* Torelli, 1929, *C. truncata* Leach, 1814, and *C. tuberculata* Costa, 1851).

Cymodoce pilosa Milne-Edwards, 1840

Distribution in this study: Stations 2, 3, 5, 10, 13, 29, 32.

General distribution: Mediterranean Sea (subregions 1, 2, 3, 5, 7 and 8), and Red Sea.

Cymodoce sp.

Material examined: Sample 7.4: 1 juvenile.

Dynamene bicolor (Rathke, 1837)

Distribution in this study: Stations 5, 6, 8, 13, 18, 24, 25, 28, 29, 32.

General distribution: Mediterranean Sea (subregions 1, 2, 3, 4, 5, 6, 7 and 8).

Remarks: Six species of this genus in the Mediterranean Sea (*D. bicolor* (Rathke, 1837), *D. bidentata* (Adams, 1800), *D. bifida* Torelli, 1930, *D. edwardsi* (Lucas, 1849), *D. magnitorata* Holdich, 1968, and *D. tubicauda* Holdich, 1968). According to Holdich (1970) and Vieira *et al.* (2016), the distribution of *D. bidentata* is restricted to the Atlantic Ocean and most Mediterranean records are due to misidentifications. However, there are records by Larwood (1940) and Elsayed & Dorgham (2019) for Alexandria (Egypt), by Shoukr *et al.* (1991) for the Suez Canal and by El-Komi *et al.* (1998) for the Suez Bay (Red Sea). In addition, the WoRMS database (WoRMS Editorial Board, 2019) displays an Atlanto-Mediterranean distribution for this species. These records were not discussed by Vieira *et al.* (2016). Therefore, the Mediterranean records of *D. bidentata* are treated as doubtful in Table 2, Table S2, Table 3, and Table 4.

Dynamene magnitorata Holdich, 1968

Distribution in this study: Stations 7, 20.

General distribution: North East Atlantic and Mediterranean Sea (subregions 1, 2, 5, 7 and 8).

Dynamene sp.

Material examined: Sample 24.2: 1 male juvenile.

Remarks: Unidentified juveniles. *Dynamene magnitorata* has been found in another locality in Beirut (20) and *D. bicolor* has been found in two other localities also in Beirut (24, 25).

Ischyromene bicarinata Harrison, 1981

Distribution in this study: Station 5.

General distribution: Mediterranean Sea (subregion 7).

Remarks: Two species of this genus are reported from the Mediterranean Sea (*I. bicarinata* Harrison, 1981, and

I. lacazei Racovitza, 1908).

Paracerceis sculpta (Holmes, 1904)

Distribution in this study: Station 26.

General distribution: Northeastern Pacific region (from California to Southern Baja California (Mexico), South Africa, Northwestern Pacific region (China, Hong Kong, Japan and Taiwan), Australia, Hawaii, Atlantic Ocean, the Mediterranean Sea (subregions 1, 2, 3, 4, 5, 7 and 8) and Suez Canal (subregion 9).

Remarks: *Paracerceis sculpta* is the only species of this genus found in the Mediterranean Sea. Considered a well-established non-indigenous species (NIS) (Ulman *et al.*, 2017; Martínez-Laiz *et al.*, 2018).

Paradella diana (Menzies, 1962)

Distribution in this study: Stations 7, 21, 26.

General distribution: Northeastern Pacific region (from California to Michoacán, Mexico), Atlantic Ocean (Florida, Puerto Rico, and Brazil), Indian Ocean (Pakistan), Australia (Western Australia and Queensland), Hong Kong, and the Mediterranean Sea (subregions 1, 2, 5, 7 and 8).

Remarks: *Paradella diana* is the only species of this genus present in the Mediterranean Sea. It is considered a non-indigenous species (NIS) (Ulman *et al.*, 2017; Martínez-Laiz *et al.*, 2018).

Pseudocerceis cf. seleneides Messana, 1988

Distribution in this study: Station 20.

General distribution: Indian Ocean (Somalia) and the Mediterranean Sea (subregion 7).

