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Hydroids (Cnidaria: Hydrozoa) from the Levant Sea (mainly Lebanon), with emphasis on alien species

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Despite the hydroid fauna of the Mediterranean Sea being considered one of the best known in the world, the eastern basin of the Mediterranean Sea remains nearly unexplored. This paper reports on 38 species collected along the Levant Sea coast (mainly Lebanon), of which three are new records for the Mediterranean and nine for the Levant Sea. Six alien species, i.e. Eudendrium carneum, Sertularia marginata, Sertularia techocarpa, Macrorhynchia philippina, Diphasia digitalis *and* Dynamena quadridentata, *are described in detail and illustrated on the basis of Levant Sea material. The last four species are considered as immigrants from the Red Sea. The synonymy of* Sertularia stechowi, *described from Japan, with* S. techocarpa *is established. Taken as a whole, the collection comprised a majority of circum-(sub)tropical species, and a reduced proportion of Atlantic–Mediterranean elements and Mediterranean endemics. The ecology (seasonality, depth distribution and habitat preference) of the indigenous species resulted similar to what is known for the more studied western Mediterranean, with some exceptions. Adding the present species inventory to the scanty published information, the total of hydroid species known from the Levant Sea rises to 70, indicating the need for future investigation in this sector of the Mediterranean Sea.*

Keywords: Hydrozoa, alien species, zoogeography, Levant Sea, Mediterranean Sea

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INTRODUCTION

Hydroids are an important component of benthic marine ecosystems, on both hard and soft bottoms (Boero, 1984; Morri *et al.*, 1991; Gili & Hughes, 1995). Many of them are known for their essential role in benthic–pelagic coupling, either by filter feeding on plankton (Gili *et al.*, 1998) or because of their metagenetic cycles, which often involve a free-swimming medusa (Boero *et al.*, 1996; Marcus & Boero, 1998). In shallow hard bottom communities of temperate seas, like the Mediterranean, hydroids can outcompete algae as major substrate occupiers during the cold season (Bianchi *et al.*, 2004) or even persist year-round to form peculiar assemblages within otherwise algae-dominated communities (Bellan-Santini *et al.*, 2002).

The hydroid fauna of the Mediterranean Sea has been said to be 'one of the better known in the world' (Boero & Bouillon, 1993) and a recent monograph with identification keys is available (Bouillon *et al.*, 2004). It must be recognized, however, that virtually all of our knowledge on Mediterranean hydroids comes from work done by French, Spanish and Italian scientists (Picard, 1958a; Medel & López-González, 1996; Boero *et al.*, 1997; and references therein), so that only the (north-)western Mediterranean and the Adriatic hydroid fauna may be considered adequately known (Boero *et al.*, 1997). The previous dearth of information on the Aegean Sea has been only partially remedied by Morri & Bianchi (1999), whereas the hydroid fauna of the Levant Sea remains little studied.

The available information on Levant Sea hydroids is summarized in the papers by Picard (1958b) and Vervoort (1993), both having studied material from Israel, and by El-Beshbeeshy (1993, 1994a, 1994b, 1995a, 1995b), who worked on the hydroids of Egypt. A number of papers deal with fouling hydroids of the Suez Canal and Mediterranean Egyptian harbours (Abdel-Hamid *et al.*, 1983, 1984; Shoukr & Abdel-Hamid, 1987; Shoukr, 1987). Also of interest are the papers on the pelagic hydromedusae of eastern Mediterranean waters (Schmidt, 1973; Lakkis & Zeidane, 1985; Goy *et al.*, 1988, 1990, 1991; Zakaria, 2004).

Thanks to the French–Lebanese co-operation programme CEDRE, expeditions to collect marine fauna were organized between 1999 and 2003 along the coasts of Lebanon (Zibrowius & Bitar, 2003). Results of these and collateral collections highlighted several points of interest: (i) sponge, isopod and bryozoan species new to science (Pérez *et al.*, 2004; Bariche & Trilles, 2006; Harmelin *et al.*, 2007; Vacelet *et al.*, 2007, 2008); (ii) lack of some 'typical' Mediterranean elements in brachiopods (Logan *et al.*, 2002); (iii) new records for the Mediterranean Sea in polychaetes (Aguado & San Martín, 2007); and (iv) occurrence of Red Sea species

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among algae (Bitar *et al.*, 2005), various invertebrates (Zibrowius & Bitar, 2003) and fish (Harmelin-Vivien *et al.*, 2005).

This paper reports on hydroids collected mostly within that project (with additions in earlier and later years). As collecting essentially aimed at a general biodiversity inventory in shallow rocky habitats, sampling was more 'faunistic' than 'ecological' in design. Nevertheless, the large amount of material obtained allowed for, beside the mere species inventory, a first analysis on some ecological traits of species occurrence, such as reproductive season and depth and habitat preference, in comparison with what is known for the more studied western Mediterranean. As the Levant Sea is currently the portion of the Mediterranean most prone to be colonized by the Red Sea immigrants (Galil, 2006), particular attention was given to the occurrence of non-indigenous or alien species (Streftaris *et al.*, 2005; Zenetos *et al.*, 2006, 2008).

MATERIALS AND METHODS

Field work

Hydroids were collected between 1999 and 2003 in Lebanon by G. Bitar and H. Zibrowius under the aegis of CEDRE. Additional samples from Lebanon were taken between 1991 and 2004 by G. Bitar, who also collected in a distant site to the north (Burj Islam, Syria) in 1999. Further, C. Morri had access to material taken in 2004 in a distant site to the south (Hadera, Israel). Altogether, 34 sites (including the two localities outside the Lebanese borders) were investigated, covering some 460 km of coastline (Figure 1); the regions of Trablus (Tripoli), Jebail (Byblos), Beirut and Saida (Sidon) were more intensively sampled. A total of a hundred and one samples were obtained, from depths ranging from near the surface down to 42 m. As samples were taken by free or SCUBA diving, the choice of sampling sites was significantly

