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Belgian Journal of Zoology

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INTRODUCTION

Ninth International Congress
on the Zoogeography and Ecology of Greece and Adjacent Regions (9ICZEGAR)
(22-25 May 2002, Thessaloniki, Greece)

Assessing Biodiversity in the Eastern Mediterranean Region: Approaches and Applications

Biodiversity, as a concept and research objective, has been the focus of the international scientific community ever since the last Tasmanian wolf (*Trylacinus cynocephalus*) disappeared in the mid-30s. Several decades later, in 1992, the Convention of Rio came as a result of the urgent need to record and conserve biodiversity. Despite its inevitable deficiencies, the Convention remains the most important tool for the conservation of biological diversity (GASTON & SPICER, 1998). Following this line of thought, the Hellenic Zoological Society organised the 9th International Congress on the Zoogeography and Ecology of Greece and Adjacent Regions (9ICZEGAR) focusing on the main topic of "Assessing Biodiversity in the Eastern Mediterranean Region: Approaches and Applications". The congress was held in Thessaloniki (Greece) from 22 to 25 May 2002.

The scope of that endeavor was (a) to assess the general inquiries on biodiversity and its three major components : taxonomy, genetics, and ecology, (b) to unfold the range of investigations that take place in the eastern Mediterranean and (c) to establish biodiversity as a mean for developing management models with viable predictions. Prior to this congress, several other important scientific conferences and papers have tackled the general concept of biodiversity (e.g. MARBENA e-conference, GRAY, 1997 ; BIANCHI & MORRI, 2000 ; JACKSON et al., 2001 ; ORME et al., 2002 ; PRICE, 2002 ; PAULY & WATSON, 2003 ; among others). The present effort, without losing any of the innate meaning, aimed to contribute significantly to the propagation of scientific research in the eastern Mediterranean as well as to the understanding of the priorities set by the scientific community for this region.

A total of 304 scientists, representing 60 research centers (Universities or Institutes) from 16 different countries, participated in the 9th ICZEGAR. During this congress, 156 papers were presented comprising 8 invited lectures, 106 oral presentations, and 42 posters that were divided into a terrestrial fauna session and an aquatic fauna session. A closer view of the abstracts of these contributions revealed a diverse array of research subjects. More specifically, 25 presentations dealt with issues of marine Biology, 23 of ichthyology, 21 of mammalian biology, 19 of freshwater ecology, 15 of soil biology, 14 of ornithology, 7 of insects, 6 of wetlands, 5 of amphibians and reptiles, and 5 of terrestrial gastropods. Moreover, there were 16 contributions dealing with molecular biology and genetics, whereas 10 presentations referred to threatened species, such as cetaceans, monk seals or loggerhead turtles.

Despite the significance of all those contributions, the Organizing Committee was forced to select a limited number of papers in order to have them published in a special issue of the Belgian Journal of Zoology. The selection was done according to the standards of the hosting journal following peer reviews from an international committee of referees. The list of referees is found at the end of this introduction. Fifty papers were submitted for review and 25 of them met the international standards imposed by the journal and are included in these proceedings.

The papers on aquatic ecosystems refer mostly to the marine environment and only few deal with freshwater biology. Summarizing the contents of those papers, there is an apparent increasing interest in certain groups of the eastern Mediterranean Sea, such as mollusks and decapods. For instance, new data are presented on the structure of the mollusk fauna on the hard substrate of the lower sublittoral zone (15-45 m depth). There are also first records of species at various locations in the eastern Mediterranean, which show a high level of spatial homogeneity in the abundance of species. A review of the fauna of exotic mollusk species in the Greek seas confirms the continuous species migrations from one geographic region (e.g. Red Sea, Indian Ocean) to another (e.g. Mediterranean). Similar information is also recorded for cephalopods, where preliminary results and an analysis of their abundance in space and time contribute significantly to our knowledge of this group in the broader region of N.E. Mediterranean. Another study of great interest focusing on deep-sea decapods of the Ionian Sea records 39 species and describes their bathymetrical distribution.

The research of deployment of artificial reefs in the Eastern Mediterranean has not started until recently. Despite the delay, the results of these efforts have so far shown the significant contribution of the artificial reefs to the reservation and upgrade of the marine environment in the N.E. Mediterranean. The region of the North Aegean Sea, though richer in nutrients than the Southern Aegean or even the Levantine Sea, is still not as rich as the Western Mediterranean. These data can induce further discussion on the value of such deployments and also on the introduction of new temporal-spatial strategies for the exploitation of similar developmental practices.

The on-growing interest of the scientific community on the subject of fishery resources and management is present in three of the papers. Two of them examine the influence of climatic changes on the reproduction of fish and substantiate the concern for the future of fish stocks in the Mediterranean. Lastly, a significant study of the functional importance of marine ecosystems, one of the three levels of biodiversity, contributes extensively to the assessment of the physical or physiological condition of the Mediterranean, a sea with particular environmental and socio-economic problems, as indicated in many F.A.O. reports.

As far as the terrestrial fauna is concerned, the selected contributions deal with soil invertebrates, birds, and mammals. In terms of soil invertebrates, changes in the community organization patterns of epiedaphic coleopterans was used to assess human impact in a protected forest reserve, while another contribution explores the effects of global climate change on the structural and functional features of a soil nematode community. The subjects of the contributions on birds range from detailed investigations of the feeding patterns and diets of owls, herons, and egrets, to the composition and species richness of bird species in protected mountain forests. Another contribution uses eggs of gulls, avocets, and terns as bioindicators for the evaluation and impact of agrochemical pollutants in Greek wetlands of international importance. Lastly, one contribution on mammals explores the major Neogene/Quaternary mammalian migrations and faunal changes in the southern Balkans that contributed to modern mammalian diversity in the eastern Mediterranean region. Two other contributions focus on voles, one investigating patterns of interpopulation variability based on allozyme variation, the other one focuses on their use as efficient bioindicators of polymetal dust emissions. Two contributions deal with carnivores in Greece, one exploring the activity patterns, movements, and home ranges of female brown bears, and one assess the population status of golden jackals.

In addition to the paper presentations, a round table was organized concerning the Protection and Management of Wild Populations of Large Mammals in Southern Balkans. Many authorities from Hellenic Universities, as well as Hellenic and international NGOs participated and exchanged basic and applied knowledge on this issue. All parties concluded that recent evaluation on the population estimates of large terrestrial mammals in Southern Balkans shows an alarming reduction. The main causes assessed were (a) human-induced habitat fragmentation and degradation resulting in small, genetically isolated populations, (b) poaching and intense hunting pressure without legal regulations, and (c) absence of a policy incorporating mammals within the larger frame of biodiversity conservation. The situation is considered critical, demanding state and public awareness through the propagation of information coming from current and ongoing research. All parties acknowledged these problems and agreed in (a) the need for collaboration between research institutions and NGOs on an international level for long-term continuous basic and applied research on threatened species, and (b) the formation of national policies for environmental protection incorporating large mammals within the frames of European action plans.

ACKNOWLEDGEMENTS

The Organizing Committee of the 9th ICZEGAR is grateful to all major and minor sponsors : the Ministry of Culture, the Egnatia Odos S.A., and the Aristotle University of Thessaloniki. We also like to express our gratitude to all the invited speakers who honoured the congress with their presence : Bailly N. (Paris, France), Boero F. (Lecce, Italy) Bouchet P. (Paris, France), Froese R. (Kiel, Germany), Goujet D. (Paris, France), Koufos G. (Thessaloniki, Greece), Lazaridou-Dimitriadou M. (Thessaloniki, Greece), Scouras Z. (Thessaloniki, Greece), Sgardelis S. (Thessaloniki, Greece), Schockaert E. (Diepenbeek, Belgium). Special thanks go to Damianidis P. and Christidis J. for their tireless work during all the stages of the organization of this congress. Lastly, we wish to thank all the referees for their valuable and instructive remarks during the selection process of the papers of this special issue of Belgian Journal of Zoology.

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Contribution to the study of the diet of four owl species (Aves, Strigiformes) from mainland and island areas of Greece

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ABSTRACT. The diets of the Barn Owl (*Tyto alba*), Little Owl (*Athene noctua*), Long-eared Owl (*Asio otus*) and Eagle Owl (*Bubo bubo*) were studied through analysis of pellets collected at 13 different continental areas and islands of Greece. The most important prey of the Barn Owl was mammals (mainly *Microtus*, *Mus*, *Apodemus*, *Rattus* and *Crocidura*), although birds and amphibians were of some importance on Antikythera island and Potidea (Central Macedonia), respectively. Average prey biomass ranged from 12.5 g to 42.8 g. The median prey biomass differed significantly between areas ($p<0.001$). The diet of the Little Owl was more diverse, consisting mainly of mammals (mostly *Microtus*, *Mus*, *Apodemus*, *Micromys* and *Crocidura*) in the Evros and Axios Deltas, mainly of insects (mostly Orthoptera and Coleoptera) in the Kitros Lagoon, Psara and Tilos islands, while birds and reptiles were common supplementary prey. Average prey biomass ranged from 0.7 g to 11.9 g. The median prey biomass differed significantly between the areas studied ($p<0.001$). The diet of the Long-eared Owl in both Nestos Delta and Porto Lagos consisted mainly of mammals (mostly *Microtus*, *Mus* and *Apodemus*), with some reptiles in the former area and birds in the latter. Average prey biomass was 18.5 g and 19.5 g respectively. The median prey biomass did not differ significantly between the two areas. The diet of the Eagle Owl in the Amvrakikos wetland consisted mostly of birds (62 % by biomass) and mammals (36 %, mainly *Rattus norvegicus*). Insects were the most important prey by numbers - 47 % (1 % by biomass). The prey diversity of the Eagle Owl was the highest while that of the Barn Owl was the lowest. Prey use by owls tended to clump by geographic area. We conclude that the owl species studied make use of prey according to the local availability and in accordance to the hunting abilities of each species.

KEY WORDS : Barn Owl *Tyto alba*, Little Owl *Athene noctua*, Long-eared Owl *Asio otus*, Eagle Owl *Bubo bubo*, diet, feeding ecology, Greece.

INTRODUCTION

Studies carried out on the diet of owls (Strigiformes) in Europe have revealed considerable geographical variation in the diet of each species (Bunn et al., 1982; Mikkola, 1983; Cramp, 1985; Taylor, 1994). Generally, prey composition and diversity in the Mediterranean area are different to those in central and northern Europe (Herrera & Hiraldo, 1976).

In Greece, nine owl species are known to occur and some of them are common in both continent and island habitats (Handrinos & Akriotis, 1997) but dietary studies are scarce. The aims of this study were : a) to describe and compare the diet and feeding ecology of the Barn Owl (*Tyto alba* (Scopoli, 1769)), Little Owl (*Athene noctua* (Scopoli, 1769)), Long-eared Owl (*Asio otus* (Linnaeus, 1758)) and Eagle Owl (*Bubo bubo* (Linnaeus, 1758)) studied in various parts of Greece and, b) to compare our results with those of studies carried out in Greece and other European countries.

MATERIAL AND METHODS

The study areas (Fig. 1) encompass different habitats. The Evros, Nestos and Axios Deltas, as well as Porto Lagos, Kitros Lagoon and Amvrakikos area are major wetlands, with a high diversity of habitats, such as saltmarshes, lagoons, reedbeds, tamarisk and riparian forest, marshes and cultivations (MEHPW, 1985; 1986a; 1986b). Potidea and Parthenio areas, both in central Macedonia, include mainly agricultural land. The study sites in Mt. Hymettus and Avlona (both near Athens) include open scrublands (phrygana) habitat and farmland. The islands of Psara (NE Aegean), Tilos (SE Aegean) and Antikythera (between Peloponese and Crete) include mainly phrygana and (to a lesser extent) farmland.

Pellets were collected opportunistically from roosts between December 1997 and August 2001 (Table 1). The material was collected out of the breeding season, mostly in winter, excepting that of the Eagle Owl collected at nests. Pellets were analyzed using reference books (Mammals : Lawrence & Brown, 1973; Chaline, 1974. Birds : Brown et al. (1987). Reptiles : Arnold & Burton (1980). Insects : Chinery (1981)). The average weight of each prey taxon was taken from the literature (Mammals : MACDONALD & BARRET (1993). Birds : PERRINS (1987). Reptiles : HELMER & SCHOLTE (1985). Insects : ZERUNIAN et al. (1982)). Because of the difficulty of distinguishing mice *Mus* spp. and *Apodemus* spp. from skulls (VOHRALIK & SOFIANIDOU, 1992), these were often not separated by species. Average prey weight for each sample was estimated by multiplying the numbers of each prey by its average weight, adding the weights produced and dividing the sum by the total numbers of prey in each sample. The trophic diversity (NB) was estimated by using the antilog of the Shannon-Weiner index, while in order to standardize the trophic diversity for comparison within and between the areas we calculated evenness index. Both were calculated on a class prey level. The Mann-Whitney U-test or Kruskall-Wallis test (where appropriate) compared the median prey weights of the same species. Cluster analysis was also performed (using Euclidean distances as distance measure and single linkage as a linkage rule) on biomass proportions of prey in order to determine geographical relationships in the owls' diet. The author names of prey identified in pellets of the owls studied are indicated in Appendix 5.

Fig. 1. – Map showing the areas where pellets of owls were collected for this study.

RESULTS

Barn Owl

In the Evros Delta, small mammals (including at least 10 species) composed 90% of the Diet of the Barn Owl (Appendix 1). The most important prey species by biomass was *Microtus rossiaemeridionalis* (37%) followed by *Mus* spp. (20%), *Crocidura suaveolens* (12%) and *Arvicola terrestris* (7%). Birds were moderately important by biomass (9%). Amphibians and arthropods formed only a minor part of this species' diet.

In Porto Lagos small mammals were also the most important prey (of at least five species, 97% by biomass). *M. rossiaemeridionalis* was by far the most important prey species (84%). The relative contributions of other mammal species were below 5%. Birds formed only a minor part of the diet in this area (2%).

TABLE 1

Number of samples collected in each study area

Area	*Tyto alba*	*Athene noctua*	*Asio otus*	*Bubo bubo*
Evros Delta	4	6	-	-
Porto Lagos	1	-	1	-
Potidea	1	-	-	-
Parthenio	1	-	-	-
Hymettus	2	-	-	-
Avlona	1	-	-	-
Antikythera	1	-	-	-
Axios Delta	-	3	-	-
Kitros Lagoon	-	1	-	-
Tilos	-	1	-	-
Psara	-	1	-	-
Nestos Delta	-	-	1	-
Amvrakikos	-	-	-	2

In Potidea, mammalian prey dominated (at least seven species, 92% by biomass). The main prey species was *M. macedonicus* (74 %). Of moderate importance were *Apodemus* spp. (7%), *C. suaveolens* (6%), birds (7%) and frogs (*Rana* spp.) (6%).

In Parthenio, various species of mammals composed the greater part of the diet, although birds, amphibians and insects were also present. The most important species by biomass were *M. rossiaemeridionalis* (35%), *M. macedonicus* (21%), *Rattus* spp. (15%), and *Apodemus sylvaticus* (12%), while birds formed 7% of the diet. Invertebrates were unimportant in the diet.

In Mt. Hymettus, at least eight mammalian species made up 92% of the diet by biomass. The most important prey species by biomass were *A. sylvaticus* (35%), *A. mystacinus* (33%) and *Microtus thomasi* (8%). Other species' participation did not exceed 5%. Birds formed 8% of the diet.

In Avlona, mammals again were the most important prey of the Barn Owl (eight species, 96% by biomass) and birds were also represented (4%). The most important species by biomass was *M. thomasi* (49%), followed by *Mus domesticus* (25%), *M. macedonicus* (8%) and A. *sylvaticus* (6%).

In Antikythera Island, the main prey consisted of three species of mammals (83% by biomass). By far the most important prey was *Rattus rattus* (73%) followed by birds (16%) and *M. domesticus* (6%). Reptiles were represented by geckoes (Gekkonidae) and formed 10% of the diet by number but only 1% by biomass.

The median prey biomass was significantly different between the seven areas (Kruskall-Wallis test, χ^2 = 304.04, df = 6, $p<0.001$). Average prey biomass ranged from 12.5 g in Potidea to 42.8 g in Antikythera. The prey diversity ranged from 1.12 in Porto Lagos to 2.14 in Antikythera, while the evenness ranged from 0.11 in Evros Delta to 0.69 in Antikythera (Table 2).

TABLE 2

Prey size and prey diversity indices of the four owl species in Greece

	N	Average	Median	Min	Max	Diversity	Eveness
			Tyto alba				
Evros	487	14.5	12.0	1.0	100	1.17	0.11
P. Lagos	116	17.2	20.0	2.0	20	1.12	0.17
Parthenio	463	18.8	20.0	1.0	150	1.31	0.20
Potidea	296	12.5	12.0	2.0	60	1.20	0.17
Avlona	94	14.8	12.0	2.0	20	1.15	0.20
Hymettus	152	22.2	20.0	6.0	80	1.20	0.27
Antikythera	106	42.8	60.0	5.0	200	2.14	0.69
			Athene noctua				
Evros	996	10.7	12.0	0.1	70	2.45	0.46
Axios	273	11.9	12.0	0.2	60	2.24	0.58
Kitros Lagoon	99	1.1	0.5	0.2	25	1.45	0.26
Tilos	154	0.7	0.5	0.1	12	1.15	0.12
Psara	74	1.1	1.0	0.1	12	1.45	0.26
			Asio otus				
Nestos	52	18.5	20.0	6.0	60	1.29	0.23
P. Lagos	83	19.5	20.0	0.5	100	1.58	0.41
			Bubo bubo				
Amvrakikos	66	108.1	3.0	1.0	800	2.88	0.77

Little Owl

The most numerous prey types of the Little Owl in Evros Delta were mammals and insects (54% and 41% by numbers respectively), although other arthropods, reptiles, birds and molluscs were also represented (Appendix 2). The most important prey were mammals (at least six species, 90% by biomass), mainly *M. rossiaemeridionalis* (54%), *Mus* spp. (13%), *Apodemus* spp. (10%) and Crocidura spp. (6%). Birds contributed 6% by biomass, insects only 2%.

