

The limit of the sea: the bathyal fauna of the Levantine Sea*

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SUMMARY: In the present study, the fish, molluscs, crustaceans and echinoderms collected at depths between 734 and 1558 m during a series of cruises conducted between 1988 and 1999 off the coast of Israel, supplemented by a photographic survey carried out southwest of Cyprus at a depth of 2900 m, were analysed. The main objectives were to determine the faunal composition of the bathybenthic assemblages in the southeastern Levantine Sea, and to compare them with the western Mediterranean assemblages in order to elucidate whether general trends in their bathymetric distribution and population density may be related to environmental/geographic factors. Considering the sampling effort, the diverse gear used and the extended period of sampling, we may assume that the low number of species and specimens recorded actually reflects a low-diversity, low-density deep water fauna. The faunal scarcity may cause a different parcelling of the populations which is reflected in bathymetric distributions that in many cases extend to greater depths than in the Western Mediterranean. The Levantine bathybenthos is composed of autochthonous, self-sustaining populations of opportunistic, eurybathic species that have settled there following the last sapropelic event.

Key words: Mediterranean Sea, Levantine Sea, bathyal, diversity, abundance, bathymetric distribution, new records, fish, Decapoda, Amphipoda, Cumacea, Mollusca.

RESUMEN: EL LÍMITE DEL MAR: LA FAUNA BATIAL DEL MAR LEVANTINO. – En este estudio se analizan los peces, los moluscos, los crustáceos y los equinodermos recolectados a profundidades entre 734 y 1558 m, durante una serie de campañas de muestreo realizadas entre 1988 y 1999 delante de las costas de Israel. Estas muestras se complementan con fotografías submarinas realizadas a 2900 m de profundidad al suroeste de Chipre. El objetivo es determinar la composición faunística de las asociaciones batipelágicas en el sureste del mar Levantino y compararla con las asociaciones del Mediterráneo occidental, con el fin de observar si existen tendencias generales en su distribución batimétrica y en las densidades de las poblaciones, de manera que puedan ser relacionadas con factores geográficos y ambientales. Considerando el esfuerzo realizado en muestreo, los diversos artes usados y el amplio período de muestreo, podemos asumir que el bajo número de especies y especímenes registrado refleja realmente la baja diversidad y la baja densidad de la fauna de las aguas profundas. La escasa fauna puede causar un distinto parcelado de las poblaciones que se refleja en su distribución batimétrica la cual en muchos casos se extiende hacia las más grandes profundidades del Mediterráneo occidental. El batibentos levantino está compuesto por especies autóctonas, poblaciones de especies oportunistas auto-sostenibles y euribáticas, que colonizaron estos fondos desde el último evento sapropélico.

Palabras clave: mar Mediterráneo, mar Levantino, batial, diversidad, abundancia, distribución batimétrica, nuevas citas, peces, Decapoda, Amphipoda, Cumacea, Mollusca.

INTRODUCTION

Undeterred by Forbes' (1844: 170) notorious observation "Zero of Animal Life probably about 300

fathoms", the scientific exploration of the Levantine bathyal biota commenced with the extensive voyages of the *Pola* (1890-1893). In 1910 the Danish Oceanographic Expedition to the Mediterranean, aboard the *Thor*, sampled nine sites along the western limits of the Levantine Sea, from Cyrenaica to

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Rhodes. However, as that expedition was concerned mainly with plankton investigations, and “dredgings were only occasionally made ... the result will thus necessarily be but poor” (Stephensen, 1915). The Lamont Geological Observatory research vessel *Vema* collected few deep benthic samples in 1958 (Barnard, 1964). Four deep-water shark species were collected in five hauls using bottom long-line at depths of 1330–1440 m off the Mediterranean coast of Israel in 1985 (Golani, 1987). The German research vessel *Meteor* [cruise 5] in 1987, collected benthic samples at sites between Crete and Israel at depths ranging between 95 and 4396 m during a ten-day sojourn (Janssen, 1989). The handful of deep sea fishes gathered persuaded Klausewitz (1989) that “this collecting trip confirmed the paucity of the deep sea fish fauna in the eastern basin of the Mediterranean”. The *Meteor* returned in 1993 [cruise 25], to collect deep-sea biota from the region between Crete, Cyprus and Egypt at depths ranging between 194 and 2812 m, as well as sea bed litter (Galil *et al.*, 1995). The fauna of Eratosthenes Seamount, south of Cyprus, was briefly sampled by the *Poseidon* [cruise 201/2] in February 1994 (Galil and Zibrowius, 1998). Among the faunistic explorations of the Levantine bathyal, only Gilat and Gelman (1984), and Jones in Priede and Bagley (2000) made use of photographic equipment to observe the deep fauna in its environment.

The meagre number and extent of the explorations prompted Fredj and Laubier (1985), in their review on the deep Mediterranean benthos, to declare that “...the southern part of the Levant Sea has practically never been studied”.