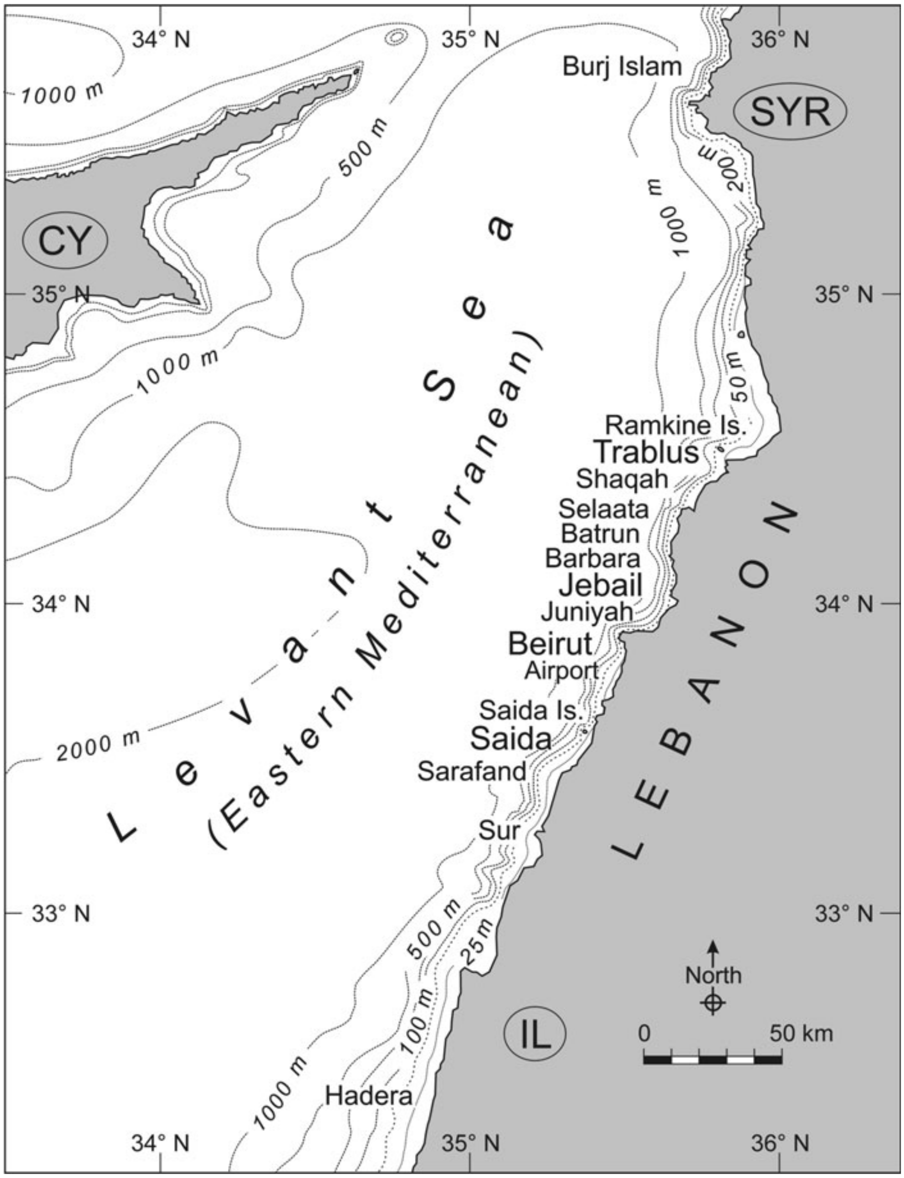

Fig. 1. Map of the sampling localities along the Levant Sea coast.

constrained by logistics (especially accessibility from shore). Dives were performed in different periods between April and November. During each dive, sampling was oriented visually; this approach has been proved most effective to establish large species inventories (Morri *et al.*, 1999).

Laboratory and data analysis

Specimens were fixed in formaldehyde 4% a few hours after sampling. Species were sorted months later, and analysed in the laboratory under both low- and high-power microscopes for taxonomic identification. Measures were taken on, and drawings were made from, fixed material. The presence of reproductive structures was noted. For some species, a number of pieces were washed with distilled water, dehydrated in graded ethanol series samples, and dried in a critical point dryer. Finally, they were coated with gold-palladium in a Balzer Union evaporator and examined with a Philips XL20 scanning electron microscope.

Data on species occurrence were organized in a presence–absence matrix. Frequency of occurrence of a given species with respect to the total number of samples (in the year, locality, season or habitat according to the case) was used as the only way available to obtain (semi-)quantitative data.

RESULTS

Diversity and systematics

A total of 38 species was found, 11 of which were Anthomedusae and 27 were Leptomedusae (Table 1). Poor conservation conditions made specific identification of a *Laomedea* species impossible. We tentatively assigned a sterile colony of *Halecium* bearing zooxanthellae in the coenosarc to the species *lankesteri. Halecium nanum*, known from Bermuda (Calder, 1991) to the north-western Mediterranean (Boero & Fresi, 1986), also has zooxanthellae and similar morphology but *H. lankesteri*, a strictly Atlantic–Mediterranean species (Peña Cantero & García Carrascosa, 2002), has already been reported from the Levant Sea by El Beshbeeshy (1994a). A positive distinction between the two species requires the observation of female gonothecae (Schuchert, 2005).

Six species can be considered as aliens: *Dynamena quadridentata*, *Diphasia digitalis* and *Sertularia thecocarpa* are recorded for the first time from the Mediterranean Sea, whereas *Eudendrium carneum* has been recorded from the western Mediterranean in recent years, but not yet from the eastern Mediterranean; *Sertularia marginata* and *Macrorhynchia philippina* had already been found in the eastern Mediterranean but no description of the Mediterranean specimens had been given before. Original drawings, SEM photographs and a detailed description of these six species, based on the Levant Sea material, are provided in the following paragraphs, as a useful addition to the scanty information available in the literature; in the case of *S. thecocarpa* descriptions and illustrations also substantiate the proposed move from the genus *Sertularella* to *Sertularia* and the synonymy with *Sertularia stechowi* Hirohito (1995).

Table 1. Taxonomic list of the species collected. Non-indigenous species are marked with*.

Subclass Anthomedusae
Order Filifera
Family Bougainvillidae
Bimeria vestita Wright, 1859
Garveia grisea (Motz-Kossowska, 1905)
Family Clavidae
Turritopsis dohrnii Weismann, 1883
Family Eudendriidae
Eudendrium carneum Clarke, 1882*
Eudendrium fragile Motz-Kossowska, 1905
Eudendrium glomeratum (Picard, 1951)
Eudendrium merulum Watson, 1985
Eudendrium racemosum (Cavolini, 1785)
Eudendrium simplex Pieper, 1884
Family Pandeidae
Amphinema rugosum (Mayer, 1900)
Order Capitata
Family Pennariidae
Pennaria disticha Goldfuss, 1820
Subclass Leptomedusae
Order Conica
Family Aglaopheniidae
Aglaophenia elongata Meneghini, 1845
Aglaophenia octodonta (Heller, 1868)
Aglaophenia picardi Svoboda, 1979
Macrorhynchia philippina (Kirchenpauer, 1872)*
Family Campanulinidae
Lafoeina tenuis G.O. Sars, 1874
Family Haleciidae
Halecium beanii (Johnston, 1838)
Halecium cf *lankesteri* (Bourne, 1890)
Halecium petrosum Stechow, 1919
Halecium pusillum (M. Sars, 1857)
Family Halopterididae
Halopteris diaphana (Heller, 1868)
Family Hebellidae
Anthohebella parasitica (Ciamician, 1880)
Family Kirchenpaueriidae
Ventromma halecioides (Alder, 1859)
Family Lafoeidae
Filellum serratum (Clarke, 1879)
Family Plumulariidae
Plumularia setacea (Linnaeus, 1758)
Family Sertulariidae
Diphasia digitalis (Busk, 1852)*
Dynamena quadridentata (Ellis & Solander, 1786)*
Sertularella ellisii (Deshayes & Milne-Edwards, 1863)
Sertularella polyzonias (Linnaeus, 1758)
Sertularia marginata (Kirchenpauer, 1864)*
Sertularia thecocarpa (Jarvis, 1922)*
Order Proboscoida
Family Campanulariidae
Campanularia hincksii Alder, 1856
Clytia gracilis (M. Sars, 1850)
Clytia hemisphaerica (Linnaeus, 1767)
Clytia linearis (Thorneley, 1899)
Laomedea sp.
Obelia dichotoma (Linnaeus, 1758)
Orthopyxis integra (MacGillivray, 1842)

Eudendrium carneum Clarke, 1882
(Figure 2G)

DESCRIPTION

Colonies dioecious, arborescent, up to 10 cm high; stem fascicled, hydrocauli arising from creeping hydrorhiza; branches alternate, occurring over entire hydrocaulus, branches up to second order, radial or planar; pedicels arising from main