Remarks. Castelló (2017b) included a descriptive note on a single collected female specimen because the features of the appendages are similar to those of the males used by Messana (1988) to describe *Pseudocerceis seleneides*. As in the case of many Sphaeromatidae, the examination of an adult male is essential to identify the species. Therefore, the identification was left open (*cf.*), pending its confirmation in the future. *Pseudocerceis seleneides* is the only species of this genus found in the Mediterranean Sea (Beirut). Its disjunct distribution means that it can be considered non-indigenous (NIS), introduced by human transport. However, it could also be a relict species (R).

Sphaeroma walkeri Stebbing, 1905

Distribution in this study: Stations 5, 21, 26.

General distribution: South Africa, Indian Ocean (Mozambique, India and Sri Lanka), Australia, China, Hong Kong, Hawaii, Atlantic Ocean (California), Mediterranean Sea (subregions 1, 2, 5, 6, 7 and 8), Suez Canal and Red Sea (subregion 9). Considered a non-indigenous species (NIS) (Ulman *et al.*, 2017; Martínez-Laiz *et al.*, 2018).

Remarks: Five species of this genus are known in the Mediterranean Sea (*S. boryi* Guérin-Méneville, 1832, *S. emarginatum* Grube, 1864, *S. serratum* Fabricius, 1787, *S. venustissimum* Monod, 1931, and *S. walkeri* Stebbing, 1905).

Species richness

It is surprising that none of the species in the examined material belong to the suborder Valvifera. Elsewhere, Valvifera commonly represents a significant percentage of the total coastal species. For example, 40 species have been cited in the Iberian Peninsula, corresponding to 18% of the total (Junoy & Castelló, 2003). Furthermore, the suborder Asellota constitutes only 10.7% of the species collected in this study. This is probably due to insufficient sampling of the habitat preferred by valviferan and asellotan isopods, namely the algal substrate. Conversely, the suborder Cymothoidea is well-represented and diverse (5 species of Anthuroidea and 11 species of Cymothoidea), as well as the suborder Sphaeromatidea, which includes 9 species of Sphaeromatidae.

Biogeography

The biogeography of the Levantine Sea is of particular interest. This region faces the Mediterranean opening of the Suez Canal, which represents the entry point of non-indigenous Indo-Pacific species, and it has even been called “Lessepsian province” (Por, 1990). The term “Lessepsian migration” (also called “Erythrean invasion”) was introduced by Por (1971, 1978). It refers to the unidirectional transit of species from the Red Sea to the Mediterranean Sea via the Suez Canal and, *sensu stricto*, does not include their passive transport. The introduction of species through human means of transport, mainly vessels, is globally acknowledged as a major pathway of introduction for marine NIS (Coll *et al.*, 2010). This pathway may include several associated transport vectors (e.g., hull fouling, ballast water, and sea chests (Ulman *et al.*, 2017)). Transport associated with marine cultures should also be considered. The discussion section will analyze these aspects, to establish a hypothesis regarding the introduction vectors of some non-indigenous species encountered in our material.

Distribution of species

To date, no exhaustive biogeographical study has been carried out of free-living isopods in the entire Mediterranean Sea. Some fairly complete regional lists do exist (e.g., Junoy & Castelló, 2003; Castelló, 2017a, for the Iberian peninsula; and Argano & Campanaro, 2010, for Italy), while other Mediterranean subregions are still insufficiently sampled. Here, an effort is made to compile all the existing data (see Table 2 and Table S2). Table 2 is intended as an inventory of the majority of Mediterranean isopod fauna, from near-shore waters to the open sea. It comprises 295 species but still excludes Epicaridea, Oniscidea and the brackish water Aselloidea of the genera *Asellus*, *Chthonasellus*, *Proasellus* (Asellidae) and *Stenasellus* (Stenasellidae). Species found on the continental shelf are the majority, but information is also available on bathyal fauna down to great depths (e.g.,

