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Bathymetric distribution of some benthic and benthopelagic species attracted to baited cameras and traps in the deep eastern Mediterranean

E. G. Jones[1,4,*], A. Tselepides[2], P. M. Bagley[1], M. A. Collins[1,3], I. G. Priede[1]

[1]University of Aberdeen, OceanLab, Newburgh, Aberdeen, AB41 6AA, Scotland, United Kingdom

[2]Institute of Marine Biology of Crete, PO Box 2214, Heraklion 71003, Crete, Greece

[3]British Antarctic Survey, High Cross, Madingley Road, Cambridge CB3 0ET, United Kingdom

[4]*Present address:* Fisheries Research Services, Marine Laboratory, PO Box 101, Victoria Road, Aberdeen AB11 9DB, Scotland, United Kingdom

ABSTRACT: A series of baited camera and trap experiments in the eastern Mediterranean Sea between 1500 and 4264 m depth attracted a variety of opportunistic scavengers, with species composition changing with increasing depth. At the shallower stations (1500 to 1800 m), decapod crustaceans and fishes, dominated by elasmobranchs such as *Hexanchus griseus*, were attracted to and actively consumed the bait. Some of these species were observed at depths exceeding their previously reported ranges. This was believed to be a result of the absence of deep-water scavengers from the adjacent Atlantic due to dispersal barriers and elevated temperatures at depth. The diversity of bait-attending fauna declined with increasing depth. Elasmobranchs were not observed below 2500 m, and below 4000 m only the caridean shrimp *Acanthephyra eximia* and the macrourid *Chalinura mediterranea* were present; at this latter depth, bait consumption was negligible. This shift in species composition was reflected in changes in first arrival times. Increasing first arrival times of *H. griseus* suggested a decline in relative abundance from 1500 to 2500 m, whilst those of *C. mediterranea* indicated an increase in relative abundance from 1800 to 4264 m.

KEY WORDS: Baited camera · Autonomous lander · *Hexanchus griseus* · *Chalinura mediterranea*

INTRODUCTION

The deep-sea environment is characterised by distinct vertical gradients of pressure, light, temperature and food availability (Carney et al. 1983, Gage & Tyler 1991). As a result of these gradients, depth-related changes in benthic and benthopelagic fauna have frequently been observed in trawl catches (Merrett & Marshall 1981, Hecker 1990, Gordon & Bergstad 1992, Fujita et al. 1995, Moranta et al. 1998). An alternative sampling technique, using free-fall baited traps and cameras, has also demonstrated both depth-related and latitudinal changes in relative abundance and diversity of opportunistic scavenging megafauna (Desbruyérès et al. 1985, Priede et al. 1994, Thurston et al. 1995, Collins et al. 1999, Yau et al. 2002). In some of these studies, the relative abundance of species attracted was inferred from differences in the time taken for the first individual to reach the baited camera (Priede & Merrett 1996, 1998). Similar methods have proved successful in shallower habitats for estimating the abundance of predatory reef fishes (Ellis & DeMartini 1995, Willis & Babcock 2000, Willis et al. 2000). Some important assumptions are necessary: that individuals are evenly dispersed across the sea floor; that they are mobile; and that the dispersal time of the odour plume is invariant between stations. The technique has its biases (see Willis & Babcock 2000), but offers a relatively low-cost method of sampling mobile fauna at great depths, as well as providing additional information on habitat and behaviour.

*Email: jonese@marlab.ac.uk

Very little is known of the ecology of deep demersal fauna in the eastern Mediterranean. These waters constitute a unique environment characterised by unusually warm temperatures of 13 to 14°C, and extreme oligotrophy (Dugdale & Wilkerson 1988, Ignatiades 1998, Psarra et al. 2000). A sharp gradient of availability of organic matter exists, related to depth and distance from the shore (Tselepides & Eleftheriou 1992, Karakassis & Eleftheriou 1998, Tselepides et al. 2000a). Compared to other areas of similar latitude and depth, there is a general scarcity of deep-sea benthos, from microbes and meiofauna (Soyer 1985, Danovaro et al. 1995) to macrofauna (Fredj & Laubier 1985, Tselepides & Eleftheriou 1992, Tselepides et al. 2000b). The lack of food, in combination with high temperatures inducing high metabolic rates, is believed to be the main reason for the impoverished benthic fauna (Pérès 1982). Some limited deep-water trawling in this region has confirmed the scarcity of ichthyofauna (Tortonese 1960, Klausewitz 1989), and baited trap deployments have not yielded the familiar scavengers, such as lysianassid amphipods (Christiansen 1989, Albertelli et al. 1992).

In this paper we describe the results of a series of baited camera and trap experiments carried out between 34 and 36.5° N and 25 and 28.5° E during the course of 2 research cruises. The results were analysed in terms of composition and distribution of benthic and benthopelagic bait-attracted species between regions, seasons and in relation to the depth gradient. In addition to simple presence and absence information, the times of first arrival of species attracted to the camera baits were compared between stations for indications of trends in relative abundance.

MATERIALS AND METHODS

A total of 11 stations were sampled in 1998, 3 in January during a cruise aboard RV 'Meteor', and a further 8 in June aboard RV 'Philia'. Fig. 1 indicates the positions of these stations and Table 1 gives details of each deployment depth and duration. In the Cretan Sea, deployments were made from 1500 m down to the maximum depth of 2490 m (in the Karpathos Basin). In the Rhodos Basin, 2 stations were sampled; one on the slope, the other at its base, between 3850 and 4000 m. Finally, 3 sets of deployments were made in the Ierapetra Basin between 3000 and 4264 m. At each station, paired deployments of the baited trap and time-lapse camera were made 1 nautical mile apart. This provided the opportunity of verifying identification of photographed species with trap samples, whilst minimising the interference between the 2 food sources.