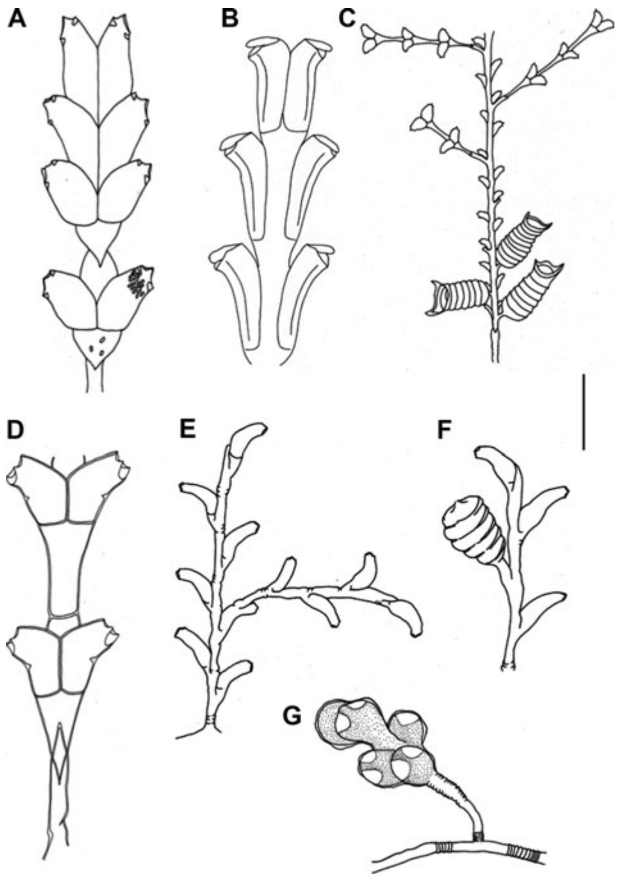

Fig. 2. Hydrothecae of *Dynamena quadridentata* (A) and *Diphasia digitalis* (B); colony of *Sertularia marginata* with gonothecae (C); hydrothecae of *Sertularia marginata* (D); colony (E) and hydrothecae (F) of *Sertularia thecocarpa*; female gonophore of *Eudendrium carneum* (G). Scale bars: (A) 200 μm; (B, E) 600 μm; (C) 1.3 mm; (D) 250 μm; (F) 550 μm; (G) 400 μm.

stem or branches of first and second order. Perisarc of main stem thick, brown, smooth or with rare rings. Branches with 5–10 rings at origin. Pedicels with 2 rings at origin, sometimes corrugated. Hydranths poorly preserved.

Gonophores styloids, arising from body of hydranth. Immature styloids placed in a circle around body of hydranth. Male blastostyle with up to 14 sporosacs, each sporosac up to 5 chambered. Sporosac with a distinct spadix over its longitudinal axis, and sometimes a terminal tubercle on its apex; distal chamber 280–300 μm in diameter, 200–210 μm in height. Mature male blastostyles with tentacles and hypostome completely reduced. Female gonophores, up to 10, arise on blastostyles, immature eggs having a bifid and curved spadix over a single egg. During egg maturation, tentacles and hypostome of the blastostyle reduce completely. During development, spadices shed. Embryos borne in perisarc-covered capsules arranged irregularly along pedicel (Figure 2G).

Nematocysts of two categories, heterotrichous microbasic euryteles and heterotrichous anisorhiza. Small microbasic euryteles (not seen discharged), 7–7.5 × 2.5–3 μm, oval, common; distributed over hydranth body, hypostome, coenosarc, and tentacles. Large heterotrichous anisorhiza (not seen discharged), 20–22 × 10–12 μm, bean shaped, distributed at the base of hydranth body and coenosarc.

Macrorhynchia philippina Kirchenpauer, 1872
(Figures 4E–H & 5)

DESCRIPTION

Colonies up to 30 cm high (Figure 5), stinging to the touch when fresh. Hydrocauli polysiphonic, strongly and irregularly branched. Branches arising from peripheral tubes of stem, with a basal part bearing median nematothecae and a distal part bearing alternate hydrocladia (Figure 4E). Axial tube of stem and distal part of branches with internodes, each with one hydrocladian apophysis and two nematothecae. Mamelon present on anterior surface of apophysis. Hydrotheca sac-shaped, upper third curving away, opening obliquely, margin with two rounded lateral cusps and a median abcauline tooth; between margin and median inferior nematotheca, a triangular thick shelf projects halfway into hydrotheca (Figure 4F, G). Median inferior nematotheca conical, reaching beyond margin of hydrotheca, with three openings (Figure 4G). Lateral nematothecae tubular, inclined forward, generally overtopping the hydrothecal margin, with one or two openings (Figure 4F). Nematothecae with mastigophores of two sizes: 63–75 × 7.5 μm (undischarged) and 13–25 × 4 μm (undischarged). Small nematocysts (mastigophores?), 5 × 2.5 μm, very abundant in polyp. Gonothecae on modified hydrocladia (phylactocarps), one per phylactocarp (Figure 4E). Phylactocarps composed of one hydrocladial segment with hydrotheca as in normal hydrocladia, followed by cylindrical segments with one or two nematothecae. Gonotheca attached to segment following hydrothecate segment, black coloured, lens-shaped (Figure 4H).

MEASUREMENTS

Hydrotheca:	total height	250–280 μm
	diameter in the middle	120–150 μm
Nematotheca:	length median free part	80–100 μm
	lateral length	80–100 μm
Gonotheca:	diameter	0.6–0.8 mm

Diphasia digitalis (Busk, 1852)
(Figure 2B)

DESCRIPTION

Stems arising from a creeping hydrorhiza, short, unbranched. Nodes transverse. Up to 3 pairs of hydrothecae on each stem; hydrothecae biseriate, paired, one pair on internode, long, tubular, adnate 3/4 adcauline length (Figure 2B). Margin quadrangular, one adcauline operculum, perisarc delicate, a low cusp at summit of a longitudinal frontal pleat extending from base of hydrotheca to margin. Gonotheca not recorded in the Levant Sea material. Coenosarc dark-brown coloured.

MEASUREMENTS

Hydrotheca:	length adcauline, adnate part	740–750 μm
	length adcauline, free part	190–230 μm
	length abcauline part	780–920 μm
	diameter at margin	300–380 μm

Dynamena quadridentata (Ellis & Solander, 1786)
(Figures 2A & 3A–C)

DESCRIPTION

Hydrorhiza creeping on *Pennaria disticha* hydrocaulus. Stem unfascicled, unbranched, reaching a maximum height of