In the Axios Delta, the most important prey were small mammals (at least eight species, 93% by biomass). The most important species were *M. rossiaemeridionalis* (39%), *Mus* spp. (12%), *Micromys minutus* (11%), *Apodemus* spp. (6%) and *Rattus* spp. (6%). Reptiles contributed 5% to the diet and insects only 1%.

In the Kitros Lagoon insects (mainly Coleoptera) were the most important prey by both number (92%) and biomass (43%), other prey consisting of mammals, Diplopoda and birds. Mammals formed 35% of the diet by biomass, represented by *Mus* spp. (23%) and *Crocidura suaveolens* (12%), while birds formed 19%.

On Tilos Island insects were again the most important prey (97% by numbers, 69% by biomass). Orthoptera (51%) and Coleoptera (14%) were the most important insect groups. Other prey consisted of mammals and reptiles. Mammals formed 27% of the diet by biomass represented by *M. domesticus* (21%) and *C. suaveolens* (5%), while reptiles contributed to 5%.

On Psara Island, insects (mainly Orthoptera and Coleoptera) were also the most important prey (92% by number, 71% by biomass). Prey also included other arthropods and mammals. Mammals formed 24% of the diet by biomass, represented by only two species, namely *M. domesticus* (15%) and *C. suaveolens* (7%).

The median prey biomass was significantly different between the five areas (Kruskall-Wallis test, $\chi^2 = 367.88$, df = 4, $p<0.001$). Average prey biomass ranged from 0.7 g on Tilos Island to 11.9 g in the Axios Delta. Prey diversity ranged from 1.15 on Tilos Island to 2.45 in Evros Delta, while the evenness ranged from 0.12 on Tilos to 0.58 in the Axios Delta (Table 2).

Long-eared Owl

In the Nestos Delta, the Long-eared Owl preyed mainly on mammals (at least five species, 87% by biomass) and secondarily on reptiles and birds (Appendix 3). The most important mammalian prey was *M. rossiaemeridionalis* (44% by biomass), followed *by M. macedonicus* (11%), *Talpa europaea* (7%), *C. suaveolens* (7%) and *Apodemus* spp. (6%). Reptiles (indeterminate snakes) formed 10% of the prey by biomass. However, because of the small sample, these results should be treated with caution.

In Porto Lagos the diet of this species consisted mainly of mammals (at least four species, 79% by biomass), but also included birds and insects. The most important mammals were *M. rossiaemeridionalis* (52%), *M. macedonicus* (17%) and *Apodemus* spp. (10%). Birds contributed 21% by biomass including small passerines and medium-sized species.

The median prey biomass did not differ significantly between the two areas (Mann-Whitney U test, Z = -1.20, n. s.). Average prey biomass was 18.5 g. and 19.5 g. in the Nestos Delta and Porto Lagos respectively. Both prey diversity and evenness were higher in the Nestos Delta (1.29 and 0.23 respectively vs. 1.58 and 0.41) (Table 2).

Eagle Owl

The Eagle Owl in Amvrakikos wetland preyed on mammals, birds, amphibians and insects (Appendix 4). While insects (mainly Orthoptera) formed 47% of the diet by number, they contributed only to 1% by biomass. Birds (of at least eight large-sized species) and mammals (at least seven species) formed 62% and 36% of the biomass of prey respectively. The most important prey species were *Rattus norvegicus* (40%), *Gallinula chloropus* (25%), Buteo buteo (11%), *Fulica atra* (10%) and *Erinaceus concolor* (7%). Because of the small size of the sample (though it included prey from two different, distant roosts), these results should not be considered representative of the diet of the species in our region. The prey diversity and evenness were 2.88 and 0.77 respectively. Average prey biomass was 108.1 g. (Table 2).

Dietary comparison between owls

The cluster analysis closely grouped the diets of Barn Owl, Little Owl and Long-eared Owl in the wetlands of northeastern Greece (group on the upper part of the cluster) (Fig. 2). The three Little Owl samples where insects predominated (Kitros Lagoon, Psara and Tilos islands) were also grouped together in the middle area of the cluster. The lower part of the cluster grouped the diets of the

Barn Owl and Eagle Owl mainly from the western part of the study area (Athens region and Amvrakikos).

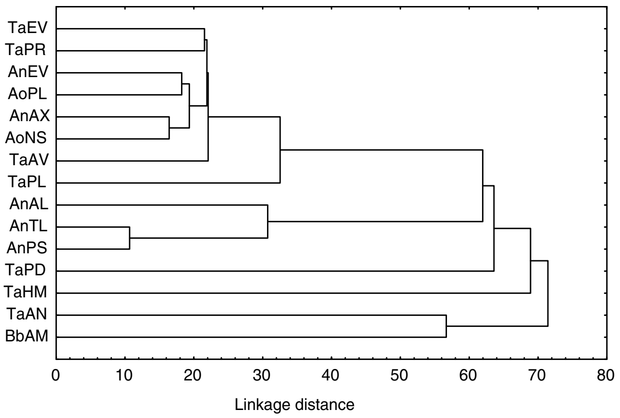

Fig. 2. – Cluster analysis of the prey of the four owl species. Ta : *Tyto alba*; An : *Athene noctua*; Ao : *Asio otus*; Bb *: Bubo bubo*. EV : Evros Delta; PR : Parthenio; PL : Porto Lagos; AX : Axios Delta; NS : Nestos Delta; AV : Avlona; AL : Kitros Lagoon; TL : Tilos; PS : Psara; PD : Potidea; HM : Hymettus; AN : Antikythera; AM : Amvrakikos.

DISCUSSION

Interspecific variation in owl diet

There were considerable differences in prey use between the four owl species. The Barn Owl preyed mainly on small mammals, while birds and amphibians were only of local importance, and, accordingly, diet showed low diversity. Although the Long-eared Owl preyed mainly on small mammals, also took other prey (particularly birds and reptiles), having a more diverse diet. The diet of the Little Owl was more variable : in two of the study areas the main prey were mammals but other prey involved resulted in relatively high diversity. In the other three areas the species took mainly insects, thus showing a more restricted diet based on small-sized prey. The Eagle Owl had the most diverse diet of all, taking many species of birds, mammals and insects, and, on average, its prey was much larger than that of the other species.

The differences in prey type and size between owl species are due to a variety of factors such as interspecific differences in morphology and hunting techniques, as well as different prey availability in different parts of the species' range (Bunn et al., 1982). The geographical distribution and consequently availability of prey species, seemed to be important in our study as revealed by the cluster analysis where diets were clumped by geographical area rather than by owl species. Despite these, there is evidence that some prey types may be selected by the species studied. Thus, the Barn Owl frequently selects shrews (Soricidae) as prey (Bunn et al, 1982; Cramp, 1985; Taylor, 1994). The Long-eared Owl, preying mainly upon small mammals, takes shrews relatively infrequently, while, on the other hand, it often takes birds, particularly in Europe (Marti, 1976; Mikkola, 1983; Cramp, 1985; Alivizatos & Goutner, 1999). In most relative studies, the Little Owl has been found to prey mainly on arthropods, particularly insects, (Zerunian et al., 1982; Mikkola, 1983; Capizzi & Luiselli, 1995) but in some Mediterranean areas small mammals are dominant in the diet (Lo Verde & Massa, 1988; Goodman, 1988; this study) The much larger Eagle Owl can take much larger prey, mainly mammals and birds (frequently including raptors and other owls) (Mikkola, 1983 : Cramp, 1985; Papageorgiou et al., 1993, Marchesi et al., 2002, Sergio et al., 2003).

Geographical variation in owl diet

In mid-European countries, voles (Microtinae) and shrews are the main prey of the Barn Owl, while in the Mediterranean countries mice (Muridae) are more important (Bohr, 1962; Cheylan, 1976; Taylor, 1994). Even on a smaller geographical scale, as in this study, there were considerable differences in the diet of the Barn Owl between the areas studied. Although mammals always made up the bulk of the diet, different species predominated in different areas. *Microtus, Mus* and to a lesser extent, *Crocidura* species were important prey in most areas, but other taxa were important locally (notably *Apodemus* spp. in Mt. Hymettus and *R. rattus* on Antikythera Island). These differences may be partly seasonal (Cambell et al., 1987; Taylor, 1994) due to different dates the pellets were collected, but they must also be due to zoogeographical reasons related to the distribution of prey species and also to the type, availability and extent of foraging habitats of the Barn Owl in each area (Dor, 1947; Yom-tov & Wool, 1997; Marti, 1988). Inevitably, habitat differences accounted for dietary differences in this study, as two of the areas sampled (Evros Delta and Porto Lagos) constitute wetlands, three (Parthenio, Potidea and Avlona) included mainly agricultural areas, while the rest (Mt. Hymettus and Antikythera Island) included mainly phryganic habitats. Of Barn Owl prey, *Microtus* spp., as well as *Mus macedonicus*, normally occur in grassland habitats, including agricultural land (Vohralik & Sofianidou, 1992), which explains their predominance as prey in areas with this habitat type. The habitat effect in prey selection is also indicated in a previous study in Mt. Hymettus where the diet of the Barn Owl comprised *M. domesticus* (39%), birds (24%) (primarily *Passer domesticus* (15%) and *Turdus merula* (5%)), A. mystacinus (19%) and *A. sylvaticus* (17%) (Tsounis & Dimitropoulos, 1992). It is likely that this study encompassed a different area, probably closer to urban environment, as suggested by the high numbers of *M. domesticus* and *P. domesticus*.

The preponderance of *M. rossiaemeridionalis* in Porto Lagos and of *M. macedonicus* in Potidea may be due to temporarily high population peaks of these species, as reported in many studies, particularly regarding *Microtus* spp. (Bunn et al., 1982; Mikkola, 1983; Taylor, 1994). It is probable that this phenomenon resulted in the considerable differences in the composition of mammalian prey of the Barn Owl in Porto Lagos found in a previous study (*Mus* spp., 32% by biomass, *M. rossiaemeridionalis* 28%, *Apodemus* spp. 10% and *C. suaveolens* 8%, Alivizatos & Goutner, 1999).

The low diversity of mammals in the diet of the Barn Owl on Antikythera Island reflected the poor mammalian fauna on the island. On the other hand, the high diversity of birds is explained mainly by the fact that the island is an important migration crossroad (Messineo et al., 2001).

Generally, the average prey biomass is within the range known for the Mediterranean countries. In our study areas the differences in average biomass of the Barn Owl prey were due to the different proportions of prey types involved in the areas studied. Low values were found where shrews and small mice were the main prey, and high where rats and birds were commonest. The highest value at Antikythera is more similar to that found in Israel and Egypt where large-sized prey such as gerbils and rats are consumed (Goodman, 1986; Yom-tov & Wool, 1997). Thus, Barn Owls, being mainly predators of small mammals, seem to exploit the most abundant or locally available prey, according to the local conditions.

The diet of the Little Owl also differed considerably in the areas studied. In the deltas the most important prey were mammals (mainly *Microtus*, followed by *Mus* and *Apodemus* spp.). In the three other areas, insects formed most of the diet. These differences could only in part be attributable to seasonal prey variability (Cramp, 1985; Zerunian et al., 1982) as the pellets from all areas were collected in winter, except on Rsara Island where they were collected in the summer. The diet of *Athene* owls varies greatly according to habitat, location and season, as found in Italy, Spain, North and South America, and differences in diet most likely reflect availability rather than prey selection (Zerunian et al., 1982; Jaksic & Marti, 1988). The predominance of *Microtus* spp. among mammalian prey was probably due to the ease of capture (lack of cover after crop harvest).

The Eagle Owl is known to take a great variety of prey, much larger on average than those of other owls. Mammals and birds are the main prey but the participation of mammals found in our study (36.2% by biomass) is the lowest reported in Europe ranging from 62% to 94% (Martinez et al., 1992). In addition, the main prey of the Eagle Owl in other Mediterranean areas is *Oryctolagus cuniculus* (Martinez et al., 1992), lacking from the diet in Greece. Insects, which usually constitute a prey taken in small numbers (Mikkola, 1983; Cramp, 1985; Papageorgiou et al., 1993), in this study are exceptionally high in their numerical representation. The differences may be due to a higher availability of other prey types in Greece and suggest a rather opportunistic foraging behaviour in this part of the region.The mammalian prey of the Long-eared Owl was rather similar in the two study areas, made up mainly by *Microtus*, *Mus* and *Apodemus* species. No conclusion can be drawn on the relative importance of birds in Porto Lagos and reptiles in the Nestos Delta in this study due to small sample sizes. In a previous study in Porto Lagos the Long-eared Owl was found to prey mainly on *Mus* spp. (35%), *Apodemus* spp. (28%), birds (16%), and only 15% on *M. rossiaemeridionalis* (Alivizatos & Goutner, 1999). The predominance of the latter species in the present study can, as in the case of the Barn Owl, be attributed either to a temporary high population increase or recent habitat changes. In Greece, mice have been recorded as the most important prey (Alivizatos & Goutner, 1999 ; Akriotis unpubl. data) but in mid-Europe voles are more important (Mikkola, 1983). Birds are often important prey in Europe but not in North America (Marti, 1976).

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APPENDIX 1

Prey of the Barn Owl in the areas studied. N: numbers; B: biomass

	EVROS DELTA			P. LAGOS			POTIDEA			PARTHENIO			HYMETTUS			AVLONA			ANTI-KYTHERA		
Prey	**N**	**% N**	**% B**	**N**	**% N**	**% B**	**N**	**% N**	**% B**	**N**	**% N**	**% B**	**N**	**% N**	**% B**	**N**	**% N**	**% B**	**N**	**% N**	**% B**
CHILOPODA	2	0.4	<0.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Scolopendra spp.	2	0.5	<0.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
INSECTA	3	0.7	<0.1	-	-	-	-	-	-	3	0.6	0.1	-	-	-	-	-	-	-	-	-
Tettigoniidae	2	0.6	<0.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Carabidae	1	0.2	<0.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Gryllotalpa gryllotalpa	-	-	-	-	-	-	-	-	-	2	0.4	<0.1	-	-	-	-	-	-	-	-	-
Scarabaeidae	-	-	-	-	-	-	-	-	-	1	0.2	<0.1	-	-	-	-	-	-	-	-	-
AMPHIBIA	1	0.2	0.4	-	-	-	7	2.4	5.7	6	1.3	2.1	-	-	-	-	-	-	-	-	-
Rana spp.	-			-	-	-	7	2.4	5.7	6	1.3	2.1	-	-	-	-	-	-	-	-	-
Anura indet.	1	0.2	0.4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
REPTILIA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11	10.4	1.2
Gekkonidae indet.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11	10.4	1.2
AVES	12	2.5	9.3	3	2.6	3.2	4	1.3	2.1	19	4.1	7.4	7	4.6	8.4	3	3.2	3.5	17	16.0	15.6
Gallinago gallinago	1	0.2	1.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Erithacus rubecula	1	0.2	0.3	1	0.9	1.1	-	-	-	-	-	-	-	-	-	1	1.1	1.0	-	-	-
Sturnus vulgaris	4	0.8	4.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Fringilla coelebs	-	-	-	2	1.7	2.1	-	-	-	3	0.7	0.7	4	2.6	4.6	2	2.1	2.7	-	-	-
Streptopelia sp.	-	-	-	-	-	-	-	-	-	1	0.2	1.7	-	-	-	-	-	-	-	-	-
Alcedo atthis	1	0.2	0.6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Turdus merula	1	0.2	1.4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Emberiza sp.	1	0.2	0.4	-	-	-	-	-	-	1	0.2	0.3	-	-	-	-	-	-	-	-	-
Parus major	-	-	-	-	-	-	1	0.3	0.4	-	-	-	-	-	-	-	-	-	-	-	-
Turdus sp.	-	-	-	-	-	-	-	-	-	-	-	-	1	0.7	2.3	-	-	-	-	-	-
Passer spp.	-	-	-	-	-	-	-	-	-	2	0.4	0.6	2	1.3	1.4	-	-	-	-	-	-
Alectoris chukar (pull.)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0.9	2.2
Porzana spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	1.9	2.2
Otus scops	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0.9	1.8
Hirundo rustica	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	1.9	0.9
Ficedula spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	1.9	0.5
Lanius spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	1.9	1.3
Miliaria calandra	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0.9	0.9
Passeriformes indet.	3	0.6	1.3	-	-	-	3	1.0	1.6	12	2.6	4.1	-	-	-	-	-	-	2	1.9	1.3
Aves indet.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	3.8	4.4
MAMMALIA	468	96.1	90.2	113	97.4	96.8	285	96.3	92.2	435	94.0	90.4	145	95.4	91.6	91	96.8	96.5	78	73.6	83.2
Neomys anomalus	10	2.1	1.4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Crocidura leucodon	26	5.3	3.0	-	-	-	2	0.7	0.4	2	0.4	0.2	2	1.3	0.5	-			-	-	-
Crocidura suaveolens	144	29.6	12.3	13	11.2	4.2	39	13.2	6.4	42	9.2	2.9	14	9.2	2.4	9	9.6	3.7	-	-	-
Crocidura spp.	-	-	-	-	-	-	-	-	-	-	-	-	3	2.0	0.6	-			-	-	-
Suncus etruscus	2	0.4	0.1	1	0.9	0.1	2	0.7	0.1	-	-	-	-	-	-	3	3.2	0.4	-	-	-
Micromys minutus	-	-	-	-	-	-	-	-	-	7	1.5	0.6	-	-	-	-	-	-	-	-	-
Microtus rossiaemeridionalis	136	27.9	38.6	78	67.2	83.7	1	0.3	0.5	150	32.9	34.6	-	-	-	-	-	-	-	-	-
Microtus guentheri	1	0.2	0.4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Apodemus spp.	18	3.7	5.1	4	3.4	4.3	13	4.4	7.1	-	-	-	5	3.3	4.3	-	-	-	-	-	-
Apodemus sylvaticus	-	-	-	-	-	-	-	-	-	54	11.8	12.4	60	39.5	34.6	4	4.2	5.5	-	-	-
Apodemus mystacinus	-	-	-	-	-	-	-	-	-	-	-	-	29	19.1	33.4	-	-	-	-	-	-
Cricetulus migratorius	-	-	-	-	-	-	-	-	-	-	-	-	2	1.3	1.2	1	1.1	1.4	-	-	-
Microtus thomasi	-	-	-	-	-	-	-	-	-	-	-	-	13	8.6	7.5	35	37.2	48.5	-	-	-
Mus domesticus	-	-	-	-	-	-	-	-	-	2	0.4	0.3	-	-	-	30	31.9	24.9	22	20.8	5.8
Mus macedonicus	-	-	-	17	14.7	4.5	224	75.7	73.5	151	33.1	20.9	15	9.9	5.2	9	9.6	7.5	-	-	-
Mus spp.	117	24.0	20.0	-	-	-	-	-	-	-	-	-	1	0.7	0.3	-	-	-	-	-	-
Mustela nivalis	1	0.2	1.4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rattus rattus	-	-	-	-	-	-	2	0.7	3.3	9	2.0	6.2	1	0.7	1.7	1	1.1	4.2	55	51.9	73.0
Rattus norvegicus	-	-	-	-	-	-	-	-	-	3	0.7	2.1	-	-	-	-	-	-	-	-	-
Rattus spp.	-	-	-	-	-	-	-	-	-	9	2.0	6.2	-	-	-	-	-	-	-	-	-
Arvicola terrestris	8	1.6	6.8	-	-	-	-	-	-	3	0.7	2.1	-	-	-	-	-	-	-	-	-
Talpa europaea	-	-	-	-	-	-	-	-	-	3	0.7	2.1	-	-	-	-	-	-	-	-	-
Oryctolagus cuniculus (juv.)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0.9	4.4
Muridae indet.	3	0.6	0.6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rodentia indet.	2	0.4	0.6	-	-	-	2	0.7	1.4	-	-	-	-	-	-	-	-	-	-	-	-
Total No of prey	486	-	-	116	-	-	296	-	-	463	-	-	152	-	-	94	-	-	106	-	-