The present study analysed the data obtained from samples collected by a box corer and a bottom trawl fitted with a plankton net during a series of cruises conducted between 1988 and 1999 as part of pollution monitoring surveys by the Israel Oceanographic and Limnological Research (IOLR) off the coast of Israel, at depths between 734 and 1558 m, supplemented by a photographic survey carried out southwest of Cyprus, at a depth of 2900 m. The main objectives were to determine the faunal composition of the bathybenthic assemblages in the southeastern Levantine Sea, and to compare them with the western Mediterranean assemblages in order to elucidate whether general trends in their bathymetric distribution and population density may be related to environmental factors. Although restricted to a small area and to the depth range mentioned above, this study has significantly increased our knowledge of the Levantine deep sea fauna.

STUDY AREA AND METHODS

The Levant Sea occupies the easternmost Mediterranean, east of the line connecting Rhodes and the coast of Cyrenaica. It is isolated from the deep Atlantic waters by the topographical and hydrological barriers posed by the shallow Gibraltar Straits and the Siculo-Tunisian sill. The Levantine deep water mass is distinguished by salinity and temperature values that are higher than in the rest of the Mediterranean ($T < 13.8^{\circ}\text{C}$, $S < 38.74$, below 700 m) (Hecht *et al.*, 1988). The Levantine Sea is ultra-oligotrophic (Berman *et al.*, 1984; Krom *et al.*, 1991): Chlorophyll *a* concentrations are as low as $0.4 \mu\text{g l}^{-1}$ nearshore, and decrease offshore to $0.05 \mu\text{g l}^{-1}$ (Berman *et al.*, 1986; Yacobi *et al.*, 1995).

The area investigated is located off the coast of Israel, at depths between 734 and 1558 m. The material was collected during monitoring surveys of two deepwater waste-dumping sites: an acidic sludge disposal site off Haifa (between $33^{\circ}00'N$ $34^{\circ}37'E$ and $33^{\circ}01'N$ $34^{\circ}47'E$), a coal fly ash disposal site off Hadera (between $32^{\circ}38'N$ $34^{\circ}02'E$ and $32^{\circ}36'N$ $34^{\circ}16'E$), and a control site off Atlit (between $32^{\circ}53'N$ $34^{\circ}10'E$ and $32^{\circ}51'N$ $34^{\circ}23'E$). The samples were collected aboard the R/V *Shikmona* (720 HP; 27 m), using a modified Agassiz benthic trawl (2.3 m width and 0.9 m height), a 45 ft Marinovitch-type deep water trawl (codend mesh 6 mm) with a 0.5 mm plankton net secured atop, and a 0.062 m^2 box-corer with an effective penetration of 40 cm (Ocean Instruments model 700 AL) (Table 1). The samples were preserved in 10% buffered formalin aboard ship. In the laboratory, the samples were washed and sieved through a $500 \mu\text{m}$ mesh, preserved in 70% alcohol, stained in Rose Bengal and sorted.

The photographic survey took place southwest of Cyprus, at depth of 2900 m. A total of 80 hours of video were recorded utilising a remote operating vehicle (Remora 6000, Phoenix).

RESULTS

Fishes

A total of 566 specimens identified to 31 species were collected during the study. Four species were new records for the eastern Mediterranean, four species were new records for the Levantine Sea and five species were newly recorded from the Israeli coast (Galil and Goren, 1994; Goren and Galil,

TABLE. 1. – List of cruises: date, location, depth, type of equipment and number of samples (n)

Date	Location	Depth (m)	Agassiz (n)	Marinovich (n)	Plankton (n)
XI 1988	Hadera	1370-1500	4		
I 1989	Haifa	1345-1450	3		
V,VI 1989	Atlit	1422-1527	5		
X1989	Haifa	1240-1441	5		
V 1990	Hadera	1400-1500	5		
VI 1990	Atlit	1400-1550	2		
V 1991	Hadera	1308-1500	9	5	
III 1993	Hadera	1387-1494	4		
IV 1993	Atlit	1435		1	
X 1993	Haifa	1360-1436		4	4
XII 1993	Hadera	1300-1500	4	1	
XII 1994	Hadera	1290-1482		8	8
I 1995	Atlit	1000-1561		8	7
X 1995	Hadera	1279-1485		12	8
XI 1995	Haifa	1224-1471		11	9
IX 1996	Atlit	1427-1562		8	6
X,XI 1996	Hadera	1281-1529		16	16
IX 1997	Hadera	1227-1454		9	7
IX 1997	Haifa	1227-1439		8	8
XI 1998	Hadera	1243-1500		14	13
X 1999	Atlit	1413-1557		7	7
X 1999	Hadera	1260-1485		14	13

1997; Goren and Galil, 2002). *Bathypterois mediterraneus* and *Nezumia sclerorhynchus* were the most common species, with nearly 38 and 27% of the specimens respectively. The Myctophidae and Macrouridae were represented by most species, with five and four species respectively (Appendix 1).