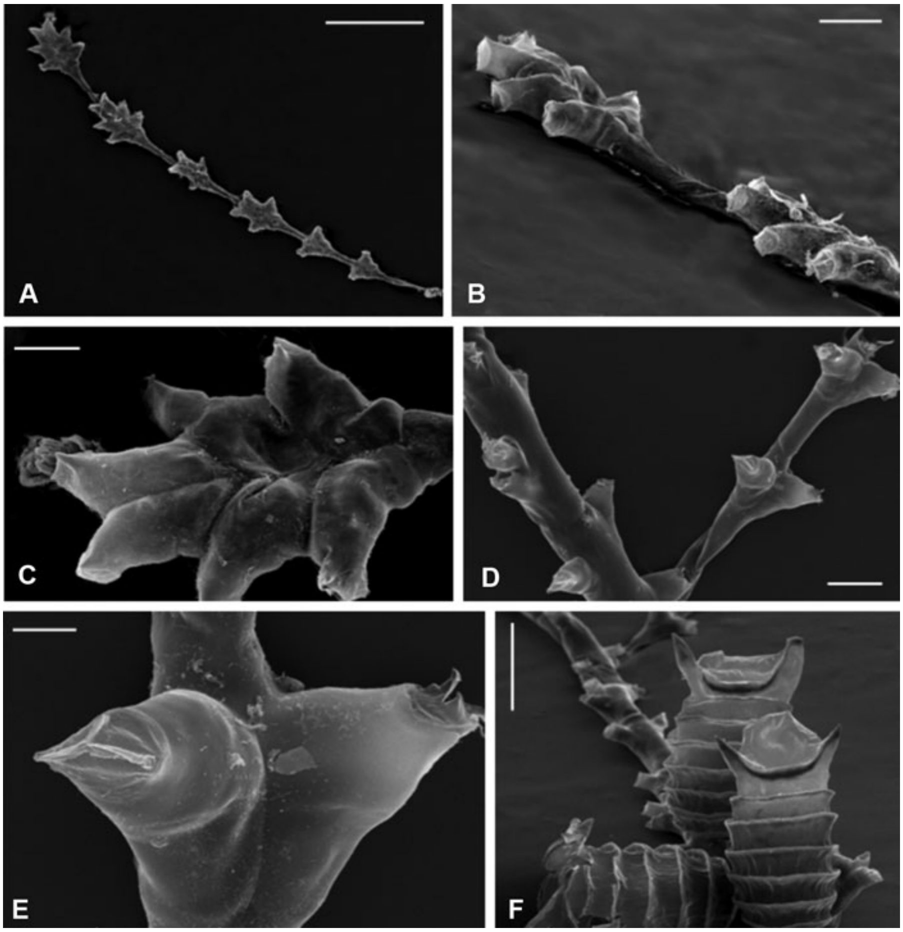

Fig. 3. Scanning electron microscopy images of *Dynamena quadridentata* colony (A) and groups of hydrothecae (B, C); *Sertularia marginata* colony (D), hydrothecae (E) and gonothecae (F). Scale bars: (A) 1 mm; (B, D) 200 μm; (C) 100 μm; (E) 50 μm; (F) 500 μm.

5 mm. Normal nodes transverse and often indistinct. Oblique hinge-joints present at the base of the stem, each forming the termination of a separate, narrow, athecate internode at irregular intervals in the distal region (Figures 2A & 3A, B). Each thecate internode bearing one to three pairs of opposite hydrothecae; the pairs in a group up to three in number, contiguous with one another and showing a difference in shape, the proximal pair being more divergent than the distal one (Figures 2A & 3B, C). Members of a pair of hydrothecae contiguous in front, separate behind. Hydrotheca tubular, narrowing to margin, bent outwards, adnate 3/4 adcauline length, with internal teeth (Figure 3C). Lateral marginal teeth broad and triangular, adcauline marginal tooth larger than the abcauline ones. Operculum composed of two flaps (Figure 3C). Gonotheca not recorded in the Levant Sea material. Nematocysts (Figure 2A): 15–20 large isorhizae (?) present at the base of the hypostome of the polyps (20–22.5 × 9–10 μm undischarged; 20–22.5 × 7.5–8 μm discharged).

MEASUREMENTS

Hydrotheca:	length adcauline, adnate part	250–300 μm
	length adcauline, free part	80–100 μm
	length abcauline part	150–200 μm
	diameter at margin	75–90 μm

Sertularia marginata (Kirchenpauer, 1864)

(Figures 2C, D & 3D–F)

DESCRIPTION

Stem unfascicled, up to 20 mm, either pinnate or simple and unbranched. Pinnate stem with a short basal athecate part terminated by a hinge-joint and a long distal thecate part bearing alternate hydrocladia (Figures 2C & 3D). Thecate part divided by slightly oblique nodes into internodes with three hydrothecae (occasionally two), one basal, axillary with the apophysis of the hydrocladium, and two subopposite (Figure 2C). The two rows of hydrocladia in one plane. Hydrocladial internodes with two hydrothecae opposite touching frontally (Figures 2C & 3D, E). Hydrotheca with an abcauline intrathecal septum, swollen below septum, narrowing to mouth above it, bent outwards and slightly forwards, adnate for over half adcauline (Figure 2D). Margin with two well developed triangular and sharp lateral teeth and a small adcauline one (Figure 3E). Internal teeth absent. Operculum composed of two flaps, the adcauline one divided in two parts (Figure 3E). Gonotheca large, drum shaped, with 6–7 transverse ribs and two rounded lateral spines sometimes very developed, aperture circular, wide provided with a circular operculum (Figures 2C & 3F).

MEASUREMENTS

Hydrotheca:	length adcauline, adnate part	150–200 μm
	length adcauline, free part	100–120 μm
	length abcauline part	180–230 μm
	diameter at margin	100–110 μm

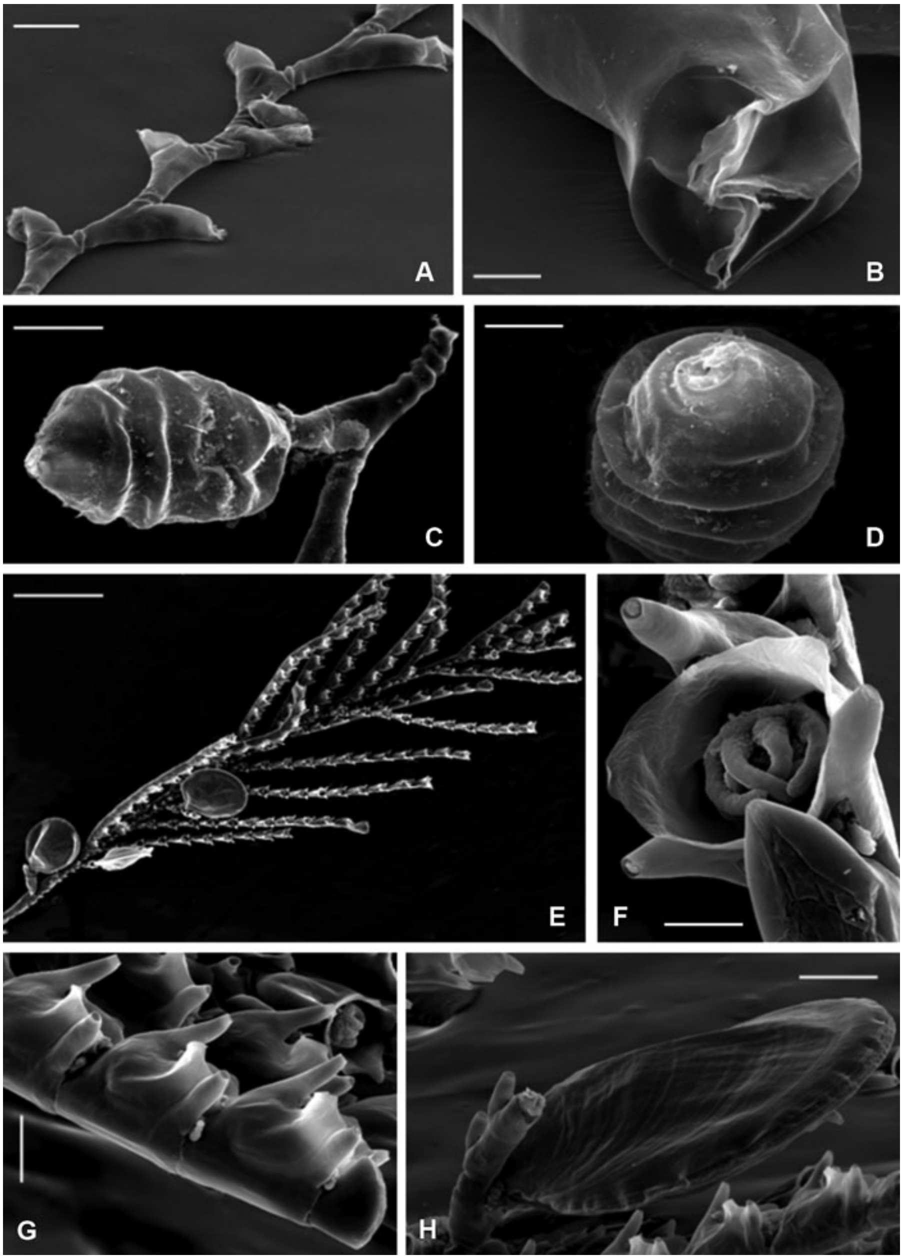

Fig. 4. Scanning electron microscopy images of *Sertularia thecocarpa* colony (A), operculum (B) and gonotheca (C, D); *Machrorhynchia philippina* colony (E), hydrothecae (F, G) and gonotheca (H). Scale bars: (A, C, H) 200 µm; (B) 25 µm; (D, G) 100 µm; (E) 1 mm; (F) 50 µm.