APPENDIX 2

Prey of the Little Owl in the areas studied N: numbers; B: biomass

	EVROS DELTA			**AXIOS DELTA**			**KITROS LAGOON**			**TILOS**			**PSARA**		
Prey	**N**	**% N**	**% B**	**N**	**% N**	**% B**	**N**	**% N**	**% B**	**N**	**% N**	**% B**	**N**	**% N**	**% B**
DIPLOPODA	-	-	-	-	-	-	3	3.0	2.9	-	-	-	-	1.4	0.6
Julidae	-	-	-	-	-	-	3	3.0	2.9	-	-	-	-	1.4	0.6
MOLLUSCA	1	0.1	<0.1	-	-	-	-	-	-	-	-	-	-	-	-
Stylommatophora indet.	1	0.1	<0.1	-	-	-	-	-	-	-	-	-	-	-	-
CHILOPODA	1	0.1	<0.1	-	-	-	-	-	-	-	-	-	-	-	-
Scolopendra sp.	1	0.1	<0.1	-	-	-	-	-	-	-	-	-	-	-	-
ARACHNIDA	2	0.2	<0.1	-	-	-	-	-	-	-	-	-	3	4.1	3.7
Aranae indet.	2	0.2	<0.1	-	-	-	-	-	-	-	-	-	-	-	-
Solifugae indet.	-	-	-	-	-	-	-	-	-	-	-	-	3	4.1	3.7
INSECTA	408	41.1	2.4	50	17.9	1.3	91	91.9	43.2	150	97.4	68.8	68	91.9	71.1
Dermaptera	56	5.6	0.2	4	1.5	0.1	2	2.0	0.4	-	-	-	1	1.4	0.2
Labiduridae	37	1.9	0.1	3	1.1	<0.1	-	-	-	-	-	-	-	-	-
Forficulidae	19	3.7	0.1	1	0.4	<0.1	2	2.0	0.4	-	-	-	1	1.4	0.2
Odonata	55	5.5	0.5	-	-	-	-	-	-	-	-	-	-	-	-
Anisoptera indet.	55	5.5	0.5	-	-	-	-	-	-	-	-	-	-	-	-
Orthoptera	154	15.4	1.2	34	12.5	1.2	-	-	-	114	74.0	50.9	60	81.1	65.8
Gryllotalpa gryllotalpa	24	2.4	0.4	21	7.7	0.7	-	-	-	-	-	-	-	-	-
Tettigoniidae	50	5.0	0.4	6	2.6	0.4	-	-	-	-	-	-	48	64.9	58.5
Acrididae	77	7.7	0.4	7	2.2	0.1	-	-	-	114	74.0	50.9	12	16.2	7.3
Hemiptera	6	0.6	<0.1	-	-	-	-	-	-	-	-	-	-	-	-
Heteroptera indet.	6	0.6	<0.1	-	-	-	-	-	-	-	-	-	-	-	-
Coleoptera	68	6.8	0.3	6	2.6	0.1	89	89.9	42.0	18	11.7	13.8	5	6.8	4.9
Staphylinidae	3	0.3	<0.1	-	-	-	4	4.0	1.9	-	-	-	-	-	-
Scarabaeidae	3	0.3	<0.1	2	0.7	<0.1	-	-	-	1	0.6	0.9	3	4.1	3.7
Curculionidae	1	0.1	<0.1	1	0.4	<0.1	-	-	-	-	-	-	-	-	-
Carabidae	49	4.9	<0.1	1	1.5	<0.1	85	85.9	40.1	3	1.9	1.3	2	2.7	1.2
Dytiscus marginalis	4	0.4	<0.1	-	-	-	-	-	-	-	-	-	-	-	-
Hydrophilus sp.	1	0.1	<0.1	-	-	-	-	-	-	-	-	-	-	-	-
Coleoptera indet.	2	0.2	<0.1	1	0.4	<0.1	-	-	-	-	-	-	-	-	-
Tenebrionidae	-	-	-	-	-	-	-	-	-	2	1.3	0.9	-	-	-
Geotrupidae	-	-	-	-	-	-	-	-	-	12	7.8	10.7	-	-	-
Dytiscidae	5	0.5	<0.1	-	-	-	-	-	-	-	-	-	-	-	-
Coccinellidae	1	0.1	<0.1	1	0.7	<0.1	-	-	-	-	-	-	-	-	-
Hymenoptera	59	5.9	0.1	-	-	-	-	-	-	15	9.7	1.3	2	2.7	0.2
Formicidae	59	5.9	0.1	-	-	-	-	-	-	15	9.7	1.3	2	2.7	0.2
Mantodea	14	1.4	0.1	1	0.4	<0.1	-	-	-	3	1.9	2.7	-	-	-
Mantidae	14	1.4	0.1	1	0.4	<0.1	-	-	-	3	1.9	2.7	-	-	-
REPTILIA	15	1.5	1.5	25	9.2	4.6	-	-	-	1	0.6	4.5	-	-	-
Podarcis taurica	13	1.3	0.5	24	8.8	3.1	-	-	-	-	-	-	-	-	-
Natrix sp.	1	0.1	0.5	-	-	-	-	-	-	-	-	-	-	-	-
Colubridae indet.	1	0.1	0.5	1	0.4	1.6	-	-	-	-	-	-	-	-	-
Lacertilia indet.	-	-	-	-	-	-	-	-	-	1	0.6	4.5	-	-	-
AVES	22	2.8	6.1	2	0.7	1.3	1	1.0	19.2	-	-	-	-	-	-
Passeriformes indet.	16	3.6	3.6	2	0.7	1.3	1	1.0	19.2	-	-	-	-	-	-
Galerida cristata	2	0.2	0.7	-	-	-	-	-	-	-	-	-	-	-	-
Sturnus vulgaris	1	0.1	0.6	-	-	-	-	-	-	-	-	-	-	-	-
Erithacus rubecula	2	0.2	0.4	-	-	-	-	-	-	-	-	-	-	-	-
Passer spp.	3	0.3	0.7	-	-	-	-	-	-	-	-	-	-	-	-
MAMMALIA	520	54.2	90.2	69	72.2	92.8	4	4.0	34.6	3	1.9	26.8	2	2.7	24.4
Crocidura suaveolens	25	2.5	5.7	8	2.9	1.5	2	2.0	11.5	1	0.6	5.4	1	1.4	7.3
Crocidura leucodon	2	0.2	0.1	-	-	-	-	-	-	-	-	-	-	-	-
Microtus rossiaemeridionalis	296	29.7	54.0	51	18.7	38.5	-	-	-	-	-	-	-	-	-
Apodemus spp.	56	5.6	10.2	10	3.7	6.3	-	-	-	-	-	-	-	-	-
Mus spp.	118	11.8	12.9	31	11.4	11.7	2	2.0	23.1	-	-	-	-	-	-
Mus domesticus	-	-	-	-	-	-	-	-	-	1	1.3	21.4	1	1.4	14.6
Rattus spp.	-	-	-	3	1.1	5.7	-	-	-	-	-	-	-	-	-
Micromys minutus	-	-	-	49	17.9	10.8	-	-	-	-	-	-	-	-	-
Suncus etruscus	-	-	-	1	0.4	0.1	-	-	-	-	-	-	-	-	-
Pipistrellus sp.	-	-	-	1	0.4	0.2	-	-	-	-	-	-	-	-	-
Muridae indet.	14	1.4	1.9	18	6.6	8.5	-	-	-	-	-	-	-	-	-
Rodentia indet.	28	2.8	5.1	25	9.2	15.8	-	-	-	-	-	-	-	-	-
Mammalia indet.	1	0.1	0.1	-	-	-	-	-	-	-	-	-	-	-	-
Total No of prey	996	-	-	273	-	-	99	-	-	154	-	-	74		

APPENDIX 3

Prey of the Long-eared Owl in the areas studied.
N: numbers; B: biomass

	NESTOS DELTA			P. LAGOS		
Prey	**N**	**% N**	**% B**	**N**	**% N**	**% B**
INSECTA	-	-	-	2	2.4	0.1
Acrididae	-	-	-	1	1.2	0.1
Tenebrionidae	-	-	-	1	1.2	0.1
REPTILIA	2	3.8	10.4	-	-	-
Colubridae indet.	2	3.8	10.4	-	-	-
AVES	1	1.9	2.1	9	10.8	21.1
Alauda arvensis	-	-	-	1	1.2	2.5
Turdus sp.	-	-	-	1	1.2	5.0
Fringilla coelebs	-	-	-	1	1.2	1.3
Carduelis sp.	-	-	-	1	1.2	0.9
Passeriformes indet.	1	1.9	2.1	4	4.8	5.0
Aves indet.	-	-	-	1	1.2	6.3
MAMMALIA	49	94.2	87.5	72	86.7	78.8
Crocidura suaveolens	11	21.1	6.9	1	1.2	0.4
Talpa europaea	2	3.8	14.6	-	-	-
Microtus rossiaemeridionalis	21	40.4	43.8	41	49.4	51.7
Apodemus spp.	3	5.8	6.3	8	9.6	10.1
Mus macedonicus	9	17.3	11.3	22	26.5	16.6
Rodentia indet.	3	5.8	4.7	-	-	-
Total No of prey	52	-	-	83	-	

APPENDIX 4

Prey of the Eagle Owl in Amvrakikos.
N: numbers; B: biomass

Prey	**N**	**% N**	**% B**
INSECTA	35	53.0	1.4
Orthoptera	31	47.0	1.3
Tettigoniidae	31	47.0	1.3
Coleoptera	4	6.1	0.1
Carabus sp.	1	1.5	<0.1
Oryctes spp.	2	3.0	0.1
Cerambyx cerdo	1	1.5	0.7
AMPHIBIA	1	1.5	0.7
Rana sp.	1	1.5	0.7
AVES	13	20.0	61.7
Buteo buteo	1	1.5	11.2
Gallinula chloropus	6	9.1	25.2
Fulica atra	1	1.5	9.8
Charadriiformes indet.	1	1.5	1.4
Columba livia	1	1.5	3.5
Streptopelia decaocto	1	1.5	2.8
Tyto alba	1	1.5	4.2
Asio otus	1	1.5	3.5
MAMMALIA	17	25.8	36.2
Erinaceus concolor	1	1.5	7.0
Sciurus vulgaris	1	1.5	2.8
Glis glis	1	1.5	1.4
Microtus thomasi	1	1.5	0.3
Rattus rattus	1	1.5	1.4
Rattus norvegicus	11	16.7	39.9
Mus sp.	1	1.5	0.2
Total No of prey	66	-	-

APPENDIX 5

Full names of prey identified in owls' pellets in this study

ARTHROPODA

Scolopendra Linnaeus 1758
Gryllotalpa gryllotalpa Linnaeus 1758
Dytiscus marginalis (Linnaeus 1758)
Hydrophilus Geoffroy 1762
Carabus Linnaeus 1758
Oryctes Illiger 1798
Cerambyx cerdo Linnaeus 1758

AMPHIBIA

Rana Linnaeus 1758

REPTILIA

Podarcis taurica Pallas 1814
Natrix Laurenti 1765

AVES

Buteo buteo (Linnaeus 1758)
Alectoris chukar (J. E. Gray 1830)
Porzana Vieillot 1816
Gallinula chloropus (Linnaeus 1758)
Fulica atra Linnaeus 1758
Gallinago gallinago (Linnaeus 1758)
Columba livia Gmelin 1789
Streptopelia decaocto (Frivaldsky 1838)
Streptopelia Bonaparte 1855
Tyto alba (Scolopi 1769)
Asio otus (Linnaeus 1758)
Otus scops (Linnaeus 1758)
Alcedo atthis (Linnaeus 1758)
Alauda arvensis Linnaeus 1758
Galerida cristata (Linnaeus 1758)
Hirundo rustica Linnaeus 1758
Lanius Linnaeus 1758
Ficedula Brisson 1760
Erithacus rubecula (Linnaeus 1758)
Turdus merula Linnaeus 1758
Turdus Linnaeus 1758
Parus major Linnaeus 1758
Emberiza calandra Linnaeus 1758
Emberiza Linnaeus 1758
Fringilla coelebs Linnaeus 1758
Carduelis Brisson 1760
Passer Brisson 1760
Sturnus vulgaris Linnaeus 1758

MAMMALIA

Erinaceus concolor Martin 1838
Neomys anomalus Cabrera 1907
Talpa europaea Linnaeus 1758
Suncus etruscus (Savi 1822)
Crocidura suaveolens (Pallas 1811)
Crocidura leucodon (Hermann 1780)
Crocidura Wagler 1832
Pipistrellus Kaup 1829
Oryctolagus cuniculus (Linnaeus 1758)
Sciurus vulgaris (Linnaeus 1758)
Glis glis (Linnaeus 1766)
Cricetulus migratorius (Pallas 1773)
Microtus rossiaemeridionalis Ognev 1924
Microtus guentheri (Danford & Alston 1880)
Microtus thomasi (Berrett-Hamilton 1903)
Arvicola terrestris (Linnaeus 1758)
Rattus norvegicus (Berkenhout 1769)
Rattus rattus (Linnaeus 1758)
Rattus Fischer 1803
Apodemus sylvaticus (Linnaeus 1758)
Apodemus Kaup 1829
Apodemus mystacinus (Danford & Alston 1877)
Micromys minutus (Pallas 1771)
Mus domesticus Swarz & Swarz 1943
Mus Linnaeus 1766
Mus macedonicus Petrov & Ruzic 1983
Mustela nivalis Linnaeus 1766

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Mollusca fauna from infralittoral hard substrate assemblages in the North Aegean Sea

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ABSTRACT. The spatial distribution of the molluscan fauna from infralittoral hard substrate assemblages in the North Aegean Sea was studied during summer 1997 and 1998. Material was collected from six stations located in Chalkidiki peninsula, plus one in Kavala Gulf. Samples were collected by means of SCUBA diving (5 replicates with a quadrate sampler covering the surface of 400cm^2). Examination of the 10917 living molluscs collected revealed 111 species, belonging to three different classes (five Polyplacophora, 85 Gastropoda and 21 Bivalvia). *Skeneopsis planorbis*, *Trapania maculata* and *Limapontia capitata* are reported for the first time as elements of the molluscan fauna in the Eastern Mediterranean or the Aegean Sea, and *Callistochiton pachylasmae*, *Raphitoma leufroyi*, *Polycera quadrilineata*, *Phyllaplysia lafonti* and *Petalifera petalifera* as elements in the North Aegean Sea. Multivariate analyses (Cluster and MDS), discriminate the sampling stations into four main groups, indicating, that apart from the rough dispersion of the molluscs, a more homogenous pattern is detectable at the middle part of the lower infralittoral zone.

KEY WORDS : *Keywords* : *Molluscs, infralittoral, Aegean Sea, hard substrate, biodiversity*

INTRODUCTION

The term ‘biodiversity’ is recently defined as the collection of genomes, species and ecosystems occurring in a geographically defined region (CBDMS, 1995). Its value as an indicator of environmental health is now largely recognized (GASTON & SPICER, 1998 ; BIANCHI & MORRI, 2000) and species diversity, i.e. composition, recognised as an important indicator of diversity across spatial scales and habitats. A considerable amount of information concerning the biodiversity of Mediterranean ecosystems has been organised and presented with reference to the classification of benthic biocenoses (PÉRÈS, 1967) or organismic assemblages (PÉRÈS, 1982), since this scheme has been considered as appropriate for that basin (AUGIER 1982).

Considering molluscs, available information during the earlier parts of the 20th century came mainly from general ecological and faunal surveys in the Eastern Mediterranean (e.g. PÉRÈS & PICARD, 1958 ; LEDOYER, 1969 ; STRACK, 1988). Throughout the last ten years, records of molluscs were included in almost all research surveys carried out in Greek waters, mainly in the Aegean and the Ionian Seas, and information is summarized in KOUTSOUBAS (1992), DELAMOTTE & VARDALA-THEODOROU (1994), ZENETOS (1997), KOUTSOUBAS et al. (2000a). However, a biotope approach, based on the molluscan fauna distributed along the continental shelf of the Greek Seas and using numerical taxonomic methods, has been attempted in very few cases and even those cover only the soft substrate assemblages (e.g. ZENETOS et al., 1991, 1997 ; KOUTSOUBAS et al. 2000b).