Three species were identified from the video records photographed southwest of Cyprus, at 2900 m, *Bathypterois mediterraneus*, *Cataetyx laticeps*, and *Chauliodus sloani* - none of which had been photographed previously in the Levantine bathyal.

Decapod crustaceans

A total of 2819 specimens identified to 19 species were collected during the study. The Mediterranean endemic geryonid crab *Chaceon mediterraneus* was photographed southwest of Cyprus, at 2900 m. In total, one species, *Levantocaris hornungae*, was described as new to science, five species were new records for the Levantine Sea and eight species were newly recorded from the Israeli coast (Galil and Clark, 1993; Galil and Goren, 1994; Appendix). *Polycheles typhlops*, *Acantheephyra eximia*, *Aristeus antennatus*, and *Geryon longipes* were the most prevalent and common species, with nearly 48, 25, 14 and 7% of the specimens respectively.

Amphipod crustaceans

A total of 673 amphipod specimens identified to 22 species were collected during the study

(Sorbe and Galil, 2002). Seventeen species constitute new records for the Levantine Sea, and four were newly recorded from the Israeli coast (Appendix 1). Four of the 22 deep-sea amphipod species collected are Mediterranean endemics. Two of the endemic species were the most frequently collected and the dominant species in the samples: *Ilerastroe ilergetes* and *Pseudotiron bouvieri* were identified in 38 and 23 of our 44 samples, with 40 and 15% of the specimens respectively. *Rhachotropis rostrata* and *Stegophaloides christianiensis* were the next most common species, each with nearly 11% of the specimens, and 23 and 22 of our samples respectively.

Cumaceans

A total of 575 specimens identified to 12 species were collected from three trawling campaigns in 1988-99. As the deep-water cumaceans of the Levantine Sea had not been studied previously, they all constitute new records (Corbera and Galil, 2001). *Procampylaspis bonnieri* was the most frequently collected and the dominant species in the samples, with 193 specimens. *Campylaspis glabra* was the next most common species, with nearly 13%, followed by *Makrokyllindrus longipes*, *Platysympus typicus* and *Procampylaspis armata*, each with nearly 11% of the specimens. These species were identified in 22, 19, 18 and 17 of our 27 samples respectively.

Molluscs

A total of 4580 molluscan specimens identified to 42 species were collected (Bogi and Galil, 2004). Four species constitute new records for the eastern Mediterranean, and 6 are newly recorded from the Levantine Sea. The most common benthic molluscs in depths greater than 1000 m off the Israeli coast are *Yoldia micrometrica*, *Kelliella abyssicola*, *Cardyomia costellata*, *Entalina tetragona*, *Benthomangelia macra*, *Benthonella tenella* and *Bathycarca pectunculoides* present in 83, 77, 76, 63, 59, 50 and 33 out of the 90 samples, with 827, 561, 437, 485, 112, 230 and 64 live specimens respectively. Much of the material examined consisted of juvenile specimens and empty shells - only 23 species were represented by living specimens, 11 of which were represented solely by juvenile specimens.

Echinoderms

Sixteen specimens of a single synallactid holothurian species, *Mesothuria intestinalis*, were collected.

DISCUSSION

Examination of the results of a total of 167 trawl hauls from a series of 22 cruises conducted between 1988 and 1999 off the coast of Israel, supplemented by a photographic survey carried out southwest of Cyprus, allows us to compare the faunal composition of the Levantine Sea bathyal with that reported from the opposite end of the Mediterranean, the Catalan Sea in the northwestern Mediterranean, where extensive surveys of the deep water fauna have resulted in a comprehensive corpus of data (Abelló and Valladares, 1988; Stefanescu *et al.*, 1992, 1993; Cartes, 1993; Cartes and Sorbe, 1993, 1997, 1999; Cartes and Sardà, 1993).

Fishes

An extensive survey of the demersal fishes of the Catalan Sea consisting of 100 samples taken at depths between 960 and 2251 m collected 31 species (Stefanescu *et al.*, 1992). Thirteen of the 20 demersal and benthopelagic fish species collected during the IOLR monitoring surveys are common to both lists. *Bathypterois mediterraneus* is by far the pre-

dominant species in both surveys, but of the next most common species in the Catalan Sea, the morid *Lepidion lepidion* and the macrourid *Coryphanoidea guentheri*, the former is absent from our samples and the latter is known from 3 specimens. *Bathypterois mediterraneus* was the dominant species also on the lower slope (1400-1600 m) in the Algerian basin (Moranta *et al.*, 1998), but of the next most common species there, *Alepocephalus rostratus* and *Coelorhynchus labiatus* [= *Caelorinchus mediterraneus*] the former is absent from our samples and the latter is known from 16 specimens. Conversely, of the next most common species in our survey, *Nezumia sclerorhynchus* and *Nettastoma melanurum*, the former is absent from the Catalan Sea samples and the latter is known from 13 specimens. In a survey of the demersal fish in the Eastern Ionian Sea at depths between 600 and 2600 m, *B. mediterraneus*, *Mora moro*, *N. sclerorhynchus* and *N. melanurum* were the most common species at depths greater than 800 m (D'Onghia *et al.*, 2004), whereas in Heraklion Bay, Crete, at 1000 m *Mora moro* was by far the most common species (Kallianiotis *et al.*, 2000).