George & Menzies, 1968; Chardy, 1974; Cartes & Sorbe 1993; Madurell & Cartes, 2003; Kavanagh *et al.*, 2006). For each geographical subregion, the respective number of species is subregion 1, 149; subregion 2, 174; subregion 3, 80; subregion 4, 61; subregion 5, 96; subregion 6, 45; subregion 7, 105; and subregion 8, 108. For the Suez Canal, 25 species have been cited. These data indicate a significant difference in species richness, with the highest levels found in the western Mediterranean subregions and the lowest in the enclosed Black Sea, the Ionian Sea, and the Adriatic Sea. The African coasts of Algeria, Tunisia and Libya have been less investigated. The French expeditions to Algeria (Lucas, 1849) represent the only major work in that subregion, and other relevant contributions are the study of Monod (1925), the descriptions of new species of Anthuridae by Negoescu (1980a, 1981), and some other study on parasitic species and their hosts (e.g., Ramdane *et al.*, 2007), as well as species records in biogeographical (e.g., Holdich, 1970; Vieira *et al.*, 2016) and ecological studies (e.g., Ayari & Afli, 2003, Pérez-Domingo *et al.*, 2008). In recent years, the number of records in subregion 8 has increased notably, especially due to the list of species from Malta (Mifsud, 2017). The list of 105 species for subregion 7 (Levantine Sea) is significantly longer than those previously compiled by Koukouras *et al.* (2001: 44 species), and Coll *et al.* (2010: 34 species). Similarly, our collection comprises 28 species, of which 15 are new to subregion 7 (Levantine Sea): *Elaphognathia bacescoi*, *Gnathia illepidus*, *Gnathia inopinata*, *Apanthura addui*, *Heptanthura cryptobia*, *Kupellonura serritelson*, *Mesanthura pacoi*, *Atarbolana beirutensis*, *Cirolana bitari*, *Cirolana manorae*, *Cirolana zibrowiusi*, *Metacirolana rotunda*, *Cymodoce fuscina*, *Cymodoce pilosa*, and *Pseudocerceis cf. seleneides*. Eight of them (*Apanthura addui*, *Atarbolana beirutensis*, *Cirolana bitari*, *Cirolana manorae*, *Cirolana zibrowiusi*, *Mesanthura pacoi*, *Metacirolana rotunda*, and *Pseudocerceis cf. seleneides*) are also new for the entire Mediterranean Sea.

Origin of Mediterranean isopod fauna

According to Rodríguez (1982), the Mediterranean region is constituted by a set of species of diverse origin, mainly ancient Tethys, Atlantic Ocean, from boreal to tropical regions, and immigrants from the Black Sea and the Red Sea. Regarding the western Mediterranean, since the beginning of the Pliocene some five million years ago, the sea has been connected to the Atlantic Ocean only via the Strait of Gibraltar. Presumably, most Mediterranean species of isopods have this origin (Coll *et al.*, 2010). In the eastern Mediterranean, according to Por (1978), marine contact existed between the Mediterranean and the central Indian Ocean until sometime in the first half of the Miocene. Later, in the Pliocene, the Red Sea was connected to the Mediterranean again but opened for the first time to the Indian Ocean, and consequently acquired mixed fauna. In the Pleistocene, various oscillations in sea level could have made possible the relicts of the Tethys and the pre-Lessepsian Red Sea species