When considering hard substrate within the infralittoral zone, three different ecological sub-zones can be recognized : a high one, which extends from 0 to 2m and is characterized by the assemblage of photophilic algae, an intermediate one extending from 2 to approximately 12m and dominated by several hydrozoans species, and a low one extending to almost 40m, where the sciaphilic algal assemblage occurs (MARINOPOULOS, 1988). Biodiversity aspects in these three sub-zones are rather well studied in the Western and Central Mediterranean (BIGGS & WILKINSON, 1966 ; BELLAN-SANTINI, 1969 ; HONG, 1983 ; RICHARDS, 1983 ; POULICEK, 1985 ; GIANGRADE, 1988) and the neighbouring Atlantic Ocean (e.g. the North Sea - KLUIJVER, 1997), but less so for the Eastern Mediterranean (PÉRÈS & PICARD, 1964 ; AUGIER, 1982 ; DAUVIN, 1993 ; BELLAN-SANTINI et al., 1994).

The present study discusses in detail the molluscan diversity, and qualitatively illustrates its spatial dispersion in the lower infralittoral hard substrate assemblages in the North Aegean Sea.

Fig. 1. – Map of the study area, showing the location of sampling sites.

MATERIAL AND METHODS

Sampling sites

Seven stations were set at different locations in the North Aegean Sea (Fig. 1). They were chosen for their dispersion in this specific biogeographical zone and their hard substrate extension and inclination (ranging from 45 to 90°). According to the maximum depth of hard substrate at each station, one to three substations were set (a-15 meters, b-30 meters and c-40 meters) in order to cover bathymetrically the entire range of the lower infralittoral zone. Basic characteristics of all stations are given in Table 1.

TABLE 1

Physical and biotic characteristics of sampling stations.

Station	**Slope (°)**	**Maximum Depth (m)**	**Prevailing Winds**	**Substations**	**Biotic Characteristics**
1 Kakia Skala	90	65	N, NE, SE	a - 15m	*Womersleyella setacea*
				b - 30m	*Womersleyella setacea*
				c - 40m	*Lithophylum* sp., *Peysonellia* sp.
2 Kelyfos	70	35	S, SW, SE, NW	a - 15m	*Padina pavonica*, *Codium bursa*
				b - 30m	*Womersleyella setacea*
3 Porto Koufo	90	50	SW	a - 15m	*Womersleyella setacea*
				b - 30m	*Womersleyella setacea*
				c - 40m	*Lithophylum* sp., *Peysonellia* sp.
4 Armenistis	50-60	35	NE	a - 15m	*Womersleyella setacea*, *Padina pavonica*
				b - 30m	*Womersleyella setacea*
5 Vourvourou	55	18	N, SE	a - 15m	*Pseudolithophylum expansum, Gelidium pectinatum, Cladocora caespitosa*
6 Eleftheronissos	70	30	NE, SE, N, S	b - 30m	*Lithothamnion* sp., *Polysiphonia* sp.
7 N.Iraklitsa	65	35	NE, NW, SE	a - 15m	*Cutleria multifida, Gelidium pectinatum*
				b - 30m	*Cutleria multifida, Gelidium pectinatum*

Sampling techniques

Physico-chemical factors

At each station measurements of the main abiotic parameters of the water column, i.e. temperature, salinity, conductivity, dissolved O_2 and pH, were carried out along the column of the water using the WTW salinity-conductivity-O_2 meter and Lovibond Checkit (pH meter) microelectronic equipment. Water clarity was also detected using the Secchi disc.

Data collection

Sampling was carried out by means of scuba diving using a modified quadrate sampler, covering a surface of 400cm^2, which is the minimum necessary for a statistically sound investigation on hard substrate benthic communities (Weinberg 1978 ; Stirn 1981). Five replicate samples (Bellan-Santini, 1969 ; Marinopoulos, 1988), were taken at each substation. All samples (75 overall) were collected by the same divers (authors), during summer months (July, August). At St.3 one more sampling attempt was performed at the depth of 30m, after one year, in order to identify annual changes in the structure of the fauna. During sampling the physiognomic aspects of the biotopes were registered by means of an underwater camera. All the samples were sieved through a 0.5mm mesh, fixed in 10% neutralized formalin and preserved in ethyl alcohol (70%). All living molluscs, after sorting, were identified to species level and counted.

Data analysis

Common biocoenotic methods were employed to analyze the data (Guille 1970 ; Hong 1983, Bakus, 1990 and others). Thus, the molluscan community structure was analysed by means of total number of species (S), average density (D - mean number of individuals/m^2), Shannon-Weaver diversity (H', $\log_2$ basis), Margalef's species richness (d) and Pielou's evenness (J') indices.

Molluscs were classified according to their distribution to organismic assemblages (summarized in Table 2) based on information derived from Pérès & Picard, 1958; Fretter & Graham, 1962; Ledoyer, 1969; SMECKEL & Portmann, 1982; Ros & Gili, 1985; Zenetos, 1993, 1997; Strack, 1988; Cattaneo-Vietti et al., 1990; Koutsoubas, 1992; Delamotte & Vardala-Theodorou, 1994).

The multivariate analysis was based on presence/absence data per sampling substation, in order to equalize the contribution of each species. Thus, cluster analysis (group average) and non-metric multidimensional scaling, based on the Bray-Curtis similarity, were performed, using PRIMER package (Clarke & Green 1988; Clarke & Warwick 1994; Digby & Kempton 1994).

The significance of the multivariate results was assessed with ANOSIM test (CLARKE, 1993).

RESULTS

Abiotic factors

The pattern of the main abiotic parameters showed slight variation in relation to bathymetry or the location of the sampling sites. Temperature values fluctuated with depth, ranging from a minimum of 16.1°C at 40m to 27.5°C at water surface. The seasonal thermocline, due to summer (sampling was performed at the end of July-beginning of August), was detected at all stations at the average depth of 25m (end of July- first days of August), with the exception of St.5 (Vourvourou), possibly due to its shallow depth (18m). Salinity and conductivity showed similar variations. Their values ranged from 29.1 to 37.8 psu and 41.1 to 51.6 μS/cm respectively, with no really significant change in relation to depth, except from St.7 (N. Iraklitsa), where a notable decrease was observed (29.1 psu). The pH values were almost constant in relation to depth in all stations (8.5 at St.1 and St.7; 7.5 at St.4 and 8.2 at the rest of the stations). Dissolved oxygen values were generally high (from 6.5-10 mg/l) with an average value of 7.5 mg/l. Water clarity exceeded 20m in all sampling sites apart from st.5 (Vourvourou), where it was reduced to 12m, probably due to the increased presence of suspended particulate organic matter in the area.

Faunal composition and zoogeographical Remarks

Examination of the collected living material (10917 individuals), revealed 111 mollusc species. Gastropoda dominate in species number (85 species) followed by Bivalvia (21 species) and Polyplacophora (five species). Within Gastropoda the taxonomic groups with the highest number of species and individuals were the prosobranch families Trochidae, Rissoidae, Cerithiidae, Muricidae and Turridae and the heterobranch family Pyramidellidae. A complete list of the species in phylogenetic order within major taxa is presented in Table 2. The total number of species ranged from 64 at St.1 to 17 at St.5. Stations 1, 2, 3 and 4 were the most species rich, with stations 5, 6 and 7 the most poor.

TABLE 2

Molluscs reported from the hard substrata infralittoral assemblages. The numerical abundance is estimated from the total number of replicates per each substation (number of individuals per $0.2m^2$). The ecological status of each species (EC), is given by HS for hard substrate, C for coralligenous, PA for photophilic algae, HP for *Posidonia oceanica* meadows, DC for detritic costs, G for caves, SS for soft sediments, VTC for coastal terrigenous mud and U for unknown demands.

taxa	**EC**	**St.1 15m**	**St.1 30m**	**St.1 40m**	**St.2 15m**	**St.2 30m**	**St.3 15m**	**St.3 30m**	**St.3 40m**	**St.3 30'm**	**St.4 15m**	**St.4 30m**	**St.5 18m**	**St.6 30m**	**St.7 15m**	**St.7 30m**
Polyplacophora																
Callistochiton pachylasmae (Monterosato, 1878)	C					1										
Callochiton septemvalvis (Montagu, 1803)	HS		1											1		1
Lepidochiton monterosatoi Kaas & Van Belle, 1981	HS	1				1	1								1	
Chiton olivaceus Spengler, 1797	HS														1	1
Acanthochitona fascicularis (Linnaeus, 1767)	HS	1									1			1	1	1
Bivalvia																
Arca tetragona Poli, 1795	HS		2	2	2	2	10	6	2	4	1	8	2	6	2	6
Barbatia pulchella (Reeve, 1844)	HS								1							
Barbatia scabra (Poli, 1795)	C	1														
Striarca lactea (Linnaeus, 1758)	HS													1		1
Musculus costulatus (Risso, 1826)		2	3			1	3	3		3	1	1				
Lithophaga lithophaga (Linnaeus, 1758)	HS											1			4	2
Modiolus barbatus (Linnaeus, 1758)	HS,HP	1	27	13	9	42	3	12	16	7	4	11		4		
Modiolus adriaticus (Lamarck, 1819)	DC,SS	23	19	1	165	49	85	28		29	97	38	6	15	6	3
Chlamys varia (Linnaeus, 1758)	HS,SS	1				3						1				3
Lima lima (Linnaeus, 1758)	HS,C					1										
Limatulla subovata (Jeffreys, 1876)	HS,DC,C				4	3		1		3	3	6				
Anomia ephippium Linnaeus, 1758	HS				1			1	2		1					
Lucinella divaricata (Linnaeus,1758)	SS	17	4			1			2		8	12				
Myrtea spinifera (Montagu, 1803)	SS						1			1	2	24		1		
Chama (Psilopus) gryphoides Linnaeus, 1758	HS	1			1		1								4	2
Acanthocardia aculeata (Linnaeus, 1758)	SS	1	2		8	4	1			2	20	21	1	4		
Acanthocardia tuberculata (Linnaeus, 1758)	SS						2	2		1			2			
Dosinia exoleta (Linnaeus, 1758)	SS	1	16			2		4		4		37				
Irus irus (Linnaeus, 1758)	C	1	1	1	3	1	4	1		2	3	21				
Lentidium mediterraneum (CostaO.G.,1839)	SS	1	7	2		2	5	11		3	3	66				
Hiatella arctica (Linnaeus, 1767)	HS,C	17	10	6	78	49	38	31	10	20	38	24	34	59	28	11
Gastropoda																
Acmaea virginea (Mueller O.F., 1776)	HS,PA				1	2										
Emarginula adriatica CostaO.G., 1829	HS,M			1												
Emarginula octaviana Coen, 1939	HS		1				1					2		1	1	1
Emarginula huzardii (Payraudeau, 1826)	HS								2							
Anatoma crispata Fleming, 1828	DC		7	3		2	1	13	5	13		1		1		
Clanculus corallinus (Gmelin, 1791)	PA	1	1					1				1				
Clanculus jussieui (Payraudeau, 1826)	PA		1													
Gibbula magus (Linnaeus, 1758)	DC	15	34	2	5	2	18	14	1	15	2	3			3	
Gibbula adansonii (Payraudeau, 1826)	SS,HP							1								
Jujubinus exasperatus (Pennant, 1777)	C	1	10	1	3	8	6	13	1	4		6			1	2
Homalopoma sanguineum (Linnaeus, 1758)	HP,C		2			5		3	5	2					1	
Tricolia pullus pullus (Linnaeus, 1758)	PA,HP						1		6							

TABLE 2 (cont.)

Molluscs reported from the hard substrata infralittoral assemblages. The numerical abundance is estimated from the total number of replicates per each substation (number of individuals per 0.2m^2). The ecological status of each species (EC), is given by HS for hard substrate, C for coralligenous, PA for photophilic algae, HP for *Posidonia oceanica* meadows, DC for detritic costs, G for caves, SS for soft sediments, VTC for coastal terrigenous mud and U for unknown demands.

taxa	**EC**	**St.1 15m**	**St.1 30m**	**St.1 40m**	**St.2 15m**	**St.2 30m**	**St.3 15m**	**St.3 30m**	**St.3 40m**	**St.3 30'm**	**St.4 15m**	**St.4 30m**	**St.5 18m**	**St.6 30m**	**St.7 15m**	**St.7 30m**
Truncatella subcylindrica (Linnaeus, 1767)	SS							1								
Benthonella tenalla (Jeffreys, 1856)	VP						3									
Bolma rugosa (Linnaeus, 1767)	PA,C							2								
Cerithium vulgatum (Bruguiere, 1792)	PA	2			1			1	2	3	8	10				1
Bittium latreillii (Payraudeau, 1826)	PA,C	1131	1880	121	340	400	414	547	90	629	254	1510	2	138	80	26
Pirenella conica (Blainville, 1826)	SS			1		1							1			
Alvania aspera (Philippi, 1844)	PA	1														
Alvania cimex (Linnaeus, 1758)	PA	8	31	2	2	1	9	23	6	5		11	3	2	5	3
Alvania discors (Allan, 1818)	SS,HP										5	4				
Alvania mamillata Risso, 1826	PA	18	88	10	3	7	12	34	16	17		23		3	3	
Alvania semistriata (Montagu, 1808)	PA						2				1			2		
Manzonia crassa (Kanmacher, 1798)	HP	2	7				1	3	1	2		1		2		
Pusillina radiata (Philippi, 1836)	PA	16	56	8	4	17	48	74	7	32	6	14	1	3	1	2
Setia turriculata Monterosato, 1884	PA		7				2			10			3			
Setia sp. juveniles	PA						8		3							
Skeneopsis planorbis (Fabricus, 1780)	U							1								
Rissoina bruguieri (Payraudeau, 1826)	HP	9	38	4	4	2	14	18		7	1	1		1	1	3
Caecum trachea (Montagu, 1803)	DC	38	33	2	4	44		20		27	45	88	5	7		
Luria lurida (Linnaeus, 1758)	PA							1								
Pseudosimnia carnea (Poiret, 1789)	C,G		1					1								
Erato voluta (Montagu, 1803)	DC						1									
Euspira macilenta (Philippi, 1884)	SS		2	1	1											
Payraudeautia intricata (Donovan, 1804)	HP				2							1				
Monophorus perversus (Linnaeus, 1758)	PA,HP	2	5									1				
Metaxia metaxae (Delle Chiaje, 1828)	HP										1	3				
Cerithiopsis tubercularis (Montagu, 1803)	DC	2	4		1	1	3	1	1	1	1	4				1
Epitonium commune (Lamarck, 1822)	PA	1														
Melanella polita (Linnaeus, 1758)	SS,HP	1	1				1	1				1				
Hadriana oretea (De Gregorio, 1885)	SS,DC							1								
Muricopsis cristata (Poiret, 1883)	PA		3													
Ocinebrina aciculata (Lamarck, 1822)	PA								1							
Buccinulum corneum (Linnaeus, 1758)	PA,DC	1														
Engina leucozona (Philippi, 1843)	PA	1														
Fasciolaria lignaria (Linnaeus, 1758)	PA								1							
Fusinus pulchellus (Philipi, 1884)	C,G				1	1										
Nassarius incrassatus (Stroem, 1768)	PA,SS		1		1									1	3	5
Nassarius limata (Chemnitz, 1795)	PA,SS		1													
Stramonita haemastoma (Linnaeus, 1758)	PA													1	1	1
Vexillum tricolor (Gmelin, 1791)	PA	1	3		1			2		1		2				
Vexillum littorale (Philippi, 1843)	PA	1														
Mitra cornicula (Linnaeus, 1758)	PA,SS,HP								1							
Conus mediterraneus *Hwass in Bruguiere, 1792*	PA		1													
Mangelia attenuata (Montagu, 1803)	SS								1							
Mangelia vauquelini (Payraudeau, 1826)	HP						2		1			1			1	
Clavus maravignai (Bivona, 1838)	SS		1													
Haedropleura septangularis (Montagu, 1803)	SS								1							
Mitrolumna olivoidea (Cantraine, 1835)	PA	1	1	1				1		1						
Raphitoma echinata (Brocchi, 1814)	C	4	22	3		3	5	10	8	1		4	2			
Raphitoma concinna (Scacchi, 1836)	PA,C								1							
Raphitoma leufroyi (Michaud, 1828)	C	2	2		2					2	1	1			1	
Philbertia densa (Monterosato, 1884)	PA										1					
Pseudotorinia architae (Costa O.G., 1841)	DC									1						
Omalogyra atomus (Philippi, 1841)	SS	1	1		1								1			
Chrysallida doliolum (Philippi, 1844)	SS	4	5							1	1	2				
Folinella excavata (Philippi, 1836)	SS	2	11	1	1	1	5	12		2		2		2		2
Odostomia conoidea (Brocchi, 1814)	SS,HP		3												1	1
Turbonilla lactea (Linnaeus, 1758)	SS		2		1			1								
Cylichnina umbilicata (Montagu, 1803)	VTC	2				1					1		1			1
Haminaea navicula (Da Costa, 1778)	SS	3	9			2	1	4		5	2					
Philine catena (Montagu, 1803)	SS,HP,DC												1			
Ascobulla fragilis (Jeffreys, 1856)	HP								1							
Limapontia capitata (Mueller, 1774)	U												1			
Umbraculum umbraculum (Roeding, 1798)	C,DC		1													
Pleurobranchus membranaceus (Montagu, 1815)	DC				1											
Phyllaplysia lafonti (Fischer P., 1798)				2												
Petalifera petallifera (Rang, 1828)	U				1											
Trapania maculata Haefelfinger, 1960				1												
Hypselodoris webbi (D'Orbignyi, 1839)	PA							1								
Discodoris atromaculata Bergh, 1880	PA,C,G									1						
Paradoris indecora Bergh, 1881	PA										1					
Polycera quadrilineata (Mueller, 1876)				1												
Dendrodoris sp.	PA												1			

The dominant species in terms of average density was the prosobranch gastropod *Bittium latreillii* (2520 individuals/m^2), followed by the bivalves *Modiolus adriaticus* (215 individuals/m^2) and *Hiatella arctica* (175 individuals/m^2), the prosobranch gastropods *Caecum trachea* (120 individuals/m^2), *Pusillina radiata* (110 individuals/m^2) and *Alvania mammilata* (90 individuals/m^2), the bivalve *Modiolus barbatus* (60 individuals/m^2) and finally the prosobranch gastropods *Gibbula magus* (45 individuals/m^2) and *Alvania cimex* (40 individuals/m^2).