Though a photographic survey by a remotely operated vehicle is limited to the large, non-burrowing, non-evasive organisms, in conjunction with qualitative data obtained by trawling, it provides a more complete view of deep-sea megafaunal communities. Among the faunistic explorations of the Levantine bathyal, only Gilat and Gelman (1984), and Jones in Priede and Bagley (2000) made use of photographic equipment to observe the deep fauna in its environment. Gilat and Gelman employed a free-fall camera positioned on top of a bait holder, taking still photographs at 5 minute intervals for 18 hours, at six sites between Israel and Cyprus. The deepest site, at 1490 m, was located off Cyprus. Jones used an autonomous unmanned lander platform equipped with cameras and sonars to track movements of fish attracted to bait in the Cretan sea (1500-2500 m), Rhodes Basin (2300 - 3850 m), and Ierapetra Basin (3080-4172 m). Both surveys utilised bait, thus attracting facultative or obligate scavengers. Off Cyprus, at 1490 m depth, the sharks *Centrophorus granulosus* and *Etmopterus spinax* were the most abundant species, constituting over 83% of the records (Gilat and Gelman, 1984). In the Cretan Sea (1500-3850 m) and Rhodes Basin (2300 - 3850 m), again sharks (*Hexanchus griseus*, *Galeus melastomus*, *Centrophorus* spp., *Centroscymnus coelolepis*, and *Etmopterus spinax*) predominated,

together with the teleost fishes *Chalinura mediterranea* and *Lepidion lepidion* (Jones in Priede and Bagley, 2000). Our survey, transacted without resorting to bait, documented the site-typical faunal complement. There is no doubt that the abundance of the Levantine deep water megafauna is remarkably low: in 80 hours of video documentation only three fishes, *B. mediterraneus*, *Cataetix laticeps* and *Chauliodes sloani*, were recorded. Although our methods were not sufficient for quantitative comparison with studies made in the western Mediterranean, the small number of species and specimens confirms the ichthyofaunal scarcity of the Levantine Sea, not only compared with the adjacent Atlantic Ocean (Haedrich and Merrett, 1988), but also with the western Mediterranean.

Decapod crustaceans

Twenty-one bathyal decapods were reported from a faunistic survey of the Catalan sea conducted between 1983 and 1985 consisting of 39 trawl samples taken between 1020 and 2011 m (Abelló and Valladares, 1988), and 28 species were identified from 57 samples trawled between 862 and 2265 m in 1988 and 1989 (Cartes, 1993). In all, 29 benthic, mesopelagic and bathypelagic decapod crustaceans have been identified from the Catalan deep sea. Fifteen of the 20 decapod species collected during the IOLR monitoring surveys are common to both localities. Of the most common species at 1350-1549 m in the Catalan sea (Cartes, 1993)—*Aristeus antennatus*, *AcanthePHYra eximia*, *Pontophilus norvegicus*, *Polycheles sculptus* and *Munida tenuimana*—only the first two species occur in our samples. The most common species in the Levantine samples, *Polycheles typhlops*, was more common on the middle slope than on the lower slope in the Catalan sea. The cold stenothermal *Sergestes arcticus* and *Pontophilus norvegicus* are absent, though the pelagic larvae of the former have been found at a depth of 10 m, and the latter was recorded at 50 m (d'Udekem d'Acoz, 1999). *Polycheles sculptus*, *Munida tenuimana* and *Munidopsis serri-cornis* [= *M. tridentata*] are known only from the western basin of the Mediterranean. *Plesionika narval*, *Munidopsis marionis* and *Bathynectes maravigna* were identified from the Levantine samples and from the western Mediterranean, but not from the surveys in the Catalan sea. In a survey of the decapod fauna of the Eastern Ionian Sea at depths between 1000 and 1500 m, *A. antennatus* was as

abundant as *P. typhlops* (Company *et al.*, 2004), whereas in the Levantine Sea *P. typhlops* is more than three times as abundant as *A. antennatus*.