Gonotheca:	length	1–1.2 mm
	maximum diameter	0.5–0.7 mm

Sertularia thecocarpa (Jarvis, 1922)
(Figures 2E, F & 4A–D)

DESCRIPTION

Colony growing on hydrocaulus of *P. disticha*, reaching 15 mm in height. Stem unfascicled, erect, rarely branched, divided into internode by oblique nodes; nodes sloping alternately in opposite direction; each internode bearing usually one hydrotheca on upper part and usually one ring just above the node (Figures 2E & 4A). Hydrothecae arranged alternately in two longitudinal rows, nearly tubular, with smooth surface, bending outwards, adnate for about a third of adcauline length; free part tapering distally. Thecal margin bearing two distinct lateral teeth; operculum composed of two identical flaps, each one sometimes divided into two identical parts (Figure 4B). Hydrothecal renovations frequent. Polyp with many small nematocysts at the base of the hypostome. Gonothecae borne on lower part of stem, arising from within the remains of hydrothecae, sometimes directly on hydrorhiza, ovate, corrugated or with five to seven transverse rings, with a low collar at distal end and a small terminal aperture (Figures 2F & 4C, D).

MEASUREMENTS

Hydrotheca:	length adcauline, adnate part	170–180 µm
	length adcauline, free part	250–280 µm
	length abcauline part	300–310 µm
	diameter at margin	150–160 µm

Fig. 5. A colony of *Macrorhynchia philippina* amidst algae in shallow water (~7 m depth): Batrun, 4 July 2003 (photograph Jean Vacelet).

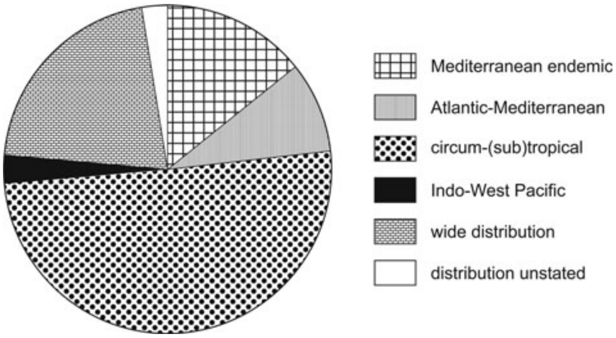

Fig. 6. Zoogeographical affinities of the hydroid fauna on the basis of the 38 species collected.

Gonotheca:	length	600–700 μm
	maximum diameter	400–450 μm
Distance from the base of one theca to the base of the subsequent one		400–420 μm
Diameter of the hydrocaulus (just below the base of the theca)		100–120 μm

REMARKS

Jarvis (1922) named *Sertularella thecocarpa* a species from the Indian Ocean characterized by the hydrothecal margin bearing two large sharply pointed lateral teeth, and gonothecae arising from a lumen of a hydrotheca. Millard & Bouillon (1973) reported the same species from the Seychelles, but did not provide a detailed description of the marginal teeth and the operculum. Owing to the presence of an operculum made of two valves, this species must be placed in the genus *Sertularia*: Jarvis was possibly confused by the division of the valves into two sections. The presence of gonothecae arising from within the hydrothecal cavity, typical of the family Syntheciidae and also reported in the sertulariid genus *Fraseroscyphus* (which has three opercular valves, however), is unusual for the genus *Sertularia* and will deserve further taxonomic investigation. *Sertularia stechowi* described by Hirohito (1995) from Sagami Bay, Japan, agrees with the characters of *S. thecocarpa*. Hirohito observed: '...each flap divided into two identical sections. Consequently the operculum is seemingly composed of four identical flaps in view from above. When the operculum is closed, however, two flaps are in contact on one edge taking shape of pyramidal roof such as operculum of four flaps would take.' We believe, therefore, that *Sertularia stechowi* is a junior synonym of *S. thecocarpa*.

Zoogeography

More than half of the species collected have a circumtropical distribution, although often extending into warm-temperate waters (Figure 6). Two of the three new Mediterranean records, *D. digitalis* and *D. quadridentata*, belong to this group, while the third, *S. thecocarpa*, was hitherto known only from the Indo-West Pacific (see remarks above). Several other species exhibit wider distributions, extending significantly into temperate waters, whereas Mediterranean

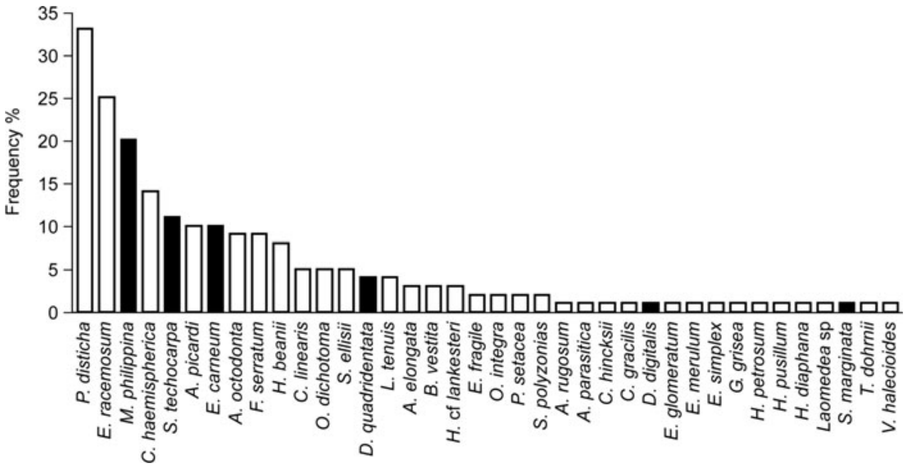

Fig. 7. Total absolute frequency of the species collected, pooling year, season and locality of collection. Species are ordered according to their frequency rank. Black bars indicate the six alien species.