Molluscs were among the dominant taxa, accounting for 60% of the mean density of the macrofauna in the sampling sites (polychaetes accounted for 20% and crustaceans 15%) and were also the richest group in terms of species composition (ANTONIADOU & CHINTIROGLOU, unpublished data).

Three of these species namely : *Skeneopsis planorbis, Limapontia capitata* and *Trapania maculata* are reported for the first time as elements of the molluscan fauna in the Eastern Mediterranean or the Aegean Sea. Five other species, namely : *Callistochiton pachylasmae*, *Raphitoma leufroyi, Phyllaplysia lafonti*, *Petalifera petalifera* and *Polycera quadrilineata*, are reported for the first time in the North Aegean Sea. For the species that are new records for the Eastern Mediterranean or the Aegean Sea some taxonomic, ecological and zoogeographical information is given below.

New Records for the Eastern Mediterranean or the Aegean Sea

GASTROPODA

PROSOBRANCHIA

Family : Skeneopsidae

Skeneopsis planorbis (Fabricius O., 1780)

Skeneopsis planorbis, FRETTER & GRAHAM 1962 : 550, Fig. 290.

Material : Station 3 (Porto-Koufo), 1 specimen, 30m, bottom covered with the Rhodophycea *Womersleyella setacea*

Distribution : Mediterranean : various areas of the Western and Central Mediterranean (SABELLI et al., 1990) ; Eastern Atlantic : Boreal region (FRETTER & GRAHAM 1962).

OPISTHOBRANCHIA

Family : Stiligeridae

Limapontia capitata (O.F. Mueller, 1773)

Limapontia nigra, PRUVOT-FOL 1954 : 205, Fig. 79a-e.

Limapontia capitata, SCMECKEL & PORTMAN 1982 : 311, Abb. 3.1.

Material : Station 5 (Vourvourou), 1 specimen, 15m, bottom covered with the Rhodophycea *Pseudolithophylum expansum, Gelidium pectinatum*

Distribution : Mediterranean : various areas of the Western and Central Mediterranean (PRUVOT-FOL, 1954 ; SMECKEL & PORTMAN, 1982) and the coasts off Turkey (SWENNEN, 1961) ; Eastern Atlantic : European coast south to Marocco (SCMECKEL & PORTMAN, 1982).

Family : Goniodorididae

Trapania maculata Haefelfinger, 1960

Trapania maculata, CERVERA & GARCIA-GOMEZ 1988 : 166, Figs 1-5.

CATTANEO-VIETTI et al. 1990 : 45, Fig. 11, Pl.1 Fig. 7.

Material : Station 5 (Vourvourou), 1 specimen, 15m, bottom covered with the Rhodophycea *Pseudolithophylum expansum, Gelidium pectinatum*

Distribution : Mediterranean : various areas of the Western Mediterranean (CATTANEO-VIETTI et al., 1990) ; Eastern Atlantic : European coasts (BROWN & PICTON, 1976 ; CERVERA & GARCIA-GOMEZ, 1989).

Structural analysis

Diversity indices showed a variation in different sampling sites, with species richness (d) values ranging from 3.79 to 5.73, community diversity (H') values ranging from 1.28 to 3.62, and evenness (J') values from 0.24 to 0.79 (Fig. 2). The diversity values were quite low as a consequence of the great density values of the species *Bittium latreillii* recorded in most of the sampling stations. Furthermore, the high density of very few species (e.g. *Modiolus adriaticus, Hiatella arctica, Caecum trachea, Pusillina radiata, Alvania cimex, Modiolus barbatus, Gibbula magus, Alvania mammilata*) strongly influenced diversity indices values and in particular Shannon-Weaver's diversity and Pielou's evenness. However, the above calculations after the elimination of the species *Bittium latreillii* showed high values (Fig.2 red points-dash symbols), with d' ranging from 4.2 to 7.49, H' from 2.44 to 4.34 and J' from 0.5 to 0.86.

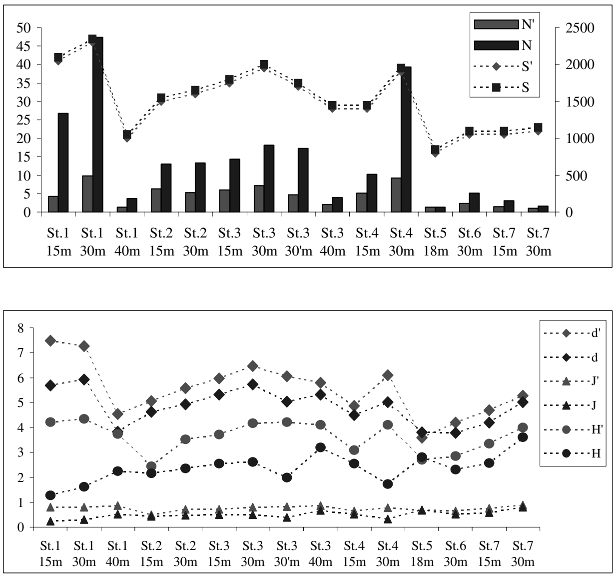

Fig. 2. – Biocoenotic parameters (up) and diversity indices (down) per substation of spatially-dispersed stations, where d is Margalef's richness, H is Shannon-Weaver index, J Pielou's evenness, S number of species/0.2m^2 and N number of individuals/0.2m^2. The dash (') indicates the above calculations after the elimination of the species *Bittium latreillii.*

Both multivariate analyses of the sampling sites, based on presence/absence data, indicate the separation of the samples in four main groups (Fig. 3). At about 40% similarity level, the samples from station 3 (c-40m) and the samples from station 5 form the first two single site groups. The third group includes the samples from stations 6 and 7 (a-15m & b-30m), while the fourth group matches the leftover stations at a 65% similarity level. The stress value for the two-dimensional MDS configuration is 0.13, so a useful picture is gained. However, a cross check of any conclusion by the superimposition of a cluster is suggested (Clarke & Warwick, 1994). The performance of a one-way ANOSIM test gave global R : 0.955 at a significance level of $p<0.1\%$, indicating an elevated degree of discrimination between the groups, confirming both Cluster and MDS. The discrimination of station 7 should probably be attributed to its slightly different abiotic characteristics (low salinity values). Its relatively moderate inclination places this station (St.7) near station 6, while the sharpest slope of stations 1, 2, 3 and 4 clusters them together. The substrate at St.5 is unique, formed by the coral *Cladocora caespitosa*. Furthermore a significant lowering in water clarity values discriminates this station from all others. At both stations 6 and 7 the sciaphilic algal assemblage is characterized by the occurrence of the Rhodophyceae *Gelidium pectinatum* and *Cutleria multifida*, while at all the other stations the dominant algae were the Rhodophyceae *Womersleyella setacea* and the Phaeophyceae *Padina pavonica* and *Codium bursa*. Furthermore at the third substation set at the depth of 40m, the dominant algae were the encrusting Rhodophyceae *Lithothamnion* sp., *Lithophyllum* sp. and *Peyssonnelia* sp.

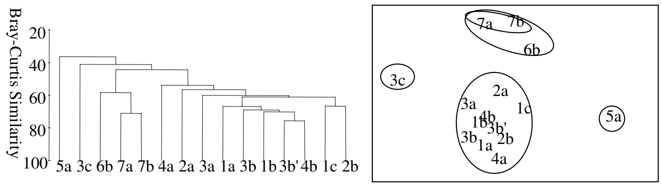

Fig. 3. – Spatial results of a cluster (left) and multidimensional scaling (right) based on Bray-Curtis similarity index on presence/absence data.

DISCUSSION

Generally speaking, Mollusca appear to be one of the most intensively studied taxa in marine habitats. However, as our revision shows, the knowledge concerning the abundance and the spatial dispersion of this taxon is very restricted. The study of hard substrate infralittoral assemblages in the North Aegean has revealed the presence of a rich molluscan community in this type of marine coastal ecosystem, while eight new records were set up for the N. Aegean molluscan fauna. These findings support previous authors' claims (e.g. Koutsoubas et al., 1997; Zenetos, 1997) that the marine biodiversity in Greek waters will be revealed to be even more rich when extended studies cover neglected geographical locations or habitats and contribute to the overthrow of the "impoverished Eastern Mediterranean theory" expressed earlier in this century (e.g. Pérès, 1967).

Comparing our results with the relevant reports from other investigators, we could focus to some major differences between the eastern and the western part of that semi-closed sea. Firstly the number of mollusc species found in this study (111) is higher than that reported from other areas of the Western and Central Mediterranean where quantitative sampling has been performed in hard substrate infralittoral assemblages [e.g. Banyuls Sur Mer (72 species) : Marinopoulos, 1988 ; Corsica (109 species) : Poulicek, 1985 ; Malta (44 species) : Richards, 1983]. The higher species richness (total number of species) found in the Aegean and Corsica, indicates that the survival ability of these assemblage is extremely high. According to Walker (1992), who expressed the hypothesis of 'over-species', the function of an ecosystem is little affected by the loss of species when there are always some representatives of all the basic functional groups in an assemblage (e.g. Gaston & Spicer, 1998). Secondly, the same also applies to density values, where 1200 individuals/m^2 had been reported from the photophilic algae assemblages off the coasts of Corsica (Poulicek, 1985). To a certain degree species with the maximum density in both aforementioned study areas *i.e.* North Aegean and Corsica, were either the same or congeneric (*Alvania mammilata, Pusillina radiata, Bittium latreillii, Hiatella arctica* – North Aegean Sea ; *Alvania cimex, Pusillina lineolata, Bittium reticulatum, Hiatella arctica* – Corsica). Thirdly a strong difference exists concerning the density of the species *Bittium latreillii.* This species was reported as one of the most abundant species from 20 meters downwards (Bellan-Santini 1969 ; Marinopoulos 1988), but as far as the western Mediterranean is concerned, it's normalized abundance (number of individuals per 5 replicates of 400cm^2) never exceeds 90, while at our stations it reached 1880. This is the case for the two upper substations (15 and 30 meters depth), while at the third substation (40 meters) and at stations 5, 6 and 7 the numerical abundance ranged from 2 to 138 individuals. The high values of *Bittium latreillii* abundance are probably related to the branching form of the dominant algae, which serves as an excellent ecological niche for this mollusc. This particular shape offers the opportunity for quantities of organic material to be trapped in the algae, thus offering suitable conditions for the species' trophic demands (herbivore-deposit feeder according to Gambi et al., 1992).

The majority of the molluscs collected during this study, including most of the dominant species, were ecologically classified as members of the photophilic algal assemblage in various areas of the Mediterranean and the Eastern Atlantic (e.g. Table 2). However, quite few of them have been recorded in soft sediments, submarine caves and sea-grass meadows. It seems that this specific habitat (rocky infralittoral) may be suitable for soft substrate and detritic species. The branching algae, which dominate the higher and middle layers of the infralittoral, offer suitable substrate for the settlement of most photophilic algal species. In-between the thallus of the algae and the hard substrate, an amount of soft sediment is trapped, leading to an increased occurrence of species demanding soft sediments. Our multivariate results revealed that the composition of the flora had a significant effect on the faunistic discrimination of the stations. They also indicate that molluscs are qualitatively distributed more evenly in terms of similarity at the middle part (20 to 30 meters) of the lower infralittoral zone. At that depth a high similarity in terms of the dominant species of flora is detectable. This demonstrates that hard substrate with either photophilic or sciaphilic algae may be a temporary, preferential site for various reasons, such as food demands, protection from predators, spawning, settlement and early development for individuals of many infralittoral or even circalittoral molluscs belonging to other assemblages. A similar statement has been made by Poulicek (1985) who noticed an increased presence of juveniles of mollusc species belonging to other assemblages in the photophilic algal communities of the coasts of Corsica over the reproduction period.

Therefore, we can imply that the complexity of the biotopes included in the hard substrate infralittoral zone, is not only insufficiently studied but also its importance is not well defined. The ecological approach of biodiversity, as Gaston & Spicer (1998) points out, is a firm component to its total definition. Consequently, the fact that these assemblages hold a very rich fauna (Mollusca in this specific case) of typical hard but also of soft substrate, reveals that they can play a key role for the maintenance of biodiversity of the broader geographical area.

Lack of knowledge on a quantitative basis makes it difficult to formulate general testimonials concerning the biogeography, although these would be valuable for building a broad picture of the biodiversity of the Mediterranean. These gaps were recently pointed out by Stergiou et al. (1997), verifying that the problem of insufficient and piecemeal information applies not only for the phylum Mollusca, but also for the majority of the fauna in the Mediterranean.

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Epiedaphic Coleoptera in the Dadia forest reserve (Thrace, Greece) : the effect of human activities on community organization patterns

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ABSTRACT. In this work we described and compared the community organization patterns of Coleoptera in various sites of the Dadia forest reserve, including different types of vegetation and management practices (grazing, cultivation, afforestation). Sampling was carried out every two months for a year, by means of pitfall traps. For studying diversity and community structure, we used Renyi's parametric index of diversity and fitted the geometric series model on rank/abundance data. In order to study the changes of species composition, we used the Indicator Value method (IndVal), after a tree clustering of our sampling sites.

According to our results, although the three management practices increased the diversity of epiedaphic Coleoptera, their effects on the community organization patterns were different. Grazing did not affect the species composition of the communities but altered the community structure. The communities in the ungrazed forests were over-dominated by one species, while those of the grazed sites were hierarchically structured. On the other hand, the main effect of cultivation on the coleopteran communities was a profound change in species composition. The cultivated site was dominated by characteristic species that were almost absent from all other sites. Afforestation caused intermediate changes in both community structure and composition.

Finally, although certain species of Coleoptera seemed to be good indices for assessing human impacts on natural environment, the study of changes in the community organization patterns is even more appropriate.

KEY WORDS : Diversity, community structure, indicator species, grazing, cultivation, afforestation.

INTRODUCTION

Different land use and management practices affect the variability of ecological factors in space and consequently the habitat heterogeneity, which is reflected in the communities of soil arthropods. Due to high turnover and growth rates of most species, these animals serve as probes that quickly respond to environmental change (MATTONI et al., 2000). Thus, the use of soil arthropods in monitoring for purposes of conservation biology, although limited until the beginning of the last decade, is continuously increasing.

Many bioindication studies aiming at habitat evaluation and monitoring have been based on the coleopteran fauna, focusing either on certain species or families or even on the whole order (e.g. BOHAC, 1999 ; HUMPHREY et al., 1999 ; MOLINA et al., 1999 ; MAGURA et al., 2000a ; BAUR et al., 2002). In many of these studies, the researchers have tried to assess the effect of human practices, such as grazing (GARDNER et al., 1997 ; PETIT & USHER, 1998), farming activities (KROOSS & SCHAEFER, 1998 ; KROMP, 1999 ; VARCHOLA & DUNN, 1999) and forestry practices (INGS & HARTLEY, 1999 ; MAGURA et al., 2001, 2002) on the coleopteran communities.

In the work we present here, we have tried to describe and compare the community organization patterns of epiedaphic Coleoptera at various sites of the Dadia forest reserve, which differ regarding vegetation and human activities. The Dadia forest is near the Greek-Turkish border. It is famous for the endangered and/or vulnerable populations of birds of prey, and it is under protection since 1980. Our work was part of a wider monitoring project of the protected area, which was funded by WWF-Hellas, and where several research teams worked on different animal groups as well as on vegetation. Our interest was focused on identifying the importance of three management practices, namely grazing, cultivation and afforestation, in shaping the coleopteran species assemblages. More specifically, we compared the effects of these practices on diversity, community structure and species composition of surface dwelling beetles.

MATERIAL AND METHODS

Study sites and sampling

Ten sites were sampled, including different types of vegetation and management practices (Table 1). Some of these sites were adjacent to each other, forming distinct gradients according to the management practice to which they are subject. For example, the natural pine forest, the grazed pine forest and the overgrazed meadow constituted a gradient of grazing pressure (PINE→gPINE→MEAD). The same holds for the ungrazed and the adjacent grazed area of the mixed oak forest (MOAK→gMOAK).

Another grazed site was a typical mediterranean maquis (MAQ) with a variety of shrub species, which is used as pastureland. Another case was a natural oak-pine forest, an adjacent cultivated field, and a natural hedgerow that is connected to the forest and borders the field (OAKP→HEDG→CULT). And lastly, we compared a pine afforestation (AFF) with the natural pine forest, in order to explore the effect of this management practice on the coleopteran community.

TABLE 1

Characteristics of the ten sampling sites within the Dadia protected area.

	Site	Code	Habitat characteristics	Management practice
1	Pine forest	PINE	Ungrazed dense mature forest of *Pinus brutia*	
2	Grazed pine forest	gPINE	Sparse *P. brutia* trees and grass-covered areas.	grazing
3	Overgrazed meadow	MEAD	Overgrazed grass-covered meadow with microhabitats of bare soil	
4	Mixed oak forest	MOAK	Ungrazed mature forest of *Quercus sp.*and *Carpinus orientalis.*	
5	Grazed mixed oak forest	gMOAK	Sparse trees of *Quercus sp.*, *Carpinus orientalis, Fraxinus ornus, Cornus mas*, *Acer sp.* and open grass-covered areas	grazing
6	Mediterranean shrubland	MAQ	Typical mediterrannean maquis with *Phillyrea latifolia, Juniperus oxycedrus, Erica arborea, Cistus sp.* and grass-covered areas	grazing
7	Mixed oak-pine forest	OAKP	Ungrazed mature forest of *Pinus brutia* and *Quercus frainetto*	
8	Natural hedgerow	HEDG	The species composition includes *Ulmus sp.*, *Clematis sp.*, *Rubus spp.*, *Rosa sp.* and *Prunus spinosa.*	cultivation
9	Cultivated field	CULT	Non-irrigated organic wheat cultivation	
10	Afforestation	AFF	*P. brutia* afforestation.	afforestation

Sampling was carried out by means of unbaited pitfall traps (diameter 5.4 cm, height 15 cm), every two months for one year. The traps contained 10% ethylene glycol as a killing-preserving solution. We used five traps per site (5x10=50 traps in total), which remained in the field for seven days on each sampling occasion. Samples from the whole experimental year were used for data analysis. All specimens were identified to morphospecies, while for further identification of Carabidae, Staphylinidae and Cerambycidae, expert assistance was offered by the National Museum of Natural History of Bulgaria.