Amphipod crustaceans

Fifty-two bathyal amphipod crustaceans were reported from a survey of the Catalan Sea suprabenthic bathyal communities (552 - 1808 m) conducted in 1989 and consisting of 10 hauls (Cartes and Sorbe, 1993), and 82 species were identified from 20 samples trawled between 389 and 1859 m in 1991-92 (Cartes and Sorbe, 1999), compared with the 22 species identified from 27 hauls in the Levant Sea. All but one of the amphipod species collected during the IOLR monitoring surveys, *Stegophaloides christianiensis*, have been recorded from the Catalan Sea. The dominant species on the upper part of the lower slope (1250-1355 m) in the Catalan Sea was *Rhachotropis caeca*, whereas on the lower part (1860 m) *Ilerastroe ilergetes* and *Rhachotropis caeca* predominate (Cartes and Sorbe, 1999). *Ilerastroe ilergetes* is the most common and prevalent species in the Levant Sea, present in 86% of the samples, as compared with 6.3 and 20.8% respectively in the upper and lower parts of the lower slope of the Catalan Sea. However, whereas *R. caeca* appears in 36.3% of the samples taken between 1250 and 1355 m on the Catalan slope, and its congener, *R. rostrata*, in only 4.3% of these samples, along the Levantine coast their abundance is reversed: *R. caeca* is present in 33% of the samples whereas *R. rostrata* is present in over half. The next most common species on the lower slope in the Catalan Sea, *Bathymedon* sp. A and *Andaniexix mimonectes*, are entirely absent from our samples. Only four species collected in our study are Mediterranean endemics, whereas of the 154 deep sea amphipods known from the Mediterranean as a whole, 71 are endemic species (Bellan-Santini, 1990).

Cumaceans

Twenty-eight bathyal cumacean species were reported from a survey of the muddy bottoms of the slope (552-1808 m) of the Catalan sea (Cartes and Sorbe, 1993), and 32 species were identified from 21 samples trawled between 389 and 1859 m in 1991 and 1992 (Cartes, 1997), compared with the 12 species identified from 27 hauls in the Levant Sea. All of the cumacean species collected during the

IOLR monitoring surveys have been recorded from the Catalan Sea. The dominant species on the lower slope in the Catalan Sea was *Cyclaspis longicaudata* (Cartes and Sorbe, 1993, 1997), whereas only 11 specimens were identified in our samples. The most common and abundant species in the Levantine samples, *Procampylaspis bonnieri*, was more common on the middle slope (862-989 m) than on the lower slope in the Catalan sea (Cartes and Sorbe, 1993). The characteristic bathyal cumacean assemblage in the western Mediterranean, consisting of *C. longicaudata*, *P. bonnieri*, *P. armata*, *Bathycuma brevirostre* and *Platysympus typicus*, is somewhat modified in the Levant Sea, where *C. longicaudata* is replaced by *Makrokyllindrus longipes*, the latter species again being more common on the middle slope than on the lower slope in the Catalan sea (Cartes and Sorbe, 1993, 1997).

Molluscs

Salas (1996:90) found that the molluscan fauna in the Alboran Sea “becomes scarce below 1000 m with hardly more than one living specimen per haul, and the deepest samples at 1433 ... and 1742 m ... were barren”. Di Geronimo *et al.* (2001), who examined the composition and depth range of molluscs from the bathyal thanatocoenoses of the southern Tyrrhenian Sea, have established that the most common benthic species at 1139-1536 m were, in descending order, *Benthonella tenella*, *Kelliella abyssicola*, *Ennucula corbuloides*, and *Microgloma tumidula*, of which only the first two species occur in our samples. The most common benthic molluscs at depths greater than 1000 m off the Israeli coast are the Atlanto-Mediterranean and Boreal *Benthonella tenella*, *Kelliella abyssicola*, *Yoldia micrometrica*, *Cardyomia costellata*, *Entalina tetragona*, *Benthomangelia macra*, and *Bathyarca pectunculoides*. The same species were identified by Janssen (1989) in material sampled by boxcore at a station off the Israeli coast at 1217 m. Though all are present in the southern Tyrrhenian Sea, except for the first three species, they are rather rare (Di Geronimo *et al.*, 2001).

Levantine low-diversity, low-density deep water fauna

“The floro-faunistic impoverishment of the eastern Mediterranean compared with the western Mediterranean richness in species” (Sarà, 1985) has

been generally accepted, as well as the perception of a gradational decrease from west to east that is more conspicuous for the deep benthos than for the whole fauna (Fredj and Laubier, 1985): a survey of the biota of the Balearic basin and the western and eastern Ionian Sea at depths between 1000 and 1500 m has shown that the biomass of demersal decapods was 48268, 17440 and 4376 g km² respectively (Company *et al.*, 2004).