System components and deployment methods. The AUDOS (Aberdeen University Deep Ocean Submersible) vehicle used in this study comprised an aluminium frame supporting a vertically orientated time-lapse camera (Umel) with twin flashlights, battery supply (DSPL, Deep Sea Power and Light) and a dual acoustic release system (Mors). Underwater, the frame was suspended between a mooring line providing positive buoyancy and a 2 m length of wire linked to a 120 kg ballast clump. This ballast, onto which a reference scale and bait (10 to 20 kg tuna pieces) were attached, rested on the seabed in view of the camera above. Photographs were taken at pre-set intervals of a 2.5 m area of the seabed. Ektachrome 200 ASA colour positive film was used, with a possible maximum of 800 frames. The time interval between photographs was set according to the deployment duration (Table 1). At the end of each deployment, the acoustic release system jettisoned the wire attached to the ballast clump, allowing the frame to return to the surface for recovery. Further details of the design and operation of the AUDOS vehicle used in these experiments can be found elsewhere (Bagley & Priede 1997, Priede & Bagley 2000).

At each station, the baited fish trap was deployed for between 12 and 36 h. This consisted of a rectangular metal frame (1000 × 800 × 800 mm) covered

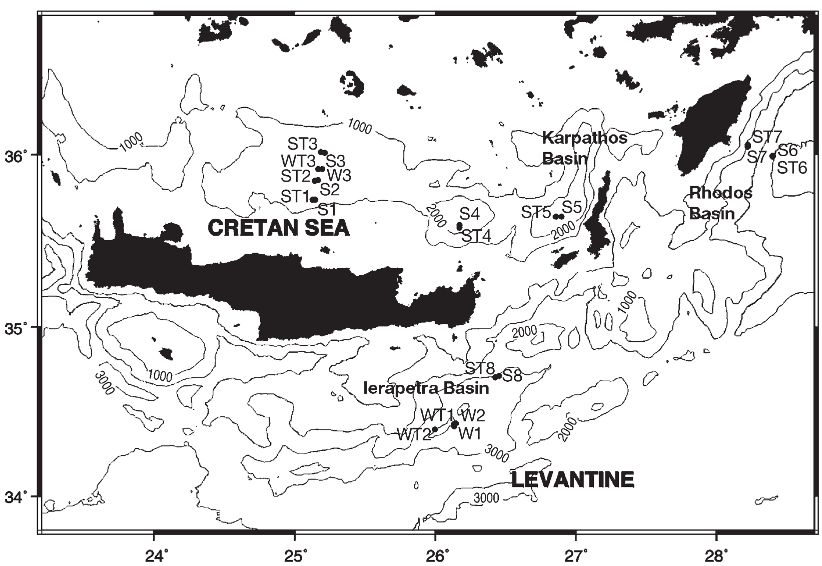

Fig. 1. Study area, showing positions of paired camera and trap deployments. All January stations have prefix W, June stations prefix S and trap deployments prefix T

with a 20 mm wire mesh, with 2 conical-shaped openings on opposite sides, one situated 100 mm above the bottom with an exterior diameter of 300 mm and an interior diameter of 150 mm, the other situated 300 mm above the bottom and with exterior diameter of 400 mm and an interior diameter of 250 mm. The trap was deployed and retrieved as a free-fall lander using glass flotation (Benthos) and an acoustic release (Mors). For each deployment, approximately 3 to 4 kg of squid and 1 kg of mackerel were used as bait.

Analysis of time-lapse photographs. Following processing, film was viewed on a microfilm viewer. Identification of species observed was made using relevant literature descriptions (e.g. Whitehead et al. 1984, Bellan-Santini et al. 1982a,b) and comparison with trap-caught specimens. Confidence in the identification of those species regularly observed in photographs and caught in the trap was high. However the identity of species rarely seen and not trapped remains tentative, but has been included for completeness. For every camera deployment, the number of each species observed in each frame was plotted over the duration of the experiment. The time of first arrival at the bait (t_{1st}) and maximum number observed in any single frame ($Max_{species}$) were then compared between region and depth.

The high numbers of certain fish species attracted allowed analysis of length frequency distributions based on total body length measurements (tip of snout to tail) from the photographs. Only those individuals in full view and close to the reference scale were chosen, with a minimum interval of 20 min between measurements to reduce the probability of the same individual being repeatedly sampled.

Table 1. Details of baited camera and trap deployments in the eastern Mediterranean. Stations from 'Meteor' Cruise 40/3, (28 December 1997 to 18 January 1998) have prefix W to denote winter; stations from 'Philia' Cruise (2 to 18 June 1998) have prefix S to denote summer; all trap deployments have prefix T. Region, depth and duration of each deployment are given, and interval between photographs for camera deployments

Cruise Region	Stn no.	Depth (m)	Duration (h)	Interval (min)
Meteor 40/3				
Ierapetra Basin	W1	4264	115	10
	WT1	4262	20	
Ierapetra Basin	W2	4172	67	5
	WT2	4064	18	
Cretan Sea	W3	1873	92	5
	WT3	1832	25	
Philia				
Cretan Sea	S1	1503	22	2
	ST1	1511	22	
Cretan Sea	S2	1822	48	5
	ST2	1831	18	
Cretan Sea	S3	1750	24	2
	ST3	1750	12	
E. Cretan Sea	S4	2220	23	2
	ST4	2230	12	
Karpathos Basin	S5	2490	24	2
	ST5	2485	12	
Rhodos Basin	S6	3850	24	2
	ST6	4067	36	
Rhodos Basin	S7	2307	22	2
	ST7	2270	12	
Ierapetra Basin	S8	3080	24	2
	ST8	3028	12	