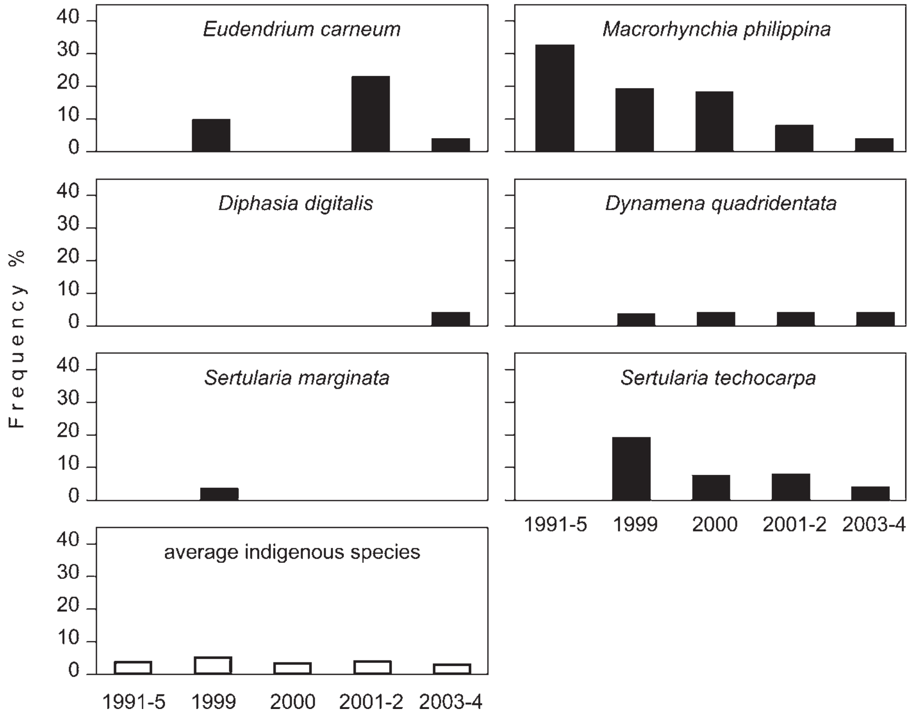

Fig. 8. Relative frequency with respect to the collection periods of the six alien species (black bars). Average indigenous species shown for comparison. Years were grouped to have roughly the same number of samples (18–23) for each period.

endemics and typical Atlantic–Mediterranean species are comparatively less represented.

Nine species are new for the Levant Sea and include widely distributed species (*Filellum serratum, Halecium beanii, Plumularia setacea* and *Sertularella polyzonias*), circum(sub)-tropical species (*E. carneum*, *Halecium pusillum* and *Lafoeina tenuis*), and Mediterranean endemics (*Garveia grisea* and *Halecium petrosum*) indistinctly.

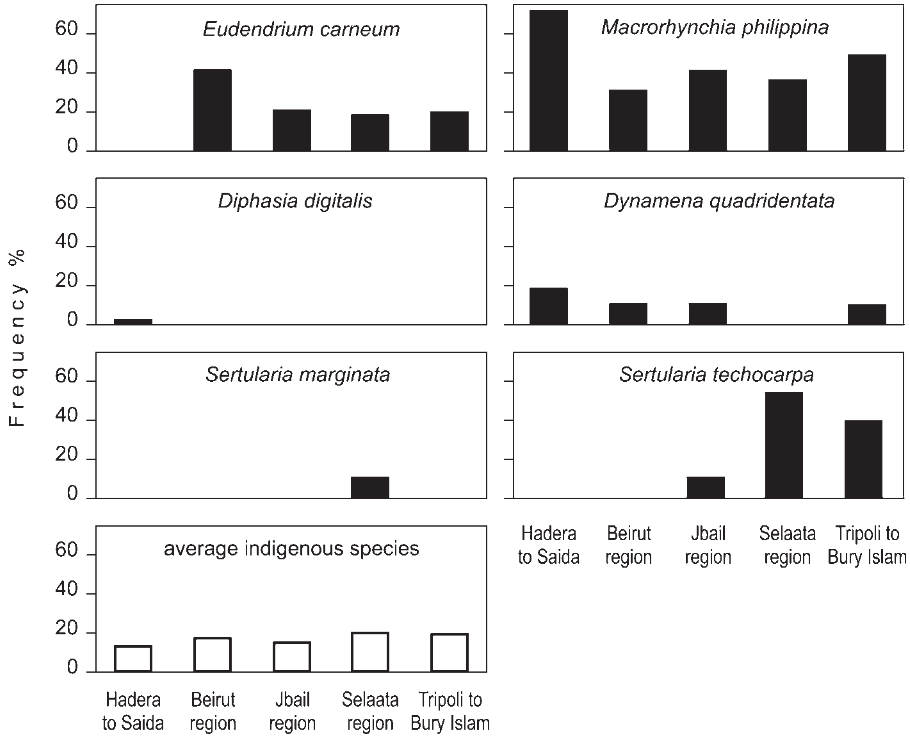

Fig. 9. Relative frequency with respect to different geographical areas (ordered south to north) of the six alien species (black bar). Average indigenous species shown for comparison. Sites were grouped to have roughly the same number of samples (16–22) for each area.

Occurrence of alien species

Three aliens out of six stand among the seven most frequent hydroid species in the present collection along the Levant coast: these are *M. philippina*, *S. thecocarpa* and *E. carneum*, in the order. *Dynamena quadridentata* is also notably frequent, whereas the latter two aliens, *D. digitalis* and *S. marginata*, were found only once (Figure 7). As a whole, the mean frequency of alien species in the present collection was greater than that of indigenous species.

One may speculate that the higher frequency of some of the aliens may be related to their earlier arrival in the Levant Sea (Figure 8). *Macrorhynchia philippina* has occurred in the region since at least the early 1990s. Hirohito (1995) included the Mediterranean within the geographical range of this species but provided no detail—perhaps he misunderstood the finding by Stechow (1919) at Suez as a Mediterranean occurrence. The first solid mention of the species in Lebanon was that by Bitar & Bitar-Kouli (1995: identification confirmed by C. Morri), who found it in polluted waters near Beirut. *Sertularia thecocarpa*, *E. carneum* and *D. quadridentata* have been first collected in 1999. Although Picard (1958b) recorded *S. marginata* from Beirut as early as in 1930, we collected it in 1999 only. Finally, *D. digitalis* was never recorded before 2004.

Macrorhynchia philippina was the most widely distributed alien species in the studied area, followed by *D. quadridentata*, which was collected everywhere but around Selaata (Figure 9). *Eudendrium carneum* was recorded only from Beirut northward, and *S. thecocarpa* from Jbail northward. The remaining two aliens were found at only one site each: *S. marginata* at Selaata and *D. digitalis* at Hadera.

Seasonality

Only *P. disticha* was continuously present throughout the sampled months (April to November), increasing its frequency in late summer and autumn; colonies were bearing gonophores from June to November (Table 2). *Macrorhynchia philippina*, *Eudendrium racemosum* and *H. beanii* were also frequently collected throughout all sampled

Table 2. Seasonality of hydroid species occurrence in the study area, averaged per months over the years 1991 to 2004. No data are available from December to March. N, number of samples per month. Species are listed in alphabetical order. *, alien species. Frequency: +, <10%; ++, 10 to 30%; +++, >30%. ^{R}, fertile.

	April (N = 5)	May (N = 8)	June (N = 11)	July (N = 17)	August (N = 5)	September (N = 16)	October (N = 18)	November (N = 4)
A. elongata	.	.	++	.	.	.	.	.
A. octodonta	++^{R}	+++^{R}	.	.	.	.	++	.
A. picardi	+++	+++^{R}	+^{R}	+	.	++	.	.
A. rugosum	.	.	.	.	.	.	+	.
A. parasitica	.	.	+	.	.	.	.	.
B. vestita	.	.	.	.	.	+	+	.
C. hincksii	.	.	.	.	.	.	+	.
C. gracilis	.	.	.	.	.	+	.	.
C. hemisphaerica	.	.	.	+	.	++	+++^{R}	.
C. linearis	.	.	.	+^{R}	.	.	++	.
*D. digitalis**	.	.	+	.	.	.	.	.
*D. quadridentata**	.	.	.	+	.	+	+	.
*E. carneum**	.	.	.	+^{R}	.	++^{R}	++^{R}	.
E. fragile	.	.	+	.	.	.	+	.
E. glomeratum	.	++	.	.	.	.	.	.
E. merulum	.	.	.	.	.	.	+	.
E. racemosum	.	++	++	++^{R}	+++	++^{R}	+++^{R}	.
E. simplex	.	.	.	.	.	.	+	.
F. serratum	.	++	.	++	.	+	++	.
G. grisea	.	.	.	.	.	+	.	.
H. beanii	.	.	+^{R}	+	.	++^{R}	+^{R}	.
H. cf *lankesteri*	.	.	+	+	.	.	+	.
H. petrosum	.	.	.	.	.	+	.	.
H. pusillum	.	+	.	.	.	.	.	.
H. diaphana	.	.	.	+	.	.	.	.
L. tenuis	.	.	.	+	.	.	++	.
Laomedea sp.	.	.	.	+	.	.	.	.
*M. philippina**	.	++	++^{R}	++	+++	++	++^{R}	++
O. dichotoma	.	.	.	+	.	++	+^{R}	.
O. integra	++	.	.	.	.	.	.	.
P. disticha	++	++	+^{R}	++^{R}	+++^{R}	+++^{R}	+++^{R}	+++^{R}
P. setacea	.	++	.	.	.	+	.	.
S. ellisii	.	.	++	+	.	.	.	.
S. polyzonias	.	++	.	.	.	.	+	.
*S. marginata**	.	.	.	.	.	.	+^{R}	.
*S. techocarpa**	.	++	.	+	.	+	++^{R}	.
T. dohrnii	.	.	.	.	.	+	.	.
V. halecioides	.	++	.	.	.	.	.	.