Data Analysis

For assessing the diversity of coleopteran communities in the different sites, we used the method of diversity ordering proposed by Renyi (1961). Renyi's parametric index of order *a* shows varying sensitivity to the rare and abundant species of a community, as the scale parameter *a* changes (Ricotta, 2000). It provides a profile of the most widely used diversity indices. For *a*=0, the index equals *log* species number, for *a*=1, it equals Shannon's index, for *a*=2, it equals Simpson's index. For *a* tending to infinite, the index is most sensitive to the abundant species. Thus, when two diversity profiles differ in the range of low *a* values, this is due to the number of species. In the range of high *a* values, differences are due to the presence of abundant species. When two diversity profiles intersect, the two communities may be ordered differently by different diversity indices. For calculations we used DivOrd (Tothmeresz, 1995).

For further insight into the community structure, we estimated the environmental constant from the rank/abundance plots, as proposed by May (1975) and Motomura (1932). In a geometric series, the abundance of species ranked from most to least abundant is :

$$n_i = N\,k\,(1\text{-}k)^{i\text{-}1}\,[1\text{-}(1\text{-}k)^s]^{\text{-}1}$$

where n_i= number of individuals of the *i*th species, N= total number of individuals, s= total number of species and k= environmental constant.

In order to study the changes of species composition at the different sites, we used the IndVal (Indicator Value) method of Dufrene & Legendre (1997). This method assigns indicator (characteristic) species to a site or a group of sites, on the basis of species relative abundance and relative frequency of occurrence in the various groups of samples. The approach requires a former classification of sample units. We obtained a typology based on a tree clustering of our sampling sites (linkage rule : unweighted pair-group centroid, distance measure : 1-Pearson r). The statistical significance of the species indicator values was also evaluated by the IndVal program by means of a randomization procedure.

RESULTS

Diversity

In Fig. 1a, we present the diversity profiles of the sites that differ due to grazing. In the case of the natural mixed oak forest and the grazed one, we can see that the diversity of the coleopteran community is much higher in the grazed forest than in the natural one. The difference of the two curves falls mainly in the range of high values of the scale parameter. This means that the difference is mostly due to the presence of abundant species in the grazed site, rather than to the higher number of species. The same holds in the case of the natural and the grazed pine forest. In comparison with these two sites, the overgrazed meadow exhibited intermediate diversity, although the number of species was higher. As regards the mediterranean pasture land, it exhibited the highest diversity of all sites.

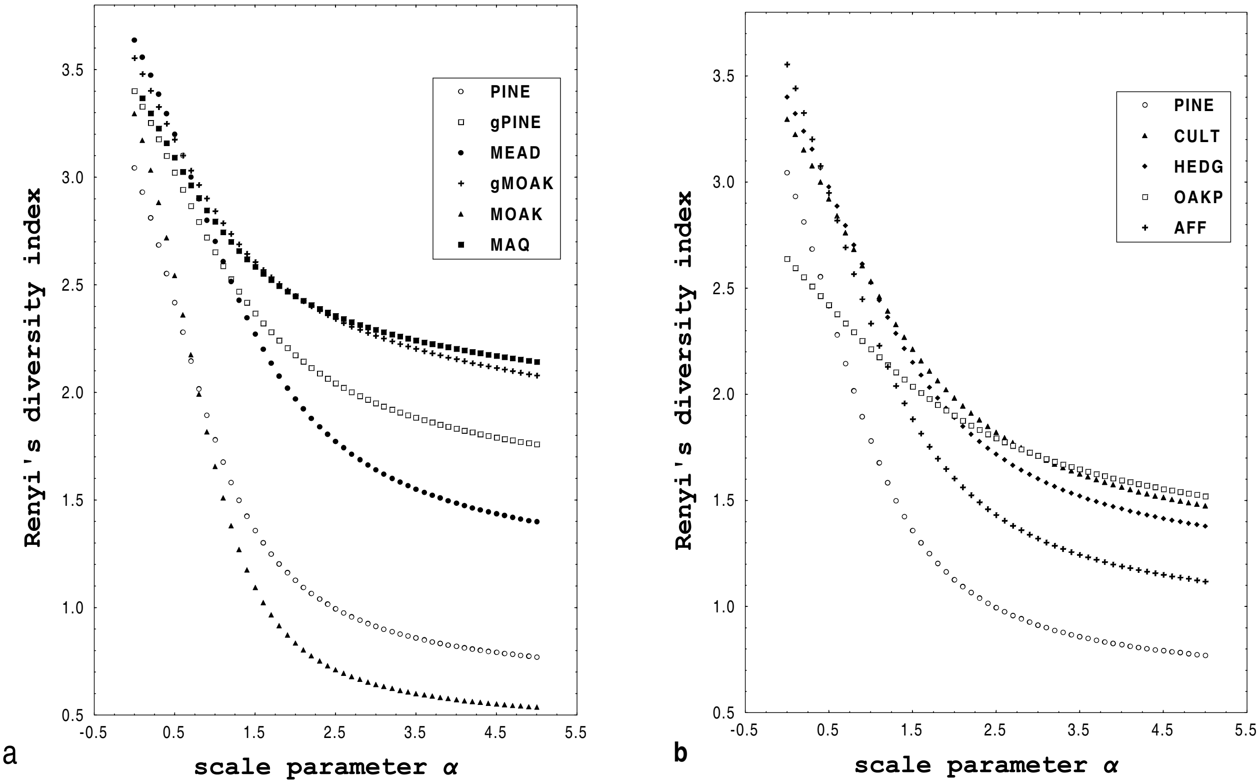

Fig. 1. – Diversity profiles of coleopteran communities (a) in PINE, gPINE, MEAD, MOAK, gMOAK, MAQ and (b) in OAKP, HEDG, CULT, AFF, PINE. PINE was also included in (b) for comparative purposes. For site codes see Table 1.

In Fig. 1b, we present the diversity profiles of the sites that differ due to the two other management practices, i.e. cultivation and afforestation. The diversity profiles of the coleopteran communities in the natural forest, the hedgerow and the cultivated field intersect, which means that the communities may be ordered differently by different diversity indices. What is obvious here is that the natural forest had the lowest diversity, and more specifically the lowest number of species, since the difference of the curves falls in the range of low values of the scale parameter. Moreover, the differences in diversity due to cultivation were not as pronounced as the ones that were caused by grazing.

As regards afforestation, the third management practice, its effect on diversity was intermediate, compared to the effects of grazing and cultivation. The afforested site was more diverse than the natural pine forest, both regarding the species number and the equitability, since the two diversity curves differ equally through the whole range of the scale parameter.

Community structure

In Fig. 2, we present the rank/abundance plots for all sites together with the values of the environmental constant (k). Comparing the natural with the grazed oak forest, we can see that in the natural forest one species overdominated the community and almost all the others were represented by very low numbers. This is the reason for the high value of the environmental constant. At the grazed site, dominance was shared by several species, and the value of the constant was very low. The same changes in community structure may also be observed in the case of the natural and the grazed pine forest, i.e. an over-domination of a single species at the natural site and a more hierarchical community structure at the grazed site. The hierarchical community structure was most obvious in the mediterranean pastureland, which exhibited the lower value of the environmental constant.

These changes of community structure cannot be observed in the case of the sites that differ due to cultivation. The values of the environmental constant were almost the same for the three sites, which means that this management practice does not induce pronounced changes in community structure as is the case with grazing.

As regards afforestation, it is obvious from the rank/abundance plots and the values of the environmental constant, that the changes in community structure were once again intermediate, compared with those induced by grazing and cultivation.

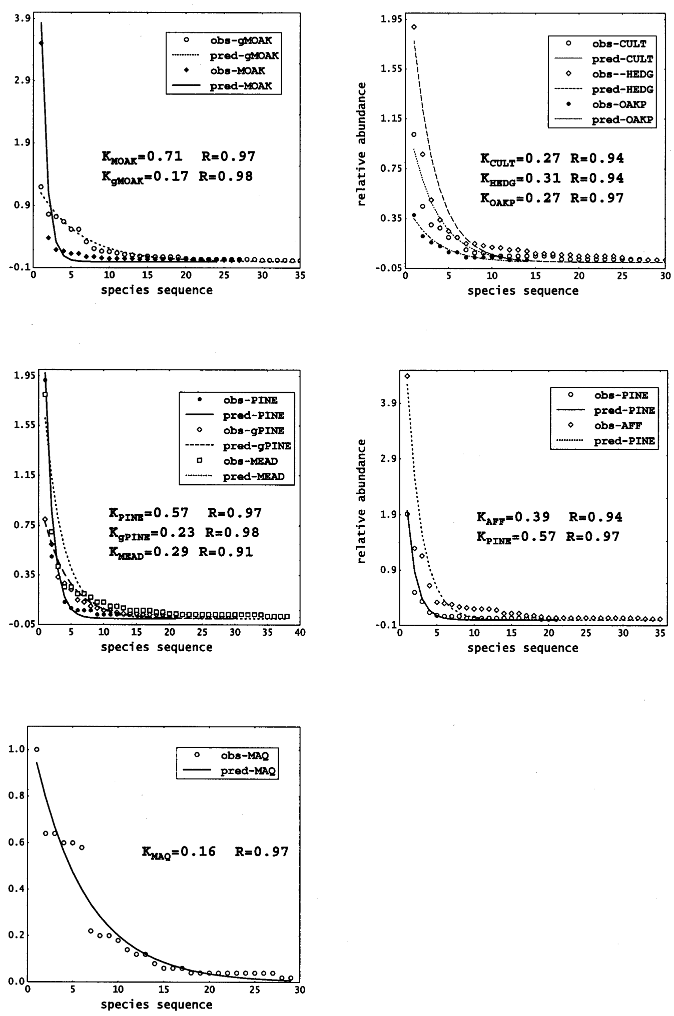

Fig. 2. – The geometric series model fitted on rank/abundance data from all sampling sites. Species are ordered from the most to the least abundant. The environmental constant (k) and the goodness of fit (R) are also noted. For site codes see Table 1.

Species composition

In order to explore changes in species composition due to the three management practices, we used the IndVal method after a tree clustering of our sites. Species recorded only on one sampling occasion were not taken into account in this analysis and thus the whole number of species recorded in this study was reduced to 34. The results are presented in Fig. 3 and Table 2. In the dendrogram of Fig. 3, we can see that the natural sites are grouped together ; the same happens with most of the grazed sites, while the cultivated field and secondly the pine afforestation are separated from all the others. These two sites have the greatest number of characteristic species. We must note here that the characteristic species of the cultivated field were also the dominant ones at this site. As regards the pine afforestation, three out of the eight characteristic species were among the five most dominant species of this site, while the other five species simply contributed to habitat specificity. The dominant species of most other sites were eurytopic species. These results imply that cultivation and, to a lesser degree, afforestation altered the species composition of the community, while this is not the case with grazing.

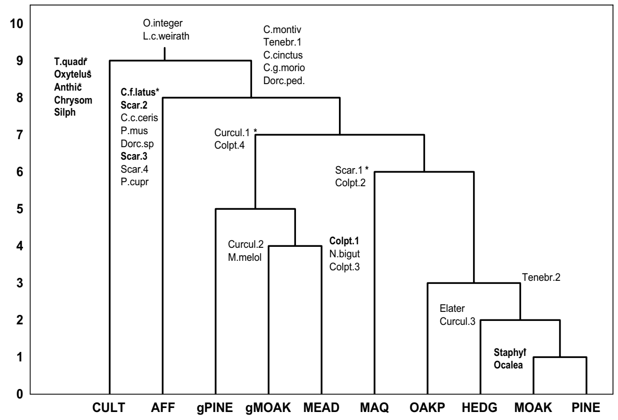

Fig. 3. – Dendrogram presenting the indicator species of each sampling site, identified by IndVal. Significant indicator species are noted by * (p<0.05). Names in bold indicate species that dominate the corresponding site. For site codes see Table 1. Species names are listed in Table 2.

TABLE 2

Species indicator values for the corresponding clustering level, i.e. the site or group of sites where the species exhibits maximum indicator value. Statistical significance is also indicated (p<0.05)

Species list	IndVal	sites	
Carabidae			
Trechus (Trechus) quadristriatus (Schrank, 1781)	58.45	CULT	*
Calathus (Calathus) fuscipes latus Audinet-Serville, 1821	44.47	AFF	*
Carabus (Procrustes) coriaceus cerisyi Dejean, 1826	31.13	AFF	ns
Laemostenus (Pristonychus) cimmerius weiratheri G. Mller, 1931	22.03	all sites	ns
Notiophilus (Latviaphilus) biguttatus (Fabricius, 1779)	18.62	MEAD	ns
Calathus (Neocalathus) cinctus (Motschulsky, 1850)	18.52	all uncultivated sites	ns
Carabus (Pachystus) graecus morio Mannerheim, 1830	16.67	all uncultivated sites	ns
Carabus (Archicarabus) montivagus Palliardi, 1825	37.04	all uncultivated sites	ns
Staphylinidae			
Oxytelus sp.	47.85	CULT	*
Staphylinidae unid.	29.22	MOAK	*
Ocypus integer Abeille, 1900	28.81	all sites	ns
Pseudocypus (s. str.) mus Brulle, 1832	26.49	AFF	ns
Ocalea sp.	23.22	MOAK	ns

TABLE 2 (cont.)

Species indicator values for the corresponding clustering level, i.e. the site or group of sites where the species exhibits maximum indicator value. Statistical significance is also indicated ($p<0.05$)

Species list	**IndVal**	**sites**	
Pseudocypus (s. str.) cupreus Rossi, 1790	13.01	AFF	ns
Scarabaeidae			
species unid.1	33.57	MAQ	*
species unid.2	32.54	AFF	ns
species unid.3	15.96	AFF	ns
species unid.4	14.86	AFF	ns
Melolontha melolontha (Linnaeus, 1758)	12.29	gMOAK	ns
Curculionidae			
species unid.1	33.33	gPINE, gMOAK, MEAD	*
species unid.2	21.76	gMOAK	ns
species unid.3	11.49	HEDG	ns
Cerambycidae			
Dorcadion sp.	23.24	AFF	ns
Dorcadion cf. pedestre (Poda, 1761)	12.96	all uncultivated sites	ns
Anthicidae			
species unid.	39.1	CULT	*
Silphidae			
species unid.	10.56	CULT	ns
Elateridae			
species unid.	16.85	HEDG	ns
Chrysomelidae			
species unid.	19.4	CULT	ns
Tenebrionidae			
species unid.1	25.93	all uncultivated sites	ns
species unid.2	16.67	forested sites and HEDG	ns
Families unidentified			
species unid.1	20.86	MEAD	ns
species unid.2	9.09	MAQ	ns
species unid.3	15.9	MEAD	ns
species unid.4	13.56	gPINE, gMOAK, MEAD	ns

DISCUSSION

Grazing

Our results showed that the diversity of the coleopteran community was much higher in the grazed than in the undisturbed part of both the deciduous and the pine forest, a result also reported by INGS & HARTLEY (1999) for carabid assemblages of forest environments. This increase of diversity may be attributed to several factors that affect the coleopteran communities, such as the light (FAHY & GORMALLY, 1998) that penetrates the overstorey, the development of ground vegetation (INGS & HARTLEY, 1999), and most importantly the high degree of structural heterogeneity induced by grazing (GARDNER et al., 1997) and the consequent changes of microclimatic conditions (RODRIGUEZ et al., 1998). Moreover, the grazed pine forest is actually a forest edge, while the overgrazed meadow is the other extreme of the forest-grass spectrum. Increased diversity of the coleopteran fauna in forest edges has been well established (MAGURA et al., 2000b ; HORVATH et al., 2002). In the overgrazed grass covered meadow, diversity was higher than that recorded at the undisturbed site but lower than that recorded at the moderately grazed site. Indeed, too much grazing reduces structural variation of vegetation and thus diversity of coleoptera (GARDNER et al., 1997), and as CONNELL (1978) pointed out, medium disturbance may indeed enhance diversity.

Diversity increase due to grazing was accompanied by changes in the hierarchical structure of the community. In the natural forest, one species over-dominated the community and almost all the others were represented by very low numbers, while in the grazed site dominance was shared by several species. As far as we know, up to now, only MOLINA et al. (1999) have reported the dominance of a single species within the forest catches as a reason accounting for the low diversity of the forest ground-dwelling community. In line with their work, we believe that the mosaic structure of vegetation at the grazed sites offers a variety of microhabitats where soil arthropods may establish and increase their local population size. Indeed, in the mediterranean pastureland, which is the most heterogeneous of all our sampling sites due to the variety of shrub species, we recorded the most diverse and hierarchically-structured community.

Regarding the species composition of the coleopteran community, according to our results, it does not seem to alter due to grazing. ELEK et al. (2001) state that the movement of forest species is prevented in more grassy sites, while RODRIGUEZ et al. (1998) claim that the habitat breadth of species correlates with the degree of disturbance at a site. However, the IndVal analysis did not reveal any characteristic forest species that disappeared in the grazed sites or vice versa, since the dominant species of both natural and grazed forests were eurytopic.

Cultivation

Apart from grazing, cultivation also had a positive result on the diversity of the coleopteran community. However, the only component of diversity that increased from the natural forest to the adjacent cultivated field was the number of species, while no pronounced changes in the community structure were recorded, as was the case with grazing. BOHAC (1999) and KROMP (1999) have also reported high species numbers of Coleopterans in arable habitats. We should also note that in the wheat cultivation that we studied there was no insecticide application, which is known to have detrimental effects for several families of beetles (WILSON et al., 1999). Moreover, the existence of the natural hedgerow at the edge of the field is very important for maintaining biodiversity, since it acts as a refuge for overwintering field species (KROMP, 1999), or relict woodland species (ASTERAKI et al., 1995), from where beetles may reinvade the adjacent field in response to changing field conditions (VARCHOLA & DUNN, 1999).