The low-diversity, low-density Levantine deep water fauna has long been presumed to be the poorest in the Mediterranean (Fredj, 1974). It was recognised that the scanty data may be due to sparse research efforts, that the “the different parts of the deep Mediterranean have not been equally sampled” (Fredj and Laubier, 1985), and that a particularly “limited amount of sampling [was] carried out in the eastern basins” (Bellan-Santini, 1990). It was even suggested that “[t]he relative species richness of ... faunas of the different sectors of Mediterranean is better correlated with the level of research effort than the true species richness” (Bellan-Santini, 1990). As late as 1989 it was still possible for Klauswitz to wonder “whether an ecological or a geographical factor may be the reason for this limited distribution or whether the low number of zoological resp. [sic] oceanographical stations and research ships in the eastern half of the Mediterranean provides the reason for the lack of records.” However, considering the sampling effort, the diverse gear used and the extended period of sampling, we may assume that the low number of species and specimens recorded does not stem solely from selective or inefficient gear, and is unlikely to increase much with additional surveys using similar sampling gear, though the number may be augmented by using other sampling methods.

Bathymetric distribution of the Levantine deep water fauna

As early as 1893 Marenzeller reported that species occur deeper in the Levant than elsewhere in the Mediterranean. Marenzeller’s records were considered suspect, an artefact resulting from a “systematic mistake on the depth measurements” that “needs to be cleared up in the future” (Fredj and Laubier, 1985: 128). Recent studies published greater depth records in the Levantine Sea than in the western Mediterranean for 14 serpulid species, with a third of the depth extensions > 400 m (Ben Eliahu and Fiege, 1996). Twenty-two fish species

were collected or photographed in the Levant Sea at depths greater than in the western Mediterranean (Goren and Galil, 1997, 2002). Several molluscs, *Crenilabium exile*, *Yoldiella philippiana*, *Bathyarca philippiana*, *Thyasira granulosa*, *Allogramma formosa*, and *Cuspidaria rostrata*, have been collected from greater depths in the Levantine Sea than in the southern Tyrrhenian Sea (Di Geronimo *et al.*, 2001). Extension of the depth records was also reported for five of the bathyal amphipods collected off the Israeli coast, in the case of *Bathymedon monoculodiformis*, for as much as 1100 m (Sorbe and Galil, 2002). The Levantine Sea bathyfaunal scarcity may cause different parcelling of the populations that is reflected in bathymetric distributions that differ from those of the western Mediterranean deep water assemblages.

Geographical and environmental factors and the Levantine deep water fauna

The Mediterranean Pleistocene bathyal assemblages are more closely related to the Atlantic bathyal than to the present-day Mediterranean deep water fauna (Barrier *et al.*, 1996). This disparity was attributed in part to the shallow Gibraltar sill that bars the deep water of the Atlantic Ocean from entering the Mediterranean, and the Mediterranean outflow that bars the entry of the deep water Atlantic fauna into the Mediterranean (Salas, 1996). The onset of the warm homothermy led to the demise of many cold stenothermic and stenohalinic species and the eventual impoverishment of the bathybenthos. In addition, the extreme oligotrophy of the Levantine Sea prevented settlement by members of the Atlantic bathyal that have been able to cross the shallow Gibraltar Straits and the Siculo-Tunisian sill (< 400 m) (Pérès, 1985). The recurring stagnant (dysoxic and anoxic) Quaternary episodes resulted in a reduction, or even extinction of deep bottom-living fauna unable to avoid annihilation by adapting to shallower depth: Van Harten (1987) reported that “Several species of deep-water ostracodes that are still common in the Western Mediterranean became extinct in the Eastern Mediterranean basin at the onset of early Holocene S1 sapropel deposition”. Bacescu (1985) believed that the bathyal bottoms of the Levant are still “unfavourable”, or even “azoic”, after the last sapropelic event, dated between 9000 and 6000 years BP, and George and Menzies (1968) suggested “that sufficient time has not elapsed to allow colonisation of the deep-sea floor”.

The bathybenthic amphipods and cumaceans are indicative because the low mobility of their adults and their lack of a pelagic larval stage would restrict their dispersal into the Levantine Sea, effectively separated from the Atlantic Ocean by the Gibraltar and Siculo-Tunisian straits. Indeed, the common amphipods and cumaceans at depths greater than 1000 m off the Israeli coast are all eurybathic Atlanto-Mediterranean and Boreal species with an upper bathymetric range enabling them to overcome that barrier. None of the species with an upper bathymetric limit set at 400 m (Bellan-Santini, 1990) were collected during the study. This is the case for the molluscan fauna as well: *K. abyssicola*, *C. costellata*, *E. tetragona* and *B. pectunculoides* are eurybathic species with upper bathymetric range well within the circalittoral (> 150 m), whereas both the more stenobathic *B. macra* and *B. tenella* have epipelagic larvae (Bouchet and Warén, 1979), enabling them to overcome the barrier posed by the shallow sills. However, 9 of the 12 thecostomate species collected in the Levantine Sea were recorded from cores dating to the upper and middle Pleistocene taken in the Ionian Sea (Grecchi, 1984) and, in fact, 12 of the 13 thecostomate species known from the western Mediterranean (Corselli and Grecchi, 1990) were collected in the present study off the coast of Israel. The evidence that the strictly epipelagic fauna is not impoverished in terms of species richness underscores the importance of the sills and/or the Quaternary extinctions in determining the character of the deep bottom-living fauna.