RESULTS

A total of 18 putative species were trapped and/or photographed in this study, and are listed in Table 2 (photographic record) and Table 3 (trapped specimens). Decapod crustaceans were the only invertebrate fauna attracted: the caridian shrimp *Acanthephyra eximia;* 2 brachyuran crabs, *Geryon longipes* and *Chaceon mediterraneus*; a mysid; a leptostracan; and a variety of amphipods. The numbers trapped are given in Table 3, although washout of the smaller species is certain to have reduced these values. In the photographs, 4 shark species and 4 teleost fishes were identified, but not all of these were trapped. As a result, the identification of certain fishes remains speculative. Of the elasmobranchs photographed, *Etmopterus spinax* and *Galeus melastomus* were trapped and photographed, whereas *Hexanchus griseus* was too large to be trapped, but was easily identifiable in photographs. A fourth species of intermediate length (estimated at between 0.5 and 1 m) was observed at 1800 m in the Cretan Sea and 2307 m in the Rhodos Basin. This was believed to be either *Centrophorus granulosus* or *Centroscymnus coelolepis.* A species of Nettastomatidae (Anguilliformes) was observed at 1503 m. *Nettastoma melanura* Rafinesque, 1810 has been caught further east in the Levant basin at 1400 m depth (Galil & Goren 1994) and in the western Mediterranean down to 1000 m (Stefanesu et al. 1992a) and was most likely to be the species photographed in this study.

Regional and seasonal variation

Due to the constraints of the sampling regime, rigorous regional and seasonal comparisons were not possible. The distribution of species numbers by region is illustrated in Fig. 2. All 18 species recorded were found in the Cretan Sea, 13 of these were also found in the Rhodos Basin and 4 species were common to all 3 regions. The 5 species exclusive to the

Table 2. Results of the 11 baited camera deployments in the eastern Mediterranean. For the species present at each station, the maximum number observed in any 1 frame during the first 24 h of the deployment is given in bold, along with the time (min, in parentheses) of first arrival at the food-fall. Prefixes as in Table 1

Species	Camera Stn no. and depth (m)										
	Cretan Sea						Rhodos Basin		Ierapetra Basin		
	S1 1503	S3 1750	S2 1822	W3 1873	S4 2220	S5 2490	S7 2307	S6 3850	S8 3080	W2 4172	W1 4264
Crustacea: Decapoda											
Acanthephyra eximia Smith, 1886	**31** (6)	**30** (10)	**191** (<5)	**85** (10)	**44** (6)	**18** (10)	**130** (4)	**20** (14)	**13** (6)	**24** (<5)	**48** (10)
Geryon longipes Milne Edwards, 1882	**16** (4)	**4** (156)	**4** (210)	**7** (25)							
Chaceon mediterraneus Manning, Holthuis, 1989					**3** (64)	**13** (75)	**9** (44)	**3** (720)	**14** (252)		
Elasmobranchii											
Etmopterus spinax (Linnaeus, 1758) (Squalidae)	**5** (10)	**5** (34)	**9** (25)	**6** (30)	**8** (18)	**4** (30)	**4** (54)				
Galeus melastomus Rafinesque, 1810 (Scyliorhinidae)	**2** (22)	**1** (90)	**1** (276)	**1** (150)							
Hexanchus griseus (Bonnaterre, 1788) (Hexanchidae)	**1** (286)	**1** (260)	**2** (285)	**1** (285)	**2** (540)		**1** (250)				
Centrophorus/Centroscymnus sp. (Squalidae)			**1** (720)				**1** (720)				
Teleostei											
Nemattostomatidae	**1** (166)										
Lepidion lepidion (Risso, 1810), *L. guntheri* (Moridae)		**1** (256)	**2** (36)	**2** (15)	**2** (60)		**2** (36)				
Chalinura mediterranea Giglioli, 1893 (Macrouridae)			**2** (380)		**1** (340)	**6** (80)		**8** (22)	**4** (106)	**26** (45)	**23** (60)

Cretan Sea were only found at the shallower depths, between 1500 and 1800 m, and were not sampled in the other regions. Deployments between 2000 and 2500 m were made in both the Cretan Sea and the Rhodos Basin and there was little difference in the species attracted. Greater numbers of *Acanthephyra eximia* and *Chaceon mediterraneus* were recorded on the Rhodos slope, and the first arrival time for *Hexanchus griseus* was less than half its arrival time in the Cretan Sea. Comparative camera and trap stations were also sampled at abyssal depths in the Rhodos and Ierapetra Basins. *A. eximia*, *Chalinura mediterranea* and *C. mediterraneus* were present in both regions. Comparative winter and summer deployments were made at 1800 m in the Cretan Sea only. The scavenger assemblage attracted was similar, apart from the absence of *C. mediterranea* and the unknown shark species.

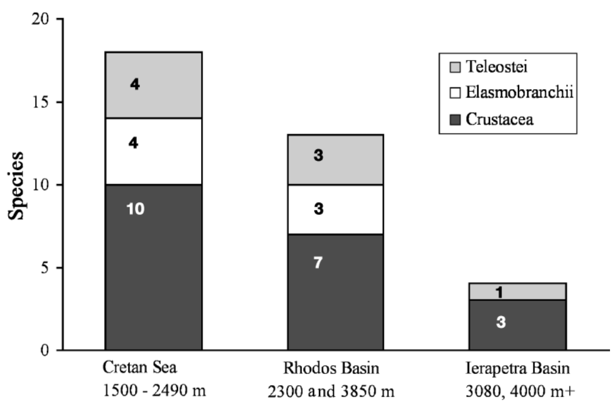

Fig. 2. Number of species observed by camera or trapped in the 3 regions sampled. Numbers of crustaceans, elasmobranchs and teleosts in each region are indicated inside bars