The most important effect of cultivation recorded in this study was the changes in species composition. Such changes are also reported by KROOSS & SCHAEFER (1998). SIEREN & FISCHER (2002) state that arable land is a suitable habitat for eurytopic species without special ecological preferences. However, the field of our study was dominated by stenotopic indicator species, the number of which was the highest one recorded at all sampling sites. This is again a completely different effect from the one induced by the previous human intervention, i.e. grazing.

Afforestation

As regards the effect of afforestation on the community patterns of Coleoptera, this was intermediate compared with the effects of grazing and cultivation. The afforested site was more diverse than the natural pine forest, regarding both the species number and the equitability. Thus, high diversity was accompanied by changes in community structure, although the latter were not as striking as the ones recorded at grazed sites. Furthermore, apart from the cultivated field, which had a completely different species composition from all other sampling sites, the coleopteran community of the afforested site was clearly discernible as well.

Our results are quite different from those of ELEK et al. (2001), who found a more abundant and species rich carabid assemblage in a native forest than in a conifer plantation. However, the fact that the native forest that they studied was a deciduous one, might be a possible explanation. Besides, there is both a geographical and a habitat associated variation in the effects of afforestation on coleopteran communities (BUTTERFIELD et al., 1995). For example, FAHY & GORMALLY (1998) imply that the low carabid diversity that they found in a conifer plantation is related to low plant species richness and consequently to low food availability, but they state that the inclusion of open areas within plantations will increase available microhabitats and thus coleopteran diversity. Indeed, in the pine plantation of our study there is no dense overstorey, because the trees are about 7 years old and of low height, and thus there are still grass covered areas between them. Based on findings of INGS & HARTLEY (1999), who believe that in mature forests or even plantations, it is the shady and humid microclimate that species are responding to, we speculate that the alteration of shade and soil moisture due to the eventual growth of trees will lead to an homogeneous microclimate and to an adverse effect on coleopteran diversity. Such an effect is reported also by KOIVULA et al. (2002) and MAGURA et al. (2002).

CONCLUSIONS

To sum up, although the three management practices increased the diversity of epiedaphic Coleoptera, their effects on the community organization patterns differed. Grazing did not affect the species composition of communities but altered the community structure. The communities of the ungrazed forests were over-dominated by one species, while those of the grazed sites were hierarchically structured. On the other hand, the main effect of cultivation on the coleopteran communities was the profound change in species composition. The cultivated site was dominated by characteristic species that were almost absent from all other sites. Afforestation caused intermediate changes in both community structure and composition.

The use of a community measure to track habitat changes is an important alternative to assessments focused on single species (MATTONI et al., 2000). Our results show that although certain species of Coleoptera had significant indicator value and seemed to be good indices for assessing human impacts on natural environments, the study of changes in the community organization patterns is even more appropriate.

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Microtus guentheri (Danford & Alston) (Rodentia, Mammalia) : a bioindicator species for estimation of the influence of polymetal dust emissions

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ABSTRACT. Chemical pollution of ecosystems resulting from human activity is an ecological factor in the living world, affecting individuals, populations, communities and ecosystems as a whole. This laboratory investigation studied the toxic effects of polymetal ferosilicic dust on *Microtus guentheri* (Rodentia, Mammalia), measuring pathological changes in blood components (haemoglobin, erythrocyte, leucocyte and platelets number, erythrocyte sedimentation rate (ESR) and white cell count). Biochemical indices were established for levels of the following blood components : blood sugar, albumin, uric acid, triglycerides, cholesterol, total protein, creatinine, calcium and inorganic phosphorus. The results obtained indicate that *Microtus guentheri* can be used as a species for evaluation of the influence of polymetal dust emission.

KEY WORDS : *Microtus guentheri*, industrial polymetal dust, bioindication, biochemical and haematological indices

INTRODUCTION

Chemical pollution of ecosystems resulting from human activity and having an influence on individuals, populations, communities and the ecosystem as a whole is an ecological factor for wildlife. Detailed analysis of the entry of various such pollutants into the environment, their concentration in selected organs and their role in development and vitality of organisms is necessary for revealing the effects of chemical pollution.

Recently, dust pollution has increased, reaching its highest values in the Northern hemisphere. During the past 20 years the atmosphere has been polluted with 240,000 t of ferosilicic dust. In the atmosphere of Sofia, Bulgaria, the current amount of polymetal microsilicic dust emissions is 0.75 – 1.0 mg/ m^3 (FeSi-45%, Fe-3,11%, Pb–2, 03%, Mn-0,25%, Cd-0,57%, MgO-1,07%, SiO-7,65%, AlO-1,76%, KO-2,60%, NaO-0,85%) (EEABG, 2002). Iron, magnesium and manganese are microelements that are absolutely necessary for hemoglobin synthesis and enzyme activity, while cadmium, lead and aluminum are not nutritionally essential elements for animals. Exposure to acutely high, or chronically low levels may induce intracellular production of metallothionein, which has an important function as a store in zinc metabolism (Chakraborty et al., 1987, Fernando et al., 1989). The high accumulation of cadmium can lead to food chain amplification (increases in concentration in animals at each step in the food chain), because metallothionein –bound cadmium has a long biological half-life in animals and because concentrations tend to increase with age (Vermeer & Castila, 1991).

The main aim of this study was to investigate the heavy metal accumulation and distribution in different organs, and the influence of polymetal microsilicic dust on some basic haematological and biochemical indices in the peripheral blood of the Guenther's vole, *Microtus guentheri* (Danford & Alston) (Rodentia, Mammalia) and to determine indices important for biological monitoring.

MATERIAL AND METHODS

Polymetal microsilicic dust emission is a waste product from iron-bearing alloy production of metallurgical works. The present laboratory eco-toxicological experiment assessed its effect on *Microtus guentheri* (Danford & Alston), which is a convenient subject for such investigations because of its high reproductive potential. Being herbivorous, it is also an important link in the trophic chain, and its stationary way of life determines the permanent influence of different pollutants on its food base.

The toxic effect of the polymetal dust was studied under experimental subchronic conditions. Eighty-five individuals were divided into one control (15 individuals) and two test groups (Group I and Group II with 35 individuals each). In order to best approximate natural conditions, the microsilicic dust was given through food in two concentrations : Group I at 5% and Group II at 10% of food quantity. Samples for analysis were taken at 30, 60 and 90 days for all groups.

The bioaccumulation and distribution of Cu, Pb, Zn, Cd, Mn and Fe in different organs and tissues were examined using an atomic absorption spectrometer (Perkin Elmer). The pathological changes caused by the toxicant to the haemoglobin content, erythrocyte, leucocyte and platelet numbers, erythrocyte sedimentation rate (ESR) and white cell count were measured using an automatic hematological counter (HC-333). The following biochemical indices were studied : blood sugar, albumin, uric acid, triglycerides, cholesterol, total protein, creatinine, calcium and inorganic phosphorus levels using the biochemical analyzer Technicon RA-1000.

RESULTS AND DISCUSSION

The concentrations of the most toxic heavy metals are presented in Table 1. The elements considered were very unevenly distributed. It seems important to recognize the pattern of distribution because this may allow an estimate of the impact on organisms, as well as give an insight into possible detoxification mechanisms. The animal's organs differed from one another in respect to heavy metal concentration. The most sensitive organs were the kidneys, where the accumulated levels of lead and cadmium were the highest (29 mg/kg Pb and 32 mg/kg Cd for Group I on the 90th day and 40 mg/kg Pb and 125 mg/kg Cd for Group II on the 90th day), and the differences in cadmium and lead concentrations between experimental and control groups are statistically significant ($t=4.36$; $p < 0,0001$).

TABLE 1

Heavy metals concentrations in the whole body and in different organs of *M. guentheri* in mg/kg dry weight

		Control				**30th Day**				**60th Day**				**90th Day**			
	N	**Fe**	**Mn**	**Pb**	**Cd**	**Fe**	**Mn**	**Pb**	**Cd**	**Fe**	**Mn**	**Pb**	**Cd**	**Fe**	**Mn**	**Pb**	**Cd**
Whole body																	
X±	10	203.4	2.6	1.7	1.4												
Sd		48.1	0.5	0.5	0.4												
Group I																	
X±	10					217.2	2.4	1.9	3.8	257.8	1.5	4.0	2.8	281.3	1.4	3.2	2.1
Sd						40.6	1.6	0.6	1.8	76.1	0.6	1.5	1.9	24.8	1.1	1.3	0.5
Group II																	
X±	8					240.0	3.5	7.4	3.9	265.3	3.0	8.3	3.1	320.8	4.0	5.8	4.6
Sd						63.8	0.4	4.3	4.3	118.0	0.5	3.0	0.5	21.0	1.4	3.2	1.6
Kidneys																	
X±	10	479.7	3.9	7.5	7.6												
Sd		46.4	0.2	7.9	3.0												
Group I																	
X±	10					507.6	12.1	19.2	86.6	470.6	5.4	22.4	53.9	659.6	14.7	28.1	31.6
Sd						144.8	4.9	7.8	72.4	162.9	3.9	7.9	27.3	170.8	6.1	21.0	10.5
Group II																	
X±	10					439.6	10.1	28.7	107.2	389.7	12.1	44.2	152.9	683.1	12.3	40.3	125.1
Sd						97.5	2.9	15.6	45.0	43.1	2.5	18.1	54.4	213.7	5.7	16.1	20.8
Liver																	
X±	10	784.4	8.7	3.8	7.6												
Sd		31.9	2.4	1.0	2.6												
Group I																	
X±	10					1064.8	8.8	3.2	20.9	901.3	6.1	5.7	71.0	1103.2	7.2	2.8	20.1
Sd						70.9	2.3	1.9	19.6	49.8	2.7	1.9	19.3	343.2	5.6	1.6	9.7
Group II																	
X±	10					868.9	9.0	5.4	37.3	645.3	8.6	10.4	48.5	800.6	8.1	10.0	114.8
Sd						237.3	2.8	3.0	23.9	155.1	2.2	3.2	12.7	407.7	2.2	5.4	8.6

Cadmium and lead cause kidney toxicity in *M. guenthery*. The results concerning the accumulation of cadmium are very interesting. In the first variant of the experiment the bioaccumulation of this element was three times higher on the 30th day than on the 90th day, confirming data obtained by Mills & Delgrano (1972) and Topashka-Ancheva et al. (1998). The high cadmium concentration on the 30th day may induce intracellular production of matallothionein, a low-molecular-weight protein rich in sulfur amino acids to which cadmium can be bound and, hence, rendered less toxic (Schreiber & Burger, 2002). At the end of the experimental period a tendency towards compensation of the toxic effect occurred but it was not entirely effective.

From an ecological point of view, the data obtained for the total bioaccumulation of these heavy metals in the body of the Guenter's vole are very important because they show an average assessment of the organism's intoxication – a fact that could be used for prognoses in biological monitoring.

The changes in the average values of basic blood indices (Table 2) have an analogous character to that of the metal data. In both test groups there was a statistically significant reduction of the average values on the 30th day (with the exception of the average number of leucocytes), followed by a significant increase on the 60th day. At the end of the experimental period a tendency towards compensation of the changes occurred but, once more, it was not entirely effective.

The average values of albumin, creatinine, cholesterol and total protein varied similarly : at the beginning of the experiment there was an initial reduction followed by evidence of a compensatory mechanism. Group II exhibited a constant increase in blood sugar and uric acid, while triglycerides showed a decrease over the experimental time period to nearly that of the control value.

The results obtained show anemic effects during the experiment, which were surmounted. On the 60th day, a dissociation of erythrocyte number and hemoglobin concentration occurred as an expression of hypochromic ane-

TABLE 2

Hematological and biochemical values in exposed and control time

Indices	Referent values n = 90	30th day n = 15		60th day n = 15		90th day n = 15	
		Group I	Group II	Group I	Group II	Group I	Group II
Hemoglobin (g/l)	161.0±9.0	123.1±5.3	136.2±4.9	160.8±2.6	149.0±8.3	169.0±9.2	178.2±6.9
Erythrocytes (10^{12}/l)	4.9±0.3	3.7±0.9	4.3±1.1	9.5±0.3	9.0±0.2	5.1±0.6	5.3±0.4
Leukocytes (10^9/l)	4.1±0.3	3.9±0.8	6.4±0.7	9.6±1.4	14.4±1.3	3.8±0.9	8.6±0.6
ESR (mm/h)	1.2±0.3	-	-	0.8±1.9	1.5±2.2	0.8±0.9	0.8±1.3
Thrombocytes (10^9/l)	268.5±9.2	198.0±7.4	212.3±8.8	430.5±9.8	456.0±8.3	268.5±9.3	316.5±9.1
Blood sugar (mmol/l)	2.6±0.1	3.6±0.4	3.2±0.2	3.7±0.4	4.0±0.2	4.6±0.2	4.2±0.3
Albumin (g/l)	43.0±0.8	-	-	40.0±0.8	33.4±0.4	42.6±0.7	44.3±0.6
Uric acide (µmol/l)	86.1±0.3	-	-	80.1±0.4	108.2±0.3	105.8±0.4	194.2±0.6
Creatinine (µmol/l)	165.2±2.5	21.2±3.5	41.3±3.3	43.0±2.9	40.3±3.1	161.2±3.9	148.4±4.1
Cholesterol (mmol/l)	2.1±0.2	1.7±0.6	1.4±0.3	2.1±0.2	2.0±0.2	2.3±0.3	2.1±0.4
Triglycerides (mmol/l)	1.2±0.3	2.7±0.3	2.9±0.2	-	-	1.7±0.4	0.9±0.5
Total protein (g/l)	82.0±1.4	71.3±1.9	72.6±1.8	80.3±1.7	74.2±1.9	86.3±2.1	93.4±2.0
Calcium (mmol/l)	1.9±0.2	2.4±0.6	2.3±0.5	2.7±0.3	2.7±0.6	-	-
Inorganic Phosphorus (mmol/l)	2.5±0.3	2.3±0.7	2.2±0.9	1.7±0.8	2.1±0.6	-	-

mia. The acceleration of blood sedimentation rate on the 60th day supported this. Evidently toxic polymetal dust irritates marrow and stimulates erythropoiesis. Many young erythrocytes with reduced hemoglobin were pushed out to the periphery. On the 30th day the average number of leukocytes in Group II was twice as high as the control value. Consequently, this index is a very good marker for the toxic action of polymetal dust.

The changes of biochemical indices show that a hyperglycemic effect occurred during the whole experiment, and its expression depended to a certain extent on dose and time. The hyperuricaemic effect in Group II was the reason for reduced elimination of uric acid because of kidney damage resulting from exposure.

Physiological triglyceridemia in *M. guentheri* was reduced during the course of the experiment. Anabolic processes were affected leading to a reduction and stunting of growth. This is also confirmed by the suppressed synthesis of triglycerides. The increased amount of cholesterol shows an acute hepatotoxic effect on the 30th day. The opposite tendency in the changes of triglycerides and cholesterol is connected with lipoprotein exchange. Evidently the synthesis of lipoproteins in the liver is reduced.

The increased level of urea shows that a nephrotoxic effect is probably occurring with an impact at the tubular level. This is why, at the beginning of the experiment, urea concentrations increase but creatinine levels do not. The polyurea observed is due to hypoglycemia. Although Cd, Fe, Mn and Mg cause damage to the liver at very high concentrations, the critical organ is generally considered to be the kidney (NYHOLM & RUELING, 2001). Nephropathy is indicated by proximal tubule cell necrosis, proteiuria, glucosuria, increased urinary cadmium and decreased cadmium content in kidneys (WHITE at al., 1978).

The pathological changes observed in the tested blood indices, as a result of synergetic action of the metal captions or ferosilicic dust show that *M. guentheri* is a good bioindicator species for the evaluation of dust emissions.

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Trophic signatures of marine organisms in the Mediterranean as compared with other ecosystems

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ABSTRACT. We compared several large marine ecosystems in terms of species numbers of fishes, sea birds, marine mammals, and cephalopods. We examined how these numbers were distributed by trophic level, from herbivores to top predators. We created group-specific trophic signatures as plots of number of species by trophic level, and used these to identify similarities and discrepancies between taxonomic groups and ecosystems. Preliminary results suggested that trophic signatures are similar for ecosystems previously known to share major features, and different for dissimilar ecosystems. In the Mediterranean, as well as in the other large marine ecosystems, fish clearly dominate the predatory trophic levels above 3.0. Preliminary signatures for cephalopods, marine mammals, and sea birds in the Mediterranean and in the North Sea indicate that these groups are restricted to trophic levels above 3.0, and are represented by many fewer species than are predatory fish. Notably, cephalopods are the only invertebrates present at higher trophic levels (>= 4). Invertebrates other than cephalopods are restricted to trophic levels below 3, with very few exceptions. Trophic signatures appear to be useful tools for better understanding of the roles that different groups of organisms play in different ecosystems. We also applied free-scale network theory to analyse the food web created by trophic links of fishes. Our preliminary results indicated that Mediterranean fishes are, on average, only two trophic links away from each other.

KEY WORDS : trophic level ; food web ; Mediterranean ; North Sea ; Baltic ; Black Sea ; Caribbean ; South China Sea

INTRODUCTION

There is wide agreement that modern fisheries management has to take into account not only prey and predators of a target species, but also their role in an overall ecosystem context (CHRISTENSEN, 1996). There also are increasing calls for ecosystem-based management as an alternative, or at least a complement, to the single-species approaches so far used exclusively, and with little success, to manage commercial fisheries (NRC, 1999). Large Marine Ecosystems (LMEs) have been identified as suitable units for management (see SHERMAN & DUDA, 1999 and http ://www.edc.uri.edu/lme/), yet our understanding of LMEs is still limited. In this study we compared the Mediterranean with five other LMEs based on the respective trophic structures of important species groups. We used signatures created by plots of number and average size of species by trophic level as conservative, long-term characteristics of LMEs. We compared these signatures between groups of organisms and between LMEs. Our first hypothesis was that a given group of organisms will show similar signatures in similar LMEs, and vice-versa. Our second hypothesis stated that different groups of organisms will have typical and different signatures. We expected that the subtropical Mediterranean would show an intermediate position between temperate LMEs (North Sea, Baltic and Black Sea) and tropical LMEs (Caribbean and South China Sea).