Bouchet and Taviani (1992) suggested that much of the Mediterranean deep-sea fauna is made-up of non-reproducing pseudopopulations that have entered the Mediterranean as meroplankton with the Atlantic inflow at Gibraltar. However, the populations of the most common benthic molluscs at depths greater than 1000 m off the Israeli coast are composed of both adult and juvenile specimens, and one species, *Yoldia micrometrica*, the most common and abundant species in the Eastern Mediterranean, is unrecorded from the westernmost part of the sea (Salas, 1996). Moreover, gravid benthic decapod crustaceans and fish were collected from the depths of the Levantine Sea (Galil and Goren, 1994; Goren and Galil, 1997; Fishelson and Galil, 2001).

Though much reduced in diversity and richness compared with the deep sea fauna of the western and central basins of the Mediterranean, the Levantine bathybenthos is composed of autochthonous, self-

sustaining populations of opportunistic, eurybathic species that have settled there following the last sapropelic event.

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APPENDIX 1. – List of species collected in the course of the IOLR deep Levantine campaigns 1988-1999 (*, New record for the eastern Mediterranean; **, New record for the Levantine Sea; ***, New record for the Israeli coast).

Fishes

- Chondrichthyes
Hexanchidae
Hexanchus griseus (Bonnaterre, 1788)
Scyliorhinidae
Galeus melastomus Rafinesque, 1810
Centrophoridae
Centrophorus granulosus (Schneider, 1801)
Dalatiidae
Etmopterus spinax (Linnaeus, 1758) *
Squalidae
Squalus acanthias Linnaeus, 1758
Squalus blainvillei (Risso, 1826)
Somniosus rostratus (Risso, 1826)
Chimaeridae
Chimaera monstrosa Linnaeus, 1758 **
Osteichthyes
Gonostomatidae
Cyclothone pygmaea Jespersen and Tåning, 1926 ***
Sternoptychidae
Argyrolepeus hemigymnus Cocco, 1829
Phosichthyidae
Vinciguerria poweriae (Cocco, 1838)
Stomiidae
Chauliodes sloani Schneider, 1801
Stomias boa (Risso, 1810)
Ipnopidae
Bathypterois mediterraneus Bauchot, 1962 ***
Myctophidae
Diaphus holti Tåning, 1918 ***
Diaphus rafinesquei (Cocco, 1838)
Electrona rissoi (Cocco, 1829) ***
Hygophum hygomii (Lütken, 1892) ***
Lampanyctus crocodilus (Risso, 1810)
Paralepididae
Paralepis speciosa Bellotti, 1878
Heterenchelyidae

- Panturichthys fowleri* (Ben Tuvia, 1953)
Nettastomatidae
Nettastoma melanurum Rafinesque, 1810
Notacanthidae
Notacanthus bonapartei Risso, 1840 **
Polyacanthonotus rissouanus (Filippi and Vérany, 1859) *
Macrouridae
Caelorinchus caelorinchus (Risso, 1810)
Caelorinchus mediterraneus (Iwamoto and Ungaro, 2002) as
Coelorhynchus labiatus (Koehler, 1896) *
Coryphaenoides guentheri (Vaillant, 1888) **
Nezumia sclerorhynchus (Valenciennes, 1838) **
Phycidae
Phycis blennoides (Brünnich, 1768)
Trachichthyidae
Hoplostethus mediterraneus Cuvier, 1829
Bythitidae
Cataetyx laticeps Koefoed, 1927 *
Ophidiidae
Ophidion barbatum Linnaeus, 1758

Crustacea

- Decapoda
Aristeidae
Aristeus antennatus (Risso, 1816)
Benthescymidae
Gennadas elegans (Smith, 1882) ***
Sergestidae
Sergia robusta (Smith, 1882)
Sergestes arachnipodus (Cocco, 1832) ***
Sergestes sargassi Ortmann, 1893 ***
Pasiphaeidae
Pasiphaea multidentata Esmark, 1866 ***
Pasiphaea sivado (Risso, 1816) ***
Oplophoridae
Acanthephyra eximia Smith, 1884
Acanthephyra pelagica (Risso, 1816)