Bathymetric distribution range of bait-attracted species

Due to the general similarities in bait-attending fauna between regions, it was considered feasible to compare all stations together for the purposes of analysing bathymetric distributions of the species observed. These were inferred from presence and absence in traps and on camera films, and are shown in Fig. 3. *Acanthephyra eximia* was photographed at baits over the entire depth range sampled, from 1500 to 4264 m. Other crustaceans had more limited ranges. The crab *Geryon longipes* was trapped between 1500

Table 3. Results of the 11 baited trap deployments in the eastern Mediterranean. Prefixes as in Table 1; x indicates species present but numbers not available

Species	Trap Stn no. and depth (m)										
	Cretan Sea						Rhodos Basin		Ierapetra Basin		
	ST1 1511	ST3 1750	ST2 1831	WT3 1832	ST4 2230	ST5 2485	ST7 2270	ST6 4067	ST8 3028	WT2 4064	WT1 4262
Crustacea: Decapoda											
Acanthephyra eximia Smith, 1886		x	10	x	x	x	x		x	x	x
Geryon longipes Milne Edwards, 1882	32	3	5								
Chaceon mediterraneus Manning & Holthuis, 1989					25	19	53		8		
Scopelocheirus hopei (Costa, 1851)		30	105	19	35	2	1				
S. polymedus Bellan-Santini, 1985	1										
Epimeria cf. *cornigera* (Fabricius, 1779)					19		6		23		
Orchomene grimaldii Chevreux, 1890			1	3	3		2				
Orchomenella nana (Kröyer, 1846)	8										
Nebaliacea		1		14	16	1	5				
Mysidacea		1			3	4	11				
Elasmobranchii											
Etmopterus spinax (Linnaeus, 1758)				1	1						
Galeus melastomus Rafinesque, 1810											
Teleostei											
Lepidion lepidion (Risso, 1810)	1	1					2				
Chalinura mediterranea Giglioli, 1893								1		12	13

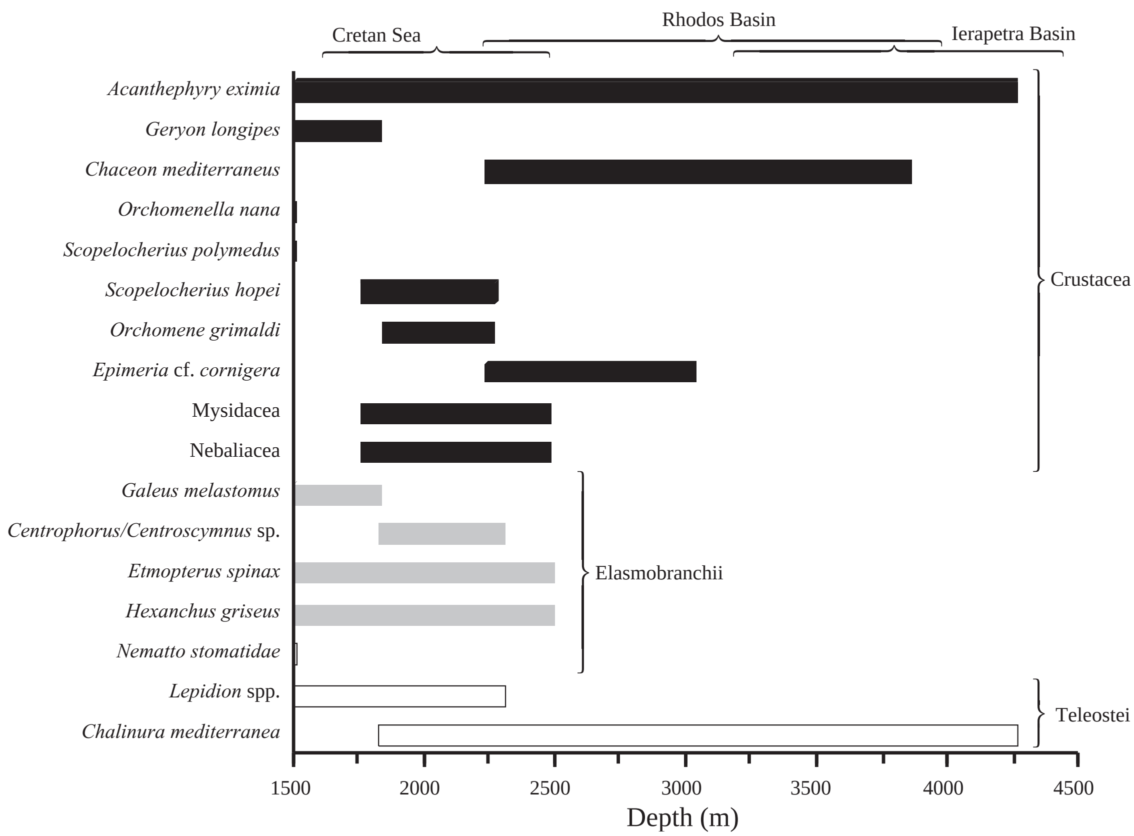

Fig. 3. Bathymetric distributions below 1500 m of crustaceans, elasmobranchs and teleosts inferred from their occurrence at baited camera and/or trap deployments. Depth ranges sampled in the 3 regions are also indicated