(Hofrichter, 2004). Now, since the opening of the Suez Canal in 1869, it has become the main entrance pathway for alien species (the other two being maritime traffic and aquaculture). International organizations are aware of the importance of monitoring the arrival of alien species. The Mediterranean Science Commission (CIESM) has already produced a series of atlases documenting alien species in the Mediterranean (crustacean decapods: Galil *et al.*, 2002; fish: Golani *et al.*, 2002; macrophytes: Verlaque *et al.*, 2015; molluscs: Zenetos *et al.*, 2004). A growing interest has been repeatedly expressed in creating additional, representative lists of introduced species because of their impact on ecosystems (e.g., Katsanevakis *et al.*, 2014). The fauna of Red Sea isopods differs considerably from that of the rest of the Indian Ocean, due to its large number of endemisms (63%, according to Kensley, 2001, including Epicaridea). Kensley (2001) noted the presence of 61 species of isopod (now 82) in the Red Sea and Gulf of Aden (equivalent to approximately 9.3% of the known Indian Ocean isopod fauna). Of these species, only 23 were introduced into the Mediterranean Sea (see Table S2 and Table 3). Their presence in the Mediterranean does not necessarily mean that they are all are also established in the Suez Canal, where 25 species are currently known (see Table S2 and Table 3). Seventeen species are reported from both the Red Sea and the Suez Canal (see Table S2 and Table 3). Moreover, only 15 of the known species from the Suez Canal have been cited in the Mediterranean Sea (see Table S2 and Table 3). Table 4 summarizes the autoecology and global distribution of the species reported in the Suez Canal and nearby areas, to establish how their presence in these areas can be explained. The transit of species is schematized in Figure 7. Doubtful records regarding *Cirolana parva*, *Dynamene bidentata*, and *Limnoria lignorum* (indicated in Table 2, Table S2, and Table 3) are mentioned in Taxonomy and Concluding remarks sections. In Table 2, doubtful records for *Nerocila swainsoni* in subregions 2 and 4 are due to the distribution given by Leach (1818) (Sea of Sicily, without distinction between the Tyrrhenian and Ionian Seas). For *Synisoma lancifer*, the doubtful record for subregion 1 is due to its possible confusion with *Synisoma capito* (Junoy & Castelló, 2003).

Discussion

About 8.1% of the species present in the Mediterranean Sea are non-indigenous (NIS). The alien species of isopods in the Mediterranean Sea listed in Zenetos *et al.* (2010) includes *Anilocra pilchardi*, *Apanthura sandalensis*, *Cymothoa indica*, *Mesanthura sp.*, *Paracerceis sculpta*, *Paradella diana*, *Sphaeroma venustissimum*, and *Sphaeroma walkeri*. Galil *et al.* (2016) added *Paranthura japonica*. *Sphaeroma venustissimum* was subsequently removed from the list of alien species (Zenetos *et al.*, 2012). Its type locality is in North West Africa and it entered the Mediterranean by natural range expansion, not by human introduction. *Mesanthura sp.* was identified by Ulman *et al.* (2017) as *M. cf. romulea* Poore & Lew-Ton,

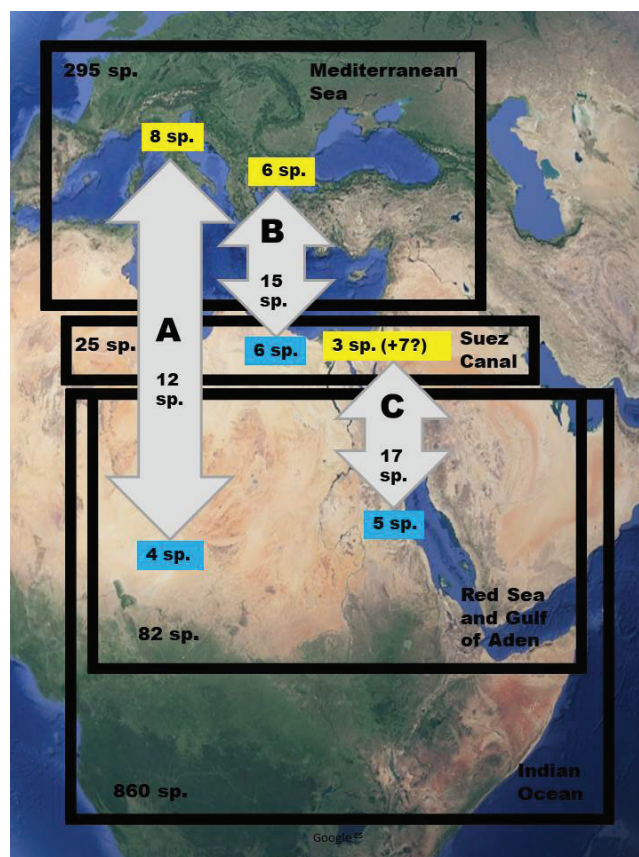


Fig. 7: Diagram showing the transit of species through the Suez Canal and nearby regions. In yellow, species of Red Sea origin introduced to the Mediterranean Sea; in blue, species of Atlanto-Mediterranean origin introduced to the Red Sea. The arrows indicate the transit of species between the areas considered: from left to right, (A) the Mediterranean Sea and the Red Sea/Gulf of Aden but not the Suez Canal, (B) the Mediterranean Sea and the Suez Canal, (C) the Suez Canal and the Red Sea/Gulf of Aden. Species with doubtful identity (*Cirolana parva*, *Dynamene bidentata*, and *Limnoria lignorum*) are not considered.