months, although not so regularly, and showed reproductive in June–July and September–October.

Clytia hemisphaerica, *C. linearis*, *E. carneum*, *Obelia dichotoma*, *S. marginata* and *S. thecocarpa* were fertile in summer and/or autumn. On the contrary, *Aglaophenia octodonta* and *A. picardi* were bearing gonothecae in spring: both are strictly Atlantic–Mediterranean species, whereas all the above mentioned species are more or less widely distributed in warm waters.

The remaining 26 species were never found fertile, and were differently frequent through the sampled months (Table 2).

Depth distribution

Although many species were only collected once, some were found frequently enough to allow for an analysis of their preferred depth-range. Four main situations can thus be distinguished (Figure 10).

(i) Six species (*A. octodonta*, *S. polyzonias*, *H. beanii*, *A. picardi*, *S. thecocarpa* and *Bimeria vestita*) seemed to prefer shallow depths, thriving from just below the sea surface down to less than 10 m.
(ii) Nine species (*Sertularella ellisii*, *Eudendrium fragile*, *H.* cf *lankesteri*, *O. dichotoma*, *L. tenuis*, *C. linearis*, *D. quadridentata*, *P. disticha* and *F. serratum*) were found from shallow waters to about 15 or 20 m.
(iii) Three species (*E. racemosum*, *C. hemisphaerica* and *M. philippina*) were also found in shallow waters but extended down to about 40 m.
(iv) *Aglaophenia elongata* was only collected between 20 and 30 m depth.

Habitat preference

The present collection consists of samples mostly from three kinds of habitats: rocky reefs, caves and harbours (Table 3).

Five species (*A. elongata*, *H.* cf *lankesteri*, *Orthopyxis integra*, *P. setacea* and *S. polyzonias*) were collected exclusively on rocky reefs in open coastal waters. *Macrorhynchia philippina* was also found in harbours but nevertheless was distinctly more frequent on rocky reefs. Five species (*B. vestita*, *F. serratum*, *L. tenuis*, *A. picardi* and *E. racemosum*) were mainly recorded in submarine caves, although mostly at the entrance or in tunnels. Three species (*E. carneum*, *Eudendrium fragile* and *H. beanii*) were more frequent in harbours and marinas. Finally, eight species (*A. octodonta*, *C. hemisphaerica*, *C. linearis*, *D. quadridentata*, *O. dichotoma*, *P. disticha*, *S. ellisii* and *S. thecocarpa*) were ubiquitous in that they showed no preference for any of the three habitats. The remaining 16 species were collected only once.

DISCUSSION

The present record of 38 species, three of which are new for the Mediterranean and nine for the Levant Sea, constitutes a significant increase in the number of hydroid species known for the eastern Mediterranean. Although this figure may appear low in absolute terms, finding nearly one-tenth of the species known for the whole Mediterranean in a single collection, as large it may be, suggests that the regional biodiversity—although lower than that of the western Mediterranean (Boero & Fresi, 1986)—may not be as low as traditionally claimed (Tortonese, 1951), provided that more studies are done. Few other species inventories for the eastern Mediterranean (Adriatic Sea excluded) are available for comparison. Picard (1958b) and Vervoort (1993) listed 13 and 25 species, respectively, from the Mediterranean coasts of Israel. El Beshbeeshy (1993, 1994a, 1994b, 1995a, 1995b) collected 19 species from Mediterranean Egyptian waters, while Abdel-Hamid *et al.* (1984) inventoried 13 species among the fouling organisms of the Suez Canal and Alexandria harbours and shipyards. Taking into account the species in common to two or more inventories, the total of hydroid species known from the Levant Sea rises to 70, with a seemingly exponential accumulation of newly found species with time (Figure 11). Morri & Bianchi (1999), who integrated pre-existing

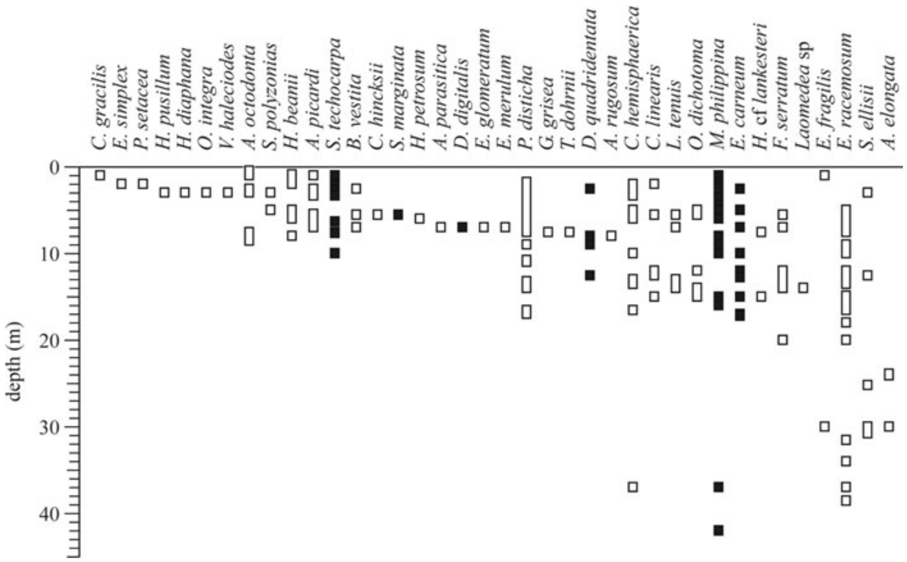

Fig. 10. Observed depth distribution of the species collected. Species are ordered according to their apparently preferred average depth. Black symbols individuate the six alien species.

Table 3. Preferred habitat of occurrence of the individual hydroid species in the study area. N, number of samples per habitat. Species are listed in order of apparent habitat preference and then alphabetically. *, alien species. Frequency: −, collected only once; +, >1 to 34%; ++, 34 to 67%; +++, >67%.