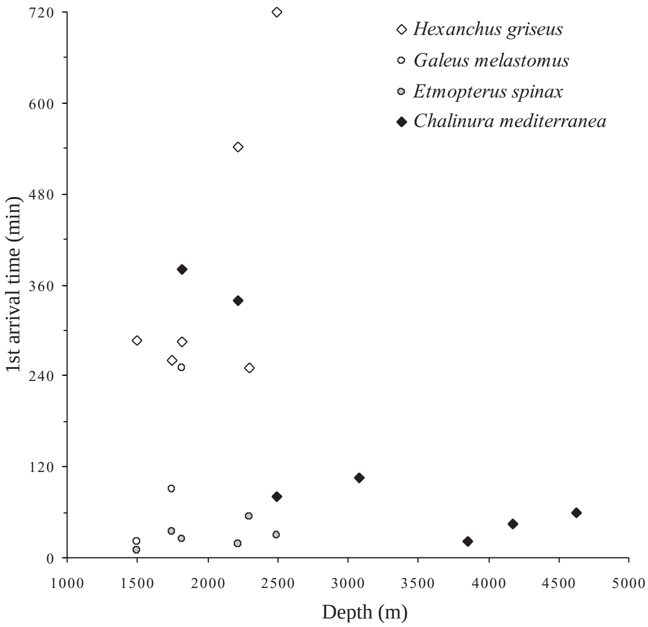

Fig. 4. Variation in first arrival time at the bait with station depth for 3 elasmo-branch species and the macrourid *Chalinura mediterranea*

and 1830 m. A second geryonid, *Chaceon mediterraneus*, was only found deeper, from 2230 m down to 3028 m. This was also the assumed identity of crabs observed on the films from the concurrent camera deployments. Although not trapped at Stn 6 (4067 m), this species was observed at the paired camera station (3850 m). A succession of amphipod species were trapped between 1500 and 3028 m (shown in Fig. 3), 1 of which, *Epimeria* cf. *cornigera*, was found in all 3 regions.

Sharks dominated the fish assemblage between 1500 and 2500 m. The catshark *Galeus melastomus* was observed from 1500 to 1830 m only. The sixgill shark *Hexanchus griseus* was by far the largest scavenger. Both *H. griseus* and the small lantern shark *Etmopterus spinax* were attracted at every station between 1500 and 2490 m. No sharks were observed at greater depths.

Between 1500 and 3080 m, 4 species of teleosts were identified, although the numbers attracted were low. The 1 species of Nemattostomatidae was photographed at 1500 m only. A morid, *Lepidion lepidion*, was photographed and trapped at the 2 shallowest stations (1503 and 1750 m). Between 1800 and 2300 m, *L. lepidion* and a second species were photographed but not trapped. This second species was thought to be *L. guentheri.* The only fish attracted to bait below 2500 m was the macrourid *Chalinura mediterranea*, which had the widest depth range of all vertebrates (from 1822 to 4264 m).

Relative abundance inferred from first arrival times

The time of first arrival (t_{1st}) for 3 elasmobranch species and *Chalinura mediterranea* are plotted against depth in Fig. 4. For *Galeus melastomus* and *H. griseus* there was a clear trend of increase in t_{1st} as depth increased. From this, a decline in relative abundance was inferred for these species with increasing depth. In contrast, a decrease in t_{1st} (Fig. 4) and corresponding increase in maximum numbers (Table 2) of *C. mediterranea* was observed with increasing depth, suggesting a higher abundance at greater depths. The maximum numbers given in Table 2 are for the first 24 h of these 2 deployments in order to be comparable with the other results. However, fish numbers continued to increase at the deepest station, reaching 49 individuals after 115 h.

Bathymetric trends in size

Length estimates of photographed fishes were made where possible. For *Etmopterus spinax* and *Chalinura mediterranea*, sufficient data were collected to allow frequency distributions to be plotted at different depths (Fig. 5). No significant change in size was detected for either species over their observed depth range. For *C. mediterranea*, the overall mean length of 198 mm (n = 328, SD = 30 mm, range = 120 to 296 mm) compared favourably with the mean length of 191 mm for trapped specimens (n = 25, SD = 27 mm, range = 155 to 260 mm). For *E. spinax*, the mean length was 332 mm (n = 125, SD = 40 mm, range = 247 to 450 mm). A limited number of length estimates were obtained for *Galeus melastomus:* mean length was 439 mm (n = 11, SD = 46 mm, range = 370 to 500 mm). Estimated total lengths for *Hexanchus griseus* ranged from 1.15 to at least 3.0 m. As a consequence of the change in species dominance with increasing depth, the average length of fishes at stations 2500 m and shallower was greater than that of fishes observed at the deeper stations.

Bait consumption and variation in numbers over time

The pattern of variation in numbers of individuals attracted to the bait over the course of each deployment differed between species and according to the scavenging activity of *Hexanchus griseus*; some examples are given in Fig. 6. *Acanthephyra eximia* was attracted to every deployment within 10 min. Typically, numbers reached a peak within the first 1 to 2 h. At shallow deployments, where the bait was attacked by *H. griseus*, shrimp numbers fluctuated until the bait was consumed. At deeper stations, where the bait was not fully consumed or remained intact, numbers declined and remained low for the rest of the deployment (Fig. 6c). A similar pattern was observed for the smaller shark *Etmopterus spinax:* peak numbers of up to 5 individuals were reached in the first few hours prior to the arrival of the sixgill sharks, declining to intermittent sightings thereafter. In contrast, the arrival rates of the 2 crab species were much slower, with numbers increasing steadily over the course of the deployment (Fig. 6b) unless the bait was completely consumed (Fig. 6a). The macrourid *Chalinura mediterranea* was only observed in any numbers at the deeper stations (2490 m and greater) and showed a similar pattern of steady build-up of individuals over the course of the deployment (Fig. 6b,c).

At all stations where sixgill sharks were attracted, the bait was consumed, although not always completely within the 24 h period. Their attacks dispersed chunks of the bait and stirred up the sediment, often attracting increased number of smaller scavengers once they had departed. At 3080 m, swarms of amphipods were visible on the surface of the bait, although the exact amount consumed was unknown since retrieval was not possible. At the 3 deeper stations, where only *Acanthephyra eximia* and *Chalinura mediterranea* were attracted, the bait appeared mostly untouched, with no indication of skin removal or reduction in size, despite the high numbers of fish and shrimp present.