1986, a species from South East Australia which can be considered NIS, awaiting confirmation of identification of the *Mesanthura* specimens. Some species (*Paracerceis sculpta*, *Paradella diana*, and *Paranthura japonica*) arrived via either maritime traffic or aquaculture, as studied in detail by Marchini *et al.* (2014) for *P. japonica*. The latter was probably introduced in the Mediterranean Sea as shellfish import from Arcachon Bay (France, Atlantic Ocean), and spread secondarily to further Mediterranean marinas (Dailianis *et al.*, 2016; Ferrario *et al.*, 2016; Ferrario *et al.*, 2017; Lavesque *et al.*, 2013; Lorenti *et al.*, 2016; Marchini *et al.*, 2014; Marchini *et al.*, 2015; Tempesti *et al.*, 2016; Ulman *et al.*, 2017). Ulman *et al.* (2017) cited seven NIS collected in marinas throughout the Mediterranean. *Ianiropsis serricaudis* (present in subregions 2 and 3) was probably introduced into the Mediterranean through the oyster trade (Marchini *et al.*, 2016). For *Sphaeroma walkeri*, Carlton & Iverson (1981) revised its introduction history and proposed a route via the Suez Canal (Omer-Cooper, 1927; Larwood, 1940) at the time of its opening. Considering the geographical distribution, it can be inferred that *Cymodoce fuscina* (found

in subregions 5 and 7) entered the Mediterranean Sea through the Suez Canal on the hulls of ships or boats. The four remaining species are widely distributed throughout the Mediterranean (*Mesanthura cf. romulea*, *Paranthura japonica*, *Paracerceis sculpta*, and *Paradella diana*).

The distribution tables of the species, by regions and subregions (Table 2 and Table S2) provide solid support for analyzing how the species recorded in the Suez Canal were able to expand to nearby areas (Table 3). In addition, the discussion is based on factors that affect the biogeographical characteristics of the species and are briefly described below. (a) Biological cycle: species that show larval stages during their development are potentially more able to move through the Canal. (b) The increase in temperature in the Levantine Sea, due to climate change, also helps species adaptation (Galil, 2006; Raitzos *et al.*, 2010; Rilov *et al.*, 2018). (c) Salinity: the dissolution of the Bitter Lakes' salt bed was complete by the 1960s (Galil, 2006) and so it no longer acted as a barrier. (d) Bathymetry: the fauna that manages to cross the canal is typical of coastal areas. Por (1971) rules out the transit of sublittoral and bathyal species. However, some Lessepsian immigrants expanded their range beyond the coastal shelf (Galil *et al.*, 2019). (e) Habitat: the fauna of muddy bottoms has more chance of crossing the canal, due to the similarity of this habitat to the bottom. (f) Water turbidity: Por (1971) dismisses the possibility that the fauna of rocky bottoms and transparent waters can pass. (g) Dispersal capacity of the species: isopods have little independent dispersal capacity. Only a few groups (e.g., Cirolanidae and some species of Sphaeromatidae) with habitats generally of muddy bottoms can transit through the canal, crossing turbid and polluted waters, unlike other groups (e.g., Asellota, Anthuridea and Valvifera) with a preference for algal substrates and clear waters. The dispersal capacity increases greatly in the case of ectoparasitic species of other organisms at particular stages of their biological cycle. For example, Aegidae, Cymothoidae and Gnathiidae parasitize fish. In terms of passive dispersion, some species take advantage of human means of transport. Species of Asellota (Janiridae or Joeropsididae) (Hobbs *et al.*, 2015; Kensley & Schotte, 2002), Anthuridea (Ulman *et al.*, 2019), Sphaeromatidae (Shoukr *et al.*, 1991; El-Komi *et al.*, 1998; Ramadan *et al.*, 2006), and Valvifera (Shoukr *et al.*, 1991; Ramadan *et al.*, 2006) can be found in the fouling of ship hulls. The presence of *Idotea* species (Valvifera) is common on floating objects (e.g., Abelló & Frankland, 1997). The Limnoriidae drill wood and, therefore, can be found mainly in floating objects (Cookson, 1991). Currently, there are almost no wooden boats and the main means of transport is rafting on driftwood transported by currents (Borges *et al.*, 2014). Anthuridea and Asellota species may also be found in oyster cultures (Faasse, 2007; Lavesque *et al.*, 2013). Species using these means of dispersion to cross the canal more easily and quickly can be termed NIS but not Lessepsian. The species that are most likely to become Lessepsian are those that are well-established in the canal (Por, 1973). For example, *Carpas styrodactylus* was reported by Glynn (1972) as