	Rocky reefs (N = 56)	Caves (N = 24)	Harbours (N = 21)
Rocky reef species			
A. elongata	+++	.	.
H. cf *lankesteri*	+++	.	.
*M. philippina**	+++	.	+
O. integra	+++	.	.
P. setacea	+++	.	.
S. polyzonias	+++	.	.
A. rugosum	−	.	.
E. glomeratum	−	.	.
E. simplex	−	.	.
H. pusillum	−	.	.
V. halecioides	−	.	.
Cave species			
B. vestita	+	+++	.
F. serratum	+	+++	.
L. tenuis	.	+++	.
A. picardi	+	++	+
E. racemosum	+	++	+
C. hincksii	.	−	.
C. gracilis	.	−	.
E. merulum	.	−	.
H. diaphana	.	−	.
Laomedea sp.	.	−	.
*S. marginata**	.	−	.
Harbour species			
*E. carneum**	+	+	+++
E. fragile	+	.	+++
H. beanii	+	.	+++
A. parasitica	.	.	−
*D. digitalis**	.	.	−
G. grisea	.	.	−
H. petrosum	.	.	−
T. dohrnii	.	.	−
Ubiquitous species			
A. octodonta	++	++	.
C. hemisphaerica	++	++	+
C. linearis	++	++	.
*D. quadridentata**	+	++	++
O. dichotoma	.	++	++
P. disticha	+	+	++
S. ellisii	++	.	++
*S. techocarpa**	++	++	.

information (Yamada, 1965; Marinopoulos, 1979), totalled 67 hydroid species (or subspecific taxa) from the Aegean Sea and nearby waters of Greece and Turkey.

Six of the species in the present collection can be qualified as aliens. *Macrorhynchia philippina* has been known from Lebanon for nearly two decades: it is now widespread and frequent in the whole area investigated and has recently been recorded also from Turkey (Çinar *et al.*, 2006). Its diffusion on coastal rocks from just below the surface to more than 40 m and the frequent reproductive status (never recorded previously in the Mediterranean) support the claim by Zenetos *et al.* (2006) that it is now fully established in the Mediterranean. *Sertularia marginata* has been known from the Levant Sea since 1930 (Picard, 1958b) but was found only once in the present collection (Selaata, October 1999).

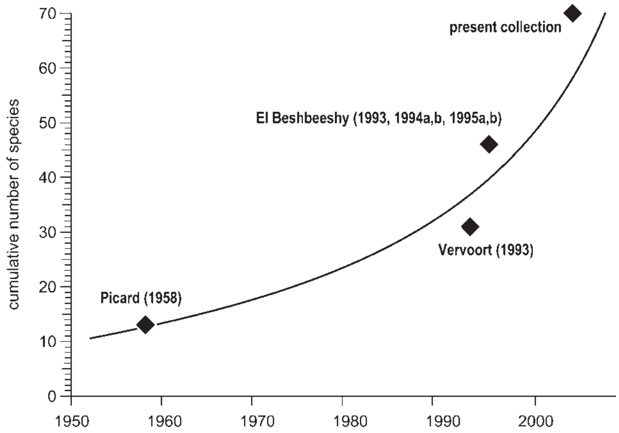

Fig. 11. Increment with time of the number of hydroid species known from the Levant, according to previously published information (Picard, 1958b; Vervoort, 1993; El Beshbeeshy, 1993, 1994a, 1994b, 1995a, 1995b) and the present collection.

Thus, notwithstanding earlier introduction, *S. marginata* may not have established as well as *M. philippina*: as no further Mediterranean records are available, the species apparently has failed to get fully naturalized in the Mediterranean or the habitat where it thrives preferentially has not yet been detected. *Eudendrium carneum* had previously been recorded in the western Mediterranean and the Adriatic (Gili, 1986; Bavestrello & Piraino, 1991; Marques *et al.*, 2000). Being particularly frequent in the present collection may be interpreted as a significant range expansion to the Levant Sea in recent years (unless it arrived there before but went unnoticed). *Dynamena quadridentata* and *Sertularia thecocarpa* have been thriving in the Levant Sea since at least 1999. Finally, *Diphasia digitalis* seems to have penetrated very recently and still inhabits a restricted range in the Levant Sea: finding it in Hadera harbour parallels the finding of the Indo-Pacific gorgonian coral *Acabaria erythraea* (Fine *et al.*, 2005).

The origins of the six alien species may not be homogeneous. *Sertularia thecocarpa* was previously known only from the Indo-West Pacific, so its penetration into the eastern Mediterranean by the route of the Suez Canal is likely. *Macrorhynchia philippina*, *D. digitalis* and *D. quadridentata* may also be Red Sea immigrants: although circumtropical in distribution, they have never been found to date in the western Mediterranean and are common in the Red Sea (Mergner & Wedler, 1977). Things are different with *E. carneum* and *S. marginata*, two circumtropical species previously known from the western Mediterranean (Bouillon *et al.*, 2004): there are several recent cases of Atlantic immigrants that have crossed the Strait of Sicily to reach the Levant Sea (Bianchi, 2007) so that a Red Sea origin for these two species cannot be taken for granted. None of these aliens has free-swimming medusa stages, so that their dispersal into the Levant Sea must have occurred as hydroids, perhaps within ship hull fouling (Morri & Boero, 1986; Shoukr, 1987).

The general warm-water affinity of these six aliens reinforces the subtropical character of the hydroid fauna of the Levant Sea. As a whole, the present collection showed a greater proportion of circum(sub)tropical species and a lowered proportion of Atlantic–Mediterranean elements and Mediterranean endemics with respect to the rest of the Mediterranean Sea (Boero & Bouillon, 1993). This picture, however, may be in part due to lack of sampling during the coldest months of the year, as most Mediterranean hydroids thrive in winter (Bavestrello *et al.*, 2006).

The ecology of the six alien hydroids in the Mediterranean Sea is outlined for the first time in the present paper. The ecology of the indigenous species is in many cases consistent with what is known for the more studied western Mediterranean. There are exceptions, however.

Some species (e.g. *Eudendrium racemosum*) showed reproductive in the same months as in the rest of the Mediterranean (Bouillon *et al.*, 2004), whereas for other species the reproductive period was extended (e.g. *Halecium beanii*) or, on the contrary, restricted (e.g. *Clytia hemisphaerica* and *C. linearis*). Among the latter, the two strictly Atlantic–Mediterranean species *Aglaophenia octodonta* and *A. picardi*, which reproduce all year round in the north-western Mediterranean, showed fertile only during spring months, thus probably avoiding the high summer temperature.

Depth distribution of the indigenous species roughly conformed to the patterns described by Boero & Fresi (1986) in the north-western Mediterranean, although *Sertularella polyzonias*, *A. picardi* and *Bimeria vestita* were restricted to shallower water in the present collection. On the contrary, *Pennaria disticha* was found deeper than usual (Morri & Boero, 1986).

As for habitat preference, considerable analogy with the western Mediterranean was found for rocky reefs (Boero & Fresi, 1986) and, to a lesser extent, submarine caves (Boero, 1985), whereas harbours have no species in common (Chimenz Gusso & Rivosecchi Taramelli, 1975; Morri & Bianchi, 1983). Four out of the six aliens (*M. philippina*, *E. carneum*, *D. digitalis* and *D. quadridentata*) were found in harbours. *Ectopleura crocea* (=*Tubularia c.*), the dominant species in western Mediterranean harbours, had been found abundant in Egyptian harbours (Abdel-Hamid *et al.*, 1983; Shoukr & Abdel-Hamid, 1987) but was not observed in the ports sampled for this study (Beirut and Trablus).

The high incidence of alien species (perhaps not just Red Sea immigrants), the apparently reduced proportion of Atlantic–Mediterranean elements and Mediterranean endemics, and the peculiarities in the ecology of indigenous species ask for future investigation on the zoogeographical and ecological traits of the hydroid fauna of the Levant Sea. Because of the sampling approach, the present collection was probably efficient only in collecting the most conspicuous and obvious species: sampling in different microhabitats would surely lead to a greater number of species.

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