DISCUSSION

The benthic and benthopelagic megafauna attracted to baited camera and trap deployments in this study consisted of decapod crustaceans and elasmobranch and teleost fishes. These taxa also dominate trawl catches in this and other regions in the Mediterranean (Kallianiotis et al. 2000, Cartes et al. 2001). Greater species diversity is found by trawling, although the dominant species in terms of biomass and numbers are similar for both methods of sampling; Stefanescu et al. (1992a) recorded 16 species of demersal fishes in the western Mediterranean between 1501 and 2250 m compared with 8 species recorded in this study. However, they found that 85% of the specimens captured came from 3 families: Chlorophthalmidae (*Bathypterois mediterraneus*), Moridae (*Lepidion lepidion* and *L. guentheri*) and Macrouridae (including *Chalinura mediterranea*). *Hexanchus griseus* dominated in terms of biomass and Macrouridae, Squalidae and Moridae were found to be the most important families in terms of species.

Camera and trap deployments encompassed 3 different regions and differing depth ranges. However, where station depths were similar the fauna attracted was broadly similar. The comparison between the Cretan Sea and Rhodos Basin suggested higher abundance of benthic and benthopelagic fauna in the latter. This was thought to be a consequence of higher productivity in this region due to a localised upwelling (Krom et al. 1992).

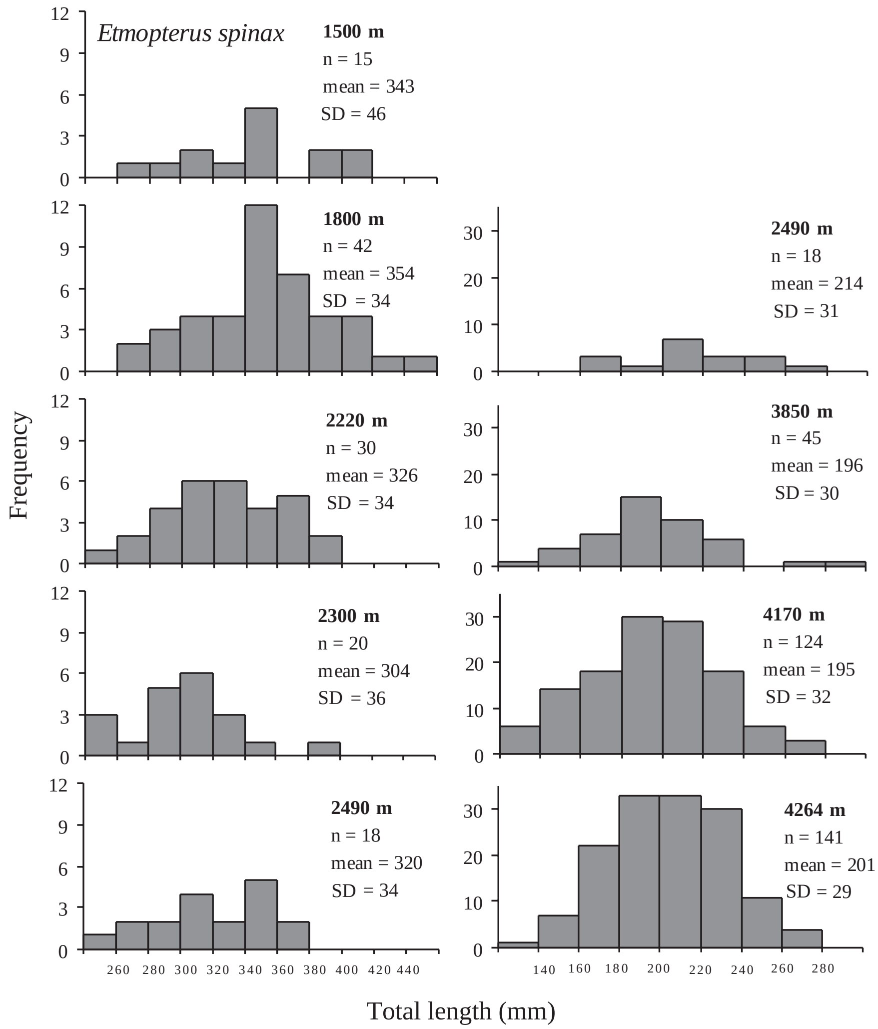

Fig. 5. *Etmopterus spinax* and *Chalinura mediterranea.* Total length-frequency distributions at stations of different depths, giving sample size, mean length and standard deviation for each depth