very abundant. However, we believe this is quite unlikely unless they have the help of human means of transport. This information is summarized for each species in Table 4. New species in the Mediterranean that are suspected to be non-indigenous (NIS) are: *Anilocra leptosoma*, *Apanthura addui*, *Carpas crosslandi*, *Ceratothoa imbricata*, *Cirolana manorae*, *Cymodoce erythraea*, *Dynamenella savignii*, *Elthusa nanoides*, *Joeropsis rathbunae*, *Livoneca redmanii*, *Metacirolana rotunda*, *Pseudocerceis cf. seleneides*, and *Synidotea variegata* (see Table 2). Therefore, the list of NIS known so far (Zenetos *et al.*, 2010; Ulman *et al.*, 2017; Martínez-Laiz *et al.*, 2018) is updated with 13 new species and a total of 23 has been reached. Information or biogeographic comments to consider these new species as NIS in the Mediterranean can be found in Table 2, Table S2, and Table 4, and in the Taxonomy and Biogeography sections or in the Discussion. The distribution of *Livoneca redmanii* is restricted to the Eastern coast of America, at least from New York to Rio de Janeiro (Trilles, 1991) and it was surprisingly identified on mugiliid fry (Mahmoud *et al.*, 2019) in the Mediterranean Sea (subregion 7). Some of the new NIS in the Mediterranean (e.g., *Carpas crosslandi*) could even be pre-Lessepsian (PL). Furthermore some species with a clear disjunct distribution, recorded from the Indian Ocean and the Mediterranean Sea (e.g., *Angeliara phreaticola*, *Apanthura addui*, *Pleurocope dasyura*, and *Pseudocerceis cf. seleneides*) may be relicts (R), from when the seas were joined. However, some caution is required, because the gaps of knowledge in the geographical distribution of single species may limit our understanding of their spreading history.

Concluding remarks: with a total of at least 295 species (excluding Epicaridea, Oniscidea, and brackish water Aselloidea), the Mediterranean isopod fauna is much more diverse than previously suggested (Koukouras *et al.*, 2001; Van der Land, 2001; Coll *et al.*, 2010). The species richness is the highest in the Western Mediterranean (subregions 1 [149 sp.] and 2 [174 sp.]), and the lowest in the Black Sea (subregion 6 [45 sp., as is to be expected in an enclosed sea]), and the Ionian Sea (subregion 4 [61 sp.]). The number of species in the African region (subregion 8 [108 sp.]) is quite high, especially due to recent studies and listings. In the other subregions, the known isopod fauna still has fairly high richness, with 80 species in the Adriatic Sea (subregion 3), 96 species in the Aegean Sea (subregion 5), and 105 species in Levantine Sea (subregion 7). In the westernmost Mediterranean Sea, closer to the Strait of Gibraltar, there may be many "Atlantic" species that have not passed the Sicily Channel. In contrast, in the eastern subregions there may be species derived from the "salty lakes" of Paratethys, especially in the Black Sea. Regional research in each of these areas is essential. In recent decades, investigations in the Aegean Sea (e.g., Bakir & Katagan, 2005; Çinar *et al.*, 2002; Çinar *et al.*, 2008; Dounas & Koukouras, 1986; Geldiay & Kocatas, 1972; Kirkim *et al.*, 2005a; Kirkim *et al.*, 2005b; Kirkim *et al.*, 2006; Kirkim *et al.*, 2010; Kitsoos & Koukouras, 2003; Koçatas, 1976; Koçatas *et al.*, 2004; Koukouras *et al.*, 1985; Koukouras *et al.*, 2001;