-
- Nematocarinidae
Nematocarinus exilis Bate, 1888 ***
- Pandalidae
Plesionika acanthonotus (Smith, 1882)**
Plesionika narval (Fabricius, 1787) ***
- Crangonidae
Aegaeon lacazei (Gourret, 1887)**
- Polychelidae
Polychelus typhlops Heller, 1862
- Galatheidae
Munidopsis marionis (A. Milne Edwards, 1882) *
- Axiidae
Levantocaris hornungae Galil and Clark, 1993
- Portunidae
Bathynectes maravigna (Prestandrea, 1839) **
- Geryonidae
Geryon longipes A. Milne Edwards, 1882**
Chaceon mediterraneus Manning and Holthuis, 1989**
- Majidae
Dorynchus thomsoni Thomson, 1873***
- Amphipoda
- Eusiridae
Eusirus longipes Boeck, 1861 **
Rhachotropis caeca Ledoyer, 1977 **
Rhachotropis grimaldii (Chevreux, 1888) **
Rhachotropis rostrata Bonnier, 1896 **
- Lepechinellidae
Lepechinella manco Barnard, 1973 **
- Leucothoidae
Leucothoe lilljorgi Boeck, 1861
- Liljeborgiidae
Idunella pirata Krapp-Schickel, 1975 **
- Lysianassidae
Orochomene grimaldii Chevreux, 1890 ***
Paracentromedon crenulatum (Chevreux, 1900) **
Tmetonyx similis (G. O. Sars, 1891) **
Tryphosella caecula (G. O. Sars, 1891) **
Tryphosites alleni Sexton, 1911 **
- Oedicerotidae
Bathymedon monoculodiformis Ledoyer, 1983**
Oediceroides pilosus Ledoyer, 1983 **
Oediceroides brevicornis Lilljeborg, **
- Pardaliscidae
Halice abyssii Boeck, 1871**
- Phoxocephalidae
Harpinia dellavallei Chevreux, 1910 ***
- Stegocephalidae
Stegophaloides christianiensis (Boeck, 1871) **
- Synopiidae
Bruzelia typica Boeck, 1871 **
Ilerastroe ilergetes (Barnard, 1964) ***
Pseudotiron bouvieri Chevreux, 1895 ***
Syrrhoë affinis Chevreux, 1908 **
- Cumacea
- Bodotriidae
Bathycuma brevirostre (Norman, 1879)***
Cyclaspis longicaudata Sars, 1864***
- Nannastacidae
Campylaspis glabra Sars, 1879***
Procampylaspis armata Bonnier, 1896***
Procampylaspis bonnieri Calman, 1906***
Procampylaspis mediterranea Ledoyer, 1988***
Styloptocuma gracillimum (Calamn, 1905)***
- Diastylidae
Diastylodes serratus (Sars, 1865) ***
Leptostylis cf. gamoi Reyss, 1972***
Makrokyllindrus longipes (Sars, 1871) ***
- Leuconidae
Leucon ensis Bishop, 1981***
- Lampropidae
Platysympus typicus (Sars, 1870) ***
- Mollusca**
- Skeneidae Clark, 1851
Akritogyra conspicua (Monterosato, 1880) *
- Rissoidae Gray, 1847
Alvania electa (Monterosato, 1874) *
Benthonella tenella (Jeffreys, 1869)
- Conidae Rafinesque, 1815
Microdrillia loprestiana (Calcara, 1841)
Benthomangelia macra (Watson, 1881) **
- Pyramidellidae Gray, 1840
Chrysalidia flexuosa (Monterosato, 1874)
Turbonilla micans (Monterosato, 1875) *
- Acteonidae D'Orbigny, 1842
Crenilabium exile (Jeffreys, 1870)
- Cylichnidae Adams, H. and A., 1854
Roxania utriculus (Brocchi, 1814)
- Yoldiidae Glibert and Van De Poel, 1965
Yoldia micrometrica (Seguenza, G., 1877)
Yoldiella philippiana (Nyst, 1845) **
- Arcidae Lamarck, 1809
Batharca pectunculoides (Sacchi, 1834)
Batharca philippiana (Nyst, 1848)
- Limidae Rafinesque, 1815
Limatula subauriculata (Montagu, 1808)
- Pectinidae Rafinesque, 1815
Cyclopecten cf. hoskynsi (Forbes, 1844) **
- Thyasiridae Dall, 1900
Thyasira granulosa (Monterosato, 1874) **
Thyasira oblonga (Monterosato, 1878) *
Thyasira eumyaria (Sars, M., 1870) **
- Semelidae Stoliczka, 1870
Abra longicallus (Scacchi, 1834)
- Kelliellidae Fischer, P., 1887
Kelliella abyssicola (Forbes, 1844)
- Lyonsiidae Fischer, P., 1887
Allogramma formosa (Jeffreys, 1882) **
- Cuspidariidae Dall, 1886
Cuspidaria rostrata (Spengler, 1793)
Cardiomyia costellata (Deshayes, 1835)
- Scaphopoda Bronn, 1862
Entalina tetragona (Brocchi, 1814)
- Echinodermata**
- Synallactidae
Mesothuria intestinalis (Ascanius and Rathke, 1805)***
-