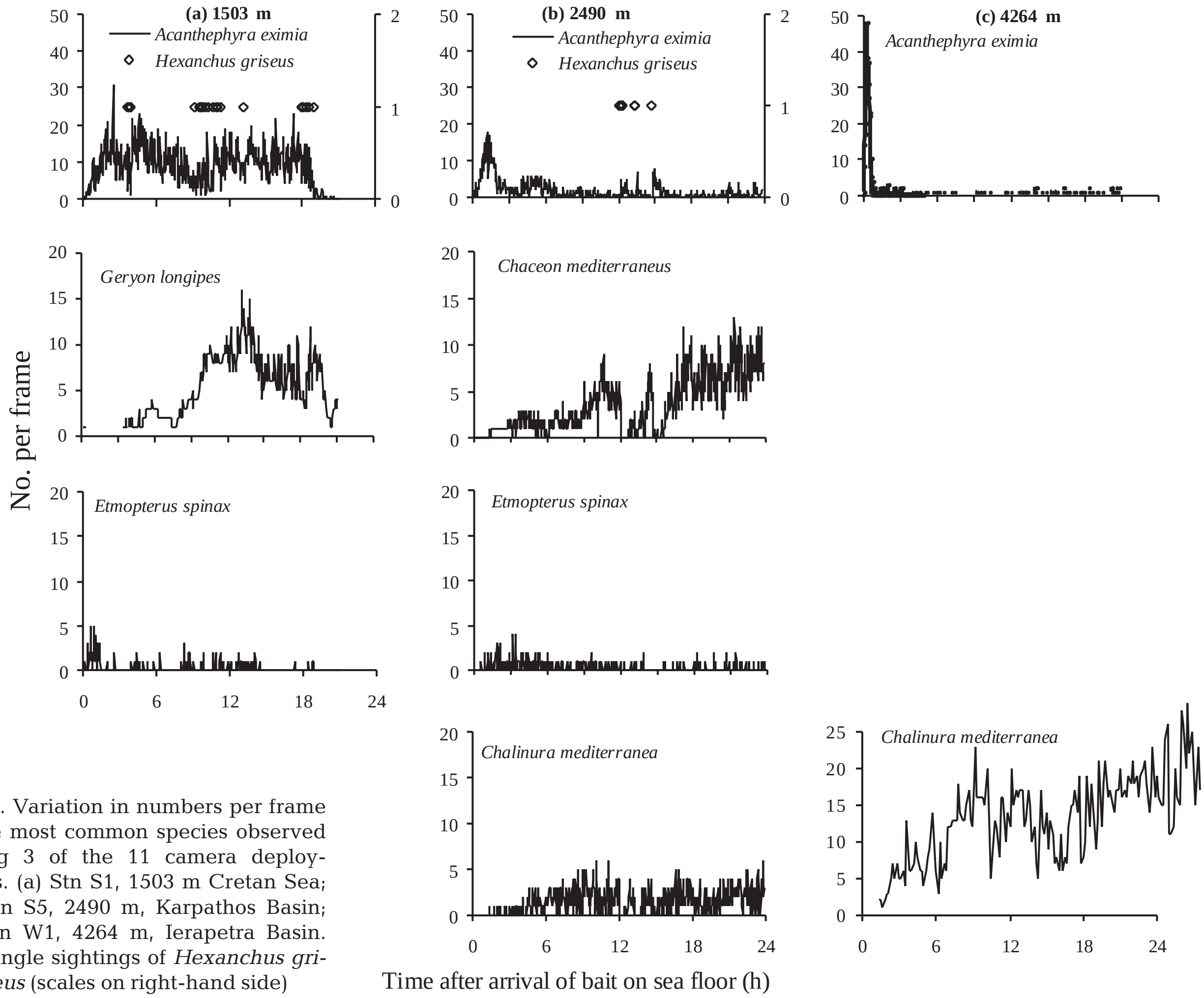

Fig. 6. Variation in numbers per frame of the most common species observed during 3 of the 11 camera deployments. (a) Stn S1, 1503 m Cretan Sea; (b) Stn S5, 2490 m, Karpathos Basin; (c) Stn W1, 4264 m, Ierapetra Basin. (◇) Single sightings of *Hexanchus griseus* (scales on right-hand side)

Bathymetric distribution

Much of the fauna of the Mediterranean Sea is believed to have originated from the Atlantic Ocean (Fredj & Laubier 1985, Bouchet & Taviani 1992). However, many of the species characteristic of baited camera experiments in the abyssal NE Atlantic were not observed here in the Mediterranean, e.g. *Coryphaenoides armatus*, zoarcids, liparids, ophidiids, deep-water eels and lysianassid amphipods such as *Eurythenes gryllus* and *Paralicella* sp. (Armstrong et al. 1992, Thurston et al. 1995, Jones et al. 1998, Henriques et al. 2002). Their absence is generally thought to be due to a combination of dispersal barriers including the shallow sill at Gibraltar, deep outflowing current, and the high temperatures at depth (13 to 14°C compared to 2 to 4°C in the Atlantic). As a consequence, some bathyal species have apparently extended their depth range into the abyssal environment. The geryonid crab *Chaceon mediterraneus* was previously noted only in the western Mediterranean from 1990 to 2830 m (Cartes 1993a), and has been trapped in the present study for the first time in the eastern Mediterranean (Koukouras et al. 2000). The specimens collected from 3028 m and observations at 3850 m extend the known depth range of this species by 1000 m. Geryonid crabs occur widely in the world's oceans, but are rare below 2000 m (Attrill et al. 1990). Temperature is believed to be the limiting factor to their distribution (Gage & Tyler 1991), and this may explain their presence here in the eastern Mediterranean, where the water is unusually warm at abyssal depths. The amphipods *Epimeria cornigera* and *Orchomenella nana* have been recorded previously in the Mediterranean down to 430 and 460 m respectively (Bellan-Santini et al. 1982b). In this study they were trapped as deep as 3028 and 2270 m respectively. The elasmobranch *Galeus melastomus* was rarely found in trawl catches below 1400 m in the western Mediterranean (Carrassón et al. 1992), but in this study it was regularly observed and also trapped down to 1830 m. Both *Etmopterus spinax* and *Hexanchus griseus* were observed at 2490 m, at the known limit of both their depth distributions. The fourth shark species observed at 1800 and 2300 m could not be identified with certainty. *Centrophorus granulosus* has been caught in this region as deep as 1000 m (Kallianiotis et al. 2000) and further east at 1490 m (Gilat & Gelman 1984), but is not thought to occur much deeper. Although not previously recorded in this region, *Centroscymnus coelolepis* was found as deep as 2251 m further west in the Catalan Sea (Carassón et al. 1992) and was thought to be the most likely identity of the shark observed in this study. *Lepidion lepidion* was observed from 1500 to 2490 m, in the Cretan Sea. Between 1822 and 2490 m a second, larger teleost, thought to be *L. guentheri*, was also photographed at the baits, but not trapped. This pattern of occurrence agrees with observations in the Catalan Sea where *L. guentheri* is rare but overlaps with *L. lepidion* over 1600 to 2239 m (Carrassón et al. 1997, Moranta et al. 1998). Below 4000 m, only *Acanthephyra eximia* and *Chalinura mediterranea* were attracted to bait. Both species have a bathyal distribution elsewhere: *A. eximia* from 200 to 2500 m in the Atlantic and Indo-Pacific (Crosnier & Forest 1973); *C. mediterranea* from 1750 to 2250 m in the NE Atlantic (Mauchline & Gordon 1984), and 1400 to 2500 m in the western Mediterranean (Stefanescu et al. 1993, Moranta et al. 1998). In the eastern Mediterranean, both species are widespread at 3000 to 4500 m, as evidenced by this and previous studies (Christiansen 1989, Albertelli et al. 1992, Della Croce & Albertelli 1995).