Koukouras *et al.*, 2002), the Marmara Sea (e.g., Bakir, 2012), Black Sea (e.g., Akbulut *et al.*, 2009; Sezgin & Çil, 2010) and Turkey in general (e.g., Bakir *et al.*, 2014) have greatly helped to broaden knowledge. As a result of the collection studied here, the number of known species in the Levantine Sea has risen to 105. Several (86) of the species found here had been previously recorded in other Mediterranean subregions. Some strangely disjunct distributions (e.g., *Gnathostenetroides laodicense*, *Joeropsis legrandi*, and *Lekanesphaera rugicauda*) with the presence of the species only in the western and eastern subregions, indicate that significant gaps of knowledge exist. Another 19 species seem to be restricted to the Levantine Sea (see Table 2). Table 4 allows the study of the species' dispersion capacity and the probability that they crossed the Suez Canal in one direction or the other (only considering species present in the Suez Canal). For the first group of five species, which coexist in the Mediterranean and the Suez Canal, *Cirolana manorae* probably crossed the Suez Canal from the Indian Ocean. At present, there are no records in the Red Sea/Gulf of Aden. This species was probably helped by maritime transport, but we cannot rule out the possibility that it reached the Mediterranean on its own. The Cirolanidae are good swimmers and mostly live on muddy bottoms. *Limnoria lignorum* is xylophagous and can easily spread in perforated hulls of vessels. This species is widely distributed in the Northern Hemisphere, and was also recorded in the Mediterranean (subregions 1, 2, 3, 4, 5, 7 and 8). Nevertheless, Cookson (1991) and Borges *et al.* (2014) restricted its distribution to the temperate and boreal Northern hemisphere, and Castelló (2011) pointed out that it was confused with *Limnoria mazzellae* on the Spanish shores. For this reason, the Mediterranean records are considered doubtful. The NIS *Paracerceis sculpta* has been thoroughly studied (e.g., Ulman *et al.*, 2017; Martínez-Laiz *et al.*, 2018). The case of *Nerocila bivittata* is that of a parasitic species that is mainly dependent on fish. It has an Atlanto-Mediterranean distribution. It has been recorded profusely in the Mediterranean, and has reached the Suez Canal (Trilles, 1991). It can be considered Anti_L. The case of *Joeropsis rathbunae* is problematic because of its geographical distribution (Bermuda Islands and the Gulf of Mexico, Mediterranean [subregion 7], and the Suez Canal), probably due to transport by vessels. Currently, it is sensible to classify it as NIS in the Mediterranean Sea, while we await further data. The second group comprises 10 species that coexist in the Mediterranean, the Suez Canal, and the Red Sea/Gulf of Aden. The two species of *Sphaeroma* (*S. serratum*, *S. walkeri*) have been studied extensively. *Sphaeroma walkeri* is widely represented in almost all Mediterranean subregions and has a cosmopolitan global distribution (Ulman *et al.*, 2017; Martínez-Laiz *et al.*, 2018). With respect to *S. serratum*, its wide distribution throughout the Atlantic European coasts and the Mediterranean since before the opening of the Suez Canal means that it can be catalogued as Anti_L. *Cymodoce spinosa*, *C. truncata* and *Dynamene edwardsi* are in the same situation as *S. serratum* (Anti_L). Any biogeographic consideration regarding *Dynamene bidentata* is