Bathymetric trends in number of species, relative abundance and size

There was a clear decline in number of species observed with increasing depth: 18 recorded at 1503 m compared with 2 at 4264 m. Amongst the fishes attracted, elasmobranchs dominated between 1500 and 2500 m, but below this depth the macrourid *Chalinura mediterranea* was the only fish present. The relationship between t_{1st} and depth for a number of fishes and decapod species reflected this change. Although lack of information on current speed variation and swimming and walking speeds for each species prevented actual abundance estimates being calculated, the trends suggested a decline in relative abundance for elasmobranchs but an increase for the macrourid. The pattern of bathymetric change in bait-attending species observed in this study has similarities to observations made in the Bay of Biscay, NE Atlantic, where *Centroscymnus coelolepis* was replaced by the macrourid *Coryphaenoides* (*Nematonurus*) *armatus* as the dominant species with increasing depth (Desbruyérès et al. 1985).

Due to the stability of physical environmental factors such as temperature, it is believed that reduced food availability with increasing depth is the principal factor responsible for the decline in species diversity. This has been demonstrated for macrobenthos in the Cretan Sea (Tselepides & Eleftheriou 1992, Tselepides et al. 2000b) and is likely to be the case for the megafauna as well. As a consequence of this decline in trophic resources and resulting change in species composition with increasing depth, a decline in fish size was apparent. This has been noted in the western Mediterranean for both fishes (Stefanescu et al. 1992b, 1993) and decapod crustaceans (Sardà & Cartes 1993). Stefanescu (1992b, 1993) found a distinct fish assemblage above 1200 m, consisting of large gadiiform fish species characterised by higher energy requirements, that were replaced at greater depths by smaller species such as *Chalinura mediterranea* with lower energy requirements.

Within-species depth-size trends have been a much-debated topic, with some believed to be an artefact of sampling techniques (Haedrich & Merrett 1990, Macpherson & Duarte 1991, Merrett & Haedrich 1997). Previous studies in the western Mediterranean have concluded that, in contrast to the adjacent Atlantic, the majority of demersal fish species between 1000 and 2250 m, including many macrourids, do not show any clear depth-size trend (Stefanescu et al 1992b). In this study, no significant difference in the size distribution of *Chalinura mediterranea* was observed between 2490 and 4264 m. A similar result was obtained for *Etmopterus spinax*, contradicting the bigger-deeper trend observed in the western basin (Carrassón et al. 1992).

Bait consumption

Although bait was visibly consumed at shallow stations, it is unlikely that necrophagy is an important feeding mode for any of the species observed. The most active scavenger of the bait was *Hexanchus griseus*, the diet of which has yet to be documented in the eastern Mediterranean. However, in the productive waters off South Africa, it is a eurytrophic predator feeding on cephalopods, crustaceans, teleosts and other elasmobranchs, with marine mammals forming an increasing part of the diet as the shark grows larger (Ebert 1994). The preferred prey of *Galeus melastomus* below 1000 m in the western Mediterranean were cephalopods, teleost fishes and decapods such as *Geryon longipes* (Carrasón et al. 1992). Scavenging was not thought to be important in its diet. *Etmopterus spinax* has a strong pelagic habit and preys mainly on cephalopods (Macpherson 1980). The diets of the teleost fish species observed have been studied in the western basins, and all have been found to be eurytrophic predators, with natantian decapods such as *Acanthephyra eximia*, *A. pelagica*, mysids, copepods and amphipods comprising important prey items (Carrassón & Matallanas 1990, 2002, Carrasón et al. 1997). It is therefore feasible that many of the fishes may have been preying on the crustaceans attracted to the bait rather than on the bait itself. The success of *A. eximia* and *Chalinuara mediterranea* at depths where the other species were absent is thought to be due to a combination of their small size, mobility and opportunistic and euryphagic feeding strategy. *A. eximia* itself has been shown to have a varied diet including natantian decapods and hyperiid amphipods (Cartes & Maynou 1998), but with an increasing trend towards scavenging and detritivory at greater depths (Cartes 1993b). This was certainly the first species to arrive at baits in almost every deployment, but numbers often declined once fishes began to arrive. This does not explain the lack of bait consumption at the deeper stations, but this may have been due to the inability of *A. eximia* to penetrate the intact skin on tuna carcasses. This phenomenon has been noted elsewhere with baited camera experiments using cetaceans (Jones et al. 1998) and mackerel (I. G. Priede pers. obs.).

This study has provided valuable new information on composition, distribution and depth ranges of natatory benthopelagic megafauna in the eastern Mediterranean. Such fauna can be difficult to catch with other sampling techniques. Whilst clearly a versatile technique for research vessels working in deep waters without the size or capability for deep-water trawling, the fauna which can be sampled is limited to sufficiently mobile opportunistic scavengers. It is possible that other species may have been observed if, for instance, the deployments had been made for longer periods with protected bait. In the NE Atlantic, long deployments with large bait attracted opportunistic scavenging echinoderms and crustaceans not observed at short 24 h deployments (Jones et al. 1998). It is also possible that some species may have been deterred by the presence of other, more aggressive scavengers, such as the larger sharks. Trawling samples a much broader range of species, although this method also has its limits and biases, and ideally a combination of these 2 techniques would allow a thorough survey of the deep fauna of this little-studied region.

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