speculative at the moment, given the uncertain status of its Mediterranean records (see the Taxonomy section). *Eurydice pulchra*, which is present in the North East Atlantic and in the Mediterranean (subregions 5, 6, 7 and 8), probably reached the Red Sea through the Suez Canal. Its absence in the Mediterranean subregions 1, 2, 3 and 4 may be due to a lack of sampling. It is considered Anti_L. *Cirolana bovina*, with a wide distribution in the Indian Ocean (South Africa, Kenya, India, Red Sea, and the Suez Canal), is only present in Mediterranean subregion 7. Therefore, it is considered NIS. According to Bruce (in WoRMS Editorial Board, 2019), for *Cirolana parva*, the Mediterranean record (subregion 8) and the records from the Suez Canal and the Red Sea should be considered inaccurate, due to misidentifications. Therefore, it is not possible to develop a sound hypothesis regarding its biogeographic distribution. *Synidotea variegata* is present in the Indian Ocean, from South Africa to Indochina. It probably reached the Red Sea transported by ships and then expanded towards the canal. It is well-established in the canal (Glynn, 1972), and was already recorded in the East Harbor of Alexandria (Ramadan *et al.*, 1998). Finally, the third group is composed of seven species that coexist in the Suez Canal and the Red Sea/Gulf of Aden. These species are candidates for future possible introduction via the Suez Canal or on the hull of vessels crossing the Canal. *Carpas stylodactylus*, with a wide but disjunct range of distribution (Caribbean Sea and South Pacific), may have been dispersed due to maritime traffic. It was probably introduced into the Suez Canal from the Red Sea. *Cirolana anadema* may even have come by its own means, as it is a genus with a habitat of muddy bottoms and good dispersion capacity and has been present in the canal for years. *Cirolana theleceps* has a distribution restricted to South Africa and it may be expanded due to maritime traffic. The type locality of *Paradella heptaphymata* is Lake Timsah (Suez Canal) and its distribution is restricted to the Suez Canal and the Red Sea. *Cymothoa exigua* is known only from the Galapagos Islands and it is considered an alien species in the Red Sea (WoRMS Editorial Board, 2019). Like *Rocinela orientalis* and *Gnathia rhinobatis*, these species are parasitic on fish, the latter of them in larval phase, which increases the probability that they can reach the Mediterranean. Furthermore, 13 species are found in both the Mediterranean Sea and the Red Sea/Gulf of Aden, but not in the Suez Canal. Among them, *Ceratothoa oxyrrynchaena* (type locality: Japan), present in the Red Sea, has a wide distribution (see Bariche & Trilles, 2005, and Table 2) but it is discontinuous (absent in the Indian Ocean). Currently, it is difficult to know if its presence in the Mediterranean (see Table 2) occurred via the Suez Canal or followed the reverse path. After studying their geographical distribution and their dispersal capacity, it can be inferred that eight of the remaining species (*Anilocra leptosoma*, *Apanthura sandalensis*, *Carpas crosslandi*, *Ceratothoa imbricata*, *Cymodoce erythraea*, *Dynamenella savignii*, *Elthusa nanoides*, and *Metacirolana rotunda*) are non-indigenous (NIS) in the Mediterranean and four species (*Cymodoce pilosa*, *Eurydice inermis*, *Idotea balthica*, and *Idotea metallica*)

are anti-Lessepsian (Anti_L). Their absence in the Suez Canal can be attributed to the fact that the Canal can be crossed by vessels. The absence of established populations of these twelve species in the Suez Canal confirms that they are neither Lessepsian nor anti-Lessepsian (by their own means) species.

In summary, the opening of the Suez Canal facilitated the exchange of isopod species. There is no clear trend to confirm a predominance of traffic in one direction or the other (see Figure 7). Species displacement was possible due to maritime traffic and there are no clearly Lessepsian species.

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Supplementary data

The following supplementary information is available on line for the article:

Table S1. Material examined, per species; see Table 1 for number codes.

Table S2. List of isopod species (excluding Epicaridea, Oniscidea, and brackish water Aselloidea) reported from the Suez Canal, Red Sea, and Gulf of Aden. Additional information: shared species with other Indian Ocean regions, and with the Mediterranean Sea, with subregions indicated in square brackets (see Figure 2 for number codes). *type locality of the species identified in this study; **doubtful record; ***uncertain validity; ****uncertain taxonomic significance; *****not in WoRMS (last accessed: 20 November 2019); abbreviations: A, absent; P, previously cited; S, found in the present study.

Table S3. Sources used in Table 2 and Table S2, by regions and subregions.