Another type of trophic signature is generated by a plot of species frequency in relation to their number of trophic links (WILLIAMS et al., 2000). Such plots can be interpreted by applying ‘small world’ or ‘free-scale network’ theories (JEONG et al., 2000 ; ALBERT & BARABASI, 2002). Within such framework species are nodes that are interconnected through trophic relationships (links). The distance or path length between two species is the number of links (k) between them. For example, a species A is one link away from species B if A is prey or predator of B ; it is two links away if A and B do not interact directly but A shares with B at least one prey or predator, etc. Analysis of non-biological free-scale networks suggested that path length will increase considerably if a certain quantity of the most connected nodes is removed, compared with a random removal of nodes, which will have little effect on path length. Here we test this prediction for the Mediterranean.

MATERIAL AND METHODS

For the purpose of this study, we used fish, cephalopods, marine mammals and sea birds as groups of organisms. We followed the LME definitions of SHERMAN & DUDA (1999). We used the Baltic and the Black Sea as analogue brackish, temperate, and species-poor ecosystems. We used the North Sea as a marine, temperate ecosystem, and we used the Caribbean and the South China Sea as examples of tropical, species-rich ecosystems.

For fishes, we used the trophic levels, maximum lengths, and LME assignments given in FishBase (FROESE & PAULY, 2000 ; www.fishbase.org). For cephalopods, we used data on distribution and food in NORMAN (2000) and in CephBase (www.cephbase.org). For marine mammals, we used trophic levels from PAULY et al. (1998). For marine birds, we used information on food and distribution from DEL HOYO et al. (1992 ; 1996), BEZZEL (1985), MELTOFTE et al. (1994), and SKOV et al. (1995). Trophic levels (trophs) were calculated from diet composition data as Troph = 1 + weighted mean troph of the food items (see CHRISTENSEN & PAULY (1992) for details, including estimation of standard errors). If no diet composition, but individual food items were known, trophic levels and their standard errors were estimated using a Monte Carlo routine described in PAULY & SA-A (2000). Both routines are implemented in the TrophLab software, which can be downloaded at www.fishbase.org/download/. If no food information was available for a given species, it was assigned the mean troph of congeners or of the respective family. For invertebrates, we relied on an estimate of Mediterranean 'macroscopic fauna' (8500 species) by the European Environment Agency (www/eea/ei/int.). We subtracted from this estimate the 691 Mediterranean species of fish, birds, cephalopods and marine mammals, and assumed that, for the purpose of this study, the remainder could be assigned to trophic levels between 2 and 3.49 (see below).

For the free-scale network analysis we used data on prey items as recorded in FishBase (FROESE & PAULY, 2000). In FishBase food items of fishes are classified into 59 categories such as diatoms, polychaetes, euphausiids, or squids/cuttlefish (SA-A et al., 2000). These categories are similar to the 'trophic species', which have been used in other food web studies and which are defined as "functional groups of taxa that share the same consumers and resources within a food web" (WILLIAMS et al., 2000). For the purpose of this study we considered 385 Mediterranean fish species as nodes and their reported food categories as links.

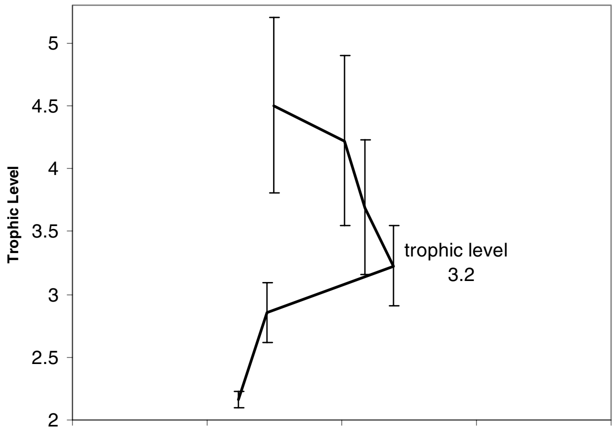

Fig. 1. – Number of fish species of the Mediterranean by trophic level. Error bars show the mean standard error of individual trophic level estimates.

RESULTS AND DISCUSSION

Fig. 1 shows the trophic signatures of 567 species of fish in the Mediterranean, plotted as number of species per 0.5 trophic level. The standard errors increase with trophic levels because second and third-level predators typically exploit a wide range of prey, from herbivores to other second or third-level predators.

Fig. 2 shows the trophic signatures of fishes in the Baltic, the Black Sea, the North Sea, the Mediterranean, the Caribbean and the South China Sea, with total number of species increasing in the same sequence. Despite the considerable differences between these ecosystems in terms of salinity, size, temperature, and species numbers, the signatures are strikingly similar : in all ecosystems fishes cover the whole range of trophic levels, from herbivores near 2.0 to top predators at above 4.5. Both herbivores and top predators contribute about or less than 5% of total species numbers. Highest species numbers always occur around troph 3.2, i.e., with first-level predators feeding mainly on herbivorous organisms. The signatures of the brackish, species-poor Baltic and Black Seas are more similar to each other than to the marine, more speciose North Sea, which has more top-predators and fewer lower-level species, resulting in a signature that cuts across that of the brackish systems. As expected, the subtropical Mediterranean takes an intermediate position between the temperate and the tropical systems. The Caribbean signature is the only one where the lower leg is bent to the right, indicating a relatively higher number of herbivorous fishes than in the other systems.

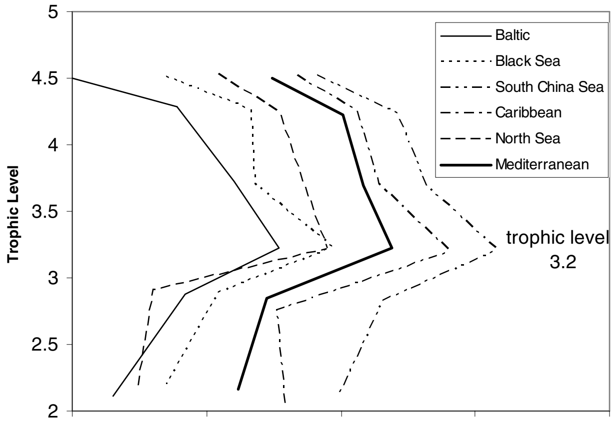

Fig. 2. – A comparison of trophic signatures of fishes in six large marine ecosystems.

Fig. 3 shows the geometric mean maximum lengths of Mediterranean fishes per half trophic level class. Most first-level predators at trophs of about 3.0 are small fishes of about 20 cm maximum length, generally feeding on zooplankton and/or small benthic invertebrates. As expected the mean maximum length increases with trophic level to 1.5 m for top-predators, but it also increases to about 27 cm for herbivores. Variation in 95% confidence limits follows the same pattern.

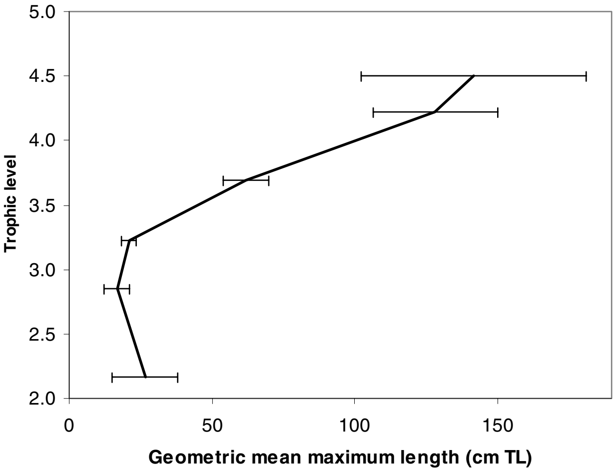

Fig. 3. – Geometric mean maximum length of Mediterranean fishes at different trophic levels, with error bars showing 95% confidence limits.

Fig. 4 shows the length signatures of all six LMEs, all with a signature roughly similar to that of the Mediterranean, with minimum mean size around trophic level 3 and an increase towards higher and lower trophic levels. Tropical systems are typically dominated by smaller species, which is shown here by the signatures of the South China Sea and the Caribbean being mostly left of the temperate systems. The subtropical Mediterranean shows again an intermediate position between temperate and tropical systems, except for the lower trophic levels where it overlaps with the tropical systems.

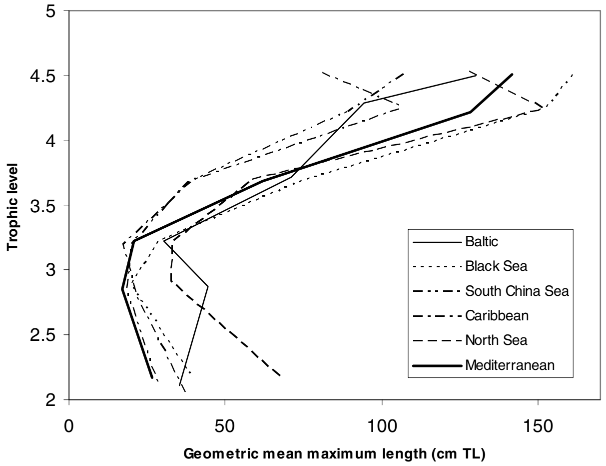

Fig. 4. – Comparison of geometric mean maximum lengths at different trophic levers for fishes in six large marine ecosystems.

Fig. 5 shows the trophic signatures of fish, cephalopods, sea birds, and marine mammals in the Mediterranean. Total species numbers of fish are an order of magnitude higher than those of the other groups. Only fish species occupy all trophic levels, whereas birds, cephalopods and mammals are restricted to levels above 3.0. Most cephalopods feed at about trophic level 3.7 (0.5 above fish), and most birds and mammals feed above 4.0, one level above fish. Because of the low number of marine mammals (17), their signature must be viewed with some caution, as improved understanding of the diet of just a few species may alter the signature. Nevertheless, the maximum at 4.2 for marine mammals shows their position as top predators in the Mediterranean, also confirmed by a plot (not shown here) of all marine mammals in the world showing a similar signature and the same maximum. Fig. 6 shows a similar graph for the North Sea, with similar signatures for the respective groups. Species numbers for fish and cephalopods in the North Sea are only about 1/3 of that in the Mediterranean, whereas numbers for sea birds and marine mammals are increased by 50% and 20%, respectively. This reflects the greater role of homoeothermic groups (i.e., marine mammals and sea birds) in colder waters.

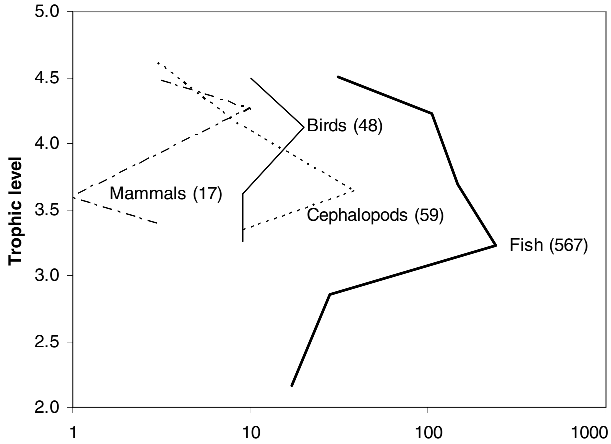

Fig. 5. – Number of species per trophic level for four groups of organisms in the Mediterranean.

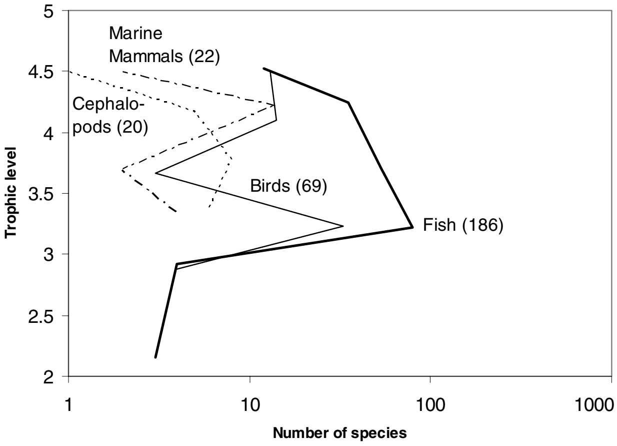

Fig. 6. – Number of species per trophic level for four groups of organisms in the North Sea.

Fig. 7 shows the sum of species per trophic level across the considered groups, resulting in the pyramid structure that is commonly encountered when plotting individual numbers (Lindeman, 1942), or biological production (Christensen & Pauly, 1992) by trophic level. Looking at Fig. 7 from a phylogenetic perspective, it appears that the four groups jointly dominating the upper trophic levels of marine ecosystems (i.e., fish, marine mammals, sea birds and cephalopods) tend to be highly derived, predatory representatives of their class or phylum, while the organisms abundant at the lower trophic levels (<3), tend to belong to stem groups, and to feed mainly on phytoplankton, benthic algae and detritus (though other invertebrates are also consumed, and cnidarians, chaetognaths and other groups of carnivorous zooplankton are actually restricted to trophic levels above 3).

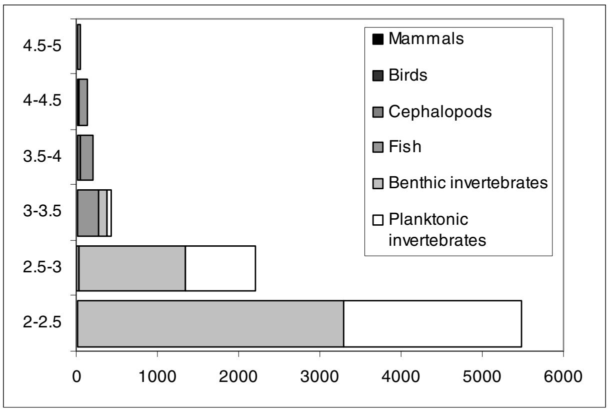

Fig. 7. – Numbers of Mediterranean species per trophic level. Note that about 7800 invertebrates are assumed, with most being herbivores, fewer being omnivores, and very few being first-order predators.

This suggests that overfishing, which tends to remove upper-trophic level animals (Pauly et al., 1998) will tend to reverse the implied evolutionary sequence, as noted in Pauly (1979), and further developed in Parsons (1996).

Feeding studies exist only for a fraction of the invertebrates in the Mediterranean or other LMEs, and thus the distribution to trophic levels shown in Fig. 7 is hypothetical. Detailed trophic studies on invertebrate species, as well as generalizations by higher taxa such as families and orders, are urgently needed for a better understanding of the foundation of LME food webs.

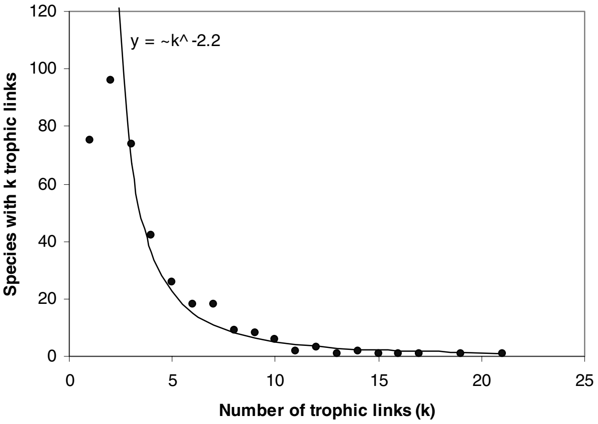

Fig. 8. – Frequency distribution of species with k trophic links, with eye-fitted curve. Note that number of species with one link is probably too high and number with two links probably too low because of a bias caused by ‘understudied’ species.

Fig. 8 shows a frequency plot of the number of trophic link categories per Mediterranean fish species. The plot shows the typical shape of a scale-free network which is roughly described by a power-law function of the form k^{-y}, and where y typically takes values between 2 and 3 (here $y = 2.2$). Thirty-two fishes (8%) preyed directly on other Mediterranean fishes and the shortest distance between them was thus one link. Analysis of ten randomly selected species showed that they had, on average, 54% of species (208.1, SE +/-16.7) within 2 links, 99% of species (380.9, SE +/-0.10) within 3 links, and all species (384) within 4 links distance from themselves. The weighted mean path length in the food web was 2.38 (SE +/-0.033) links. This agrees well with other food-web analyses, where path lengths between 1.4 and 2.7 have been found (Williams et al., 2000). Knowledge about mean path length is important as it quantifies the average number of links necessary for an effect to propagate from one species to other species. Significant effects have been shown to propagate often two and sometimes three links away from manipulated species, whereas species more than three links away from each other are functionally disconnected (Brett & Goldman, 1997; Pace et al., 1999).

It has been suggested that the removal of 5% of the nodes starting with those with highest numbers of links can double path length (Cohen, 2002). In our data set such removal of species with highest numbers of trophic links increased mean path length to 2.43 (SE +/-0.066), which is not significantly (t-test, n=740, $P<0.05$) different from 2.38. To choose a more realistic scenario we removed 38 Mediterranean fishes that were marked in FishBase as ‘highly commercial,’ many of them upper-trophic level species with many (median=5) trophic links. This removal increased mean path length to 2.45 (SE +/-0.033), which is also not significantly (t-test, n=712, $P<0.05$) different from 2.38. Thus, it appears that food webs are relatively robust towards removal of 5-10% of highly connected species. This might explain the observation that many ecosystems have apparently withstood very strong fishing pressure for a very long time. We want to stress that our application of scale-free network theory to food-web data of Mediterranean fishes is preliminary and a more thorough study of trophic relationships including non-fish species is needed to confirm or reject our results.

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The status of the Golden Jackal (*Canis aureus* L.) in Greece

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ABSTRACT. Broadcasted jackal howls were used to survey the status of the golden jackal in Greece. All sites with recent indication of jackal presence were surveyed at selected calling stations, and minimum population estimates were recorded. The results of the survey show that both populations and distribution area of the golden jackal in Greece have been declining steadily during the last three decades. The golden jackal has disappeared from Central and Western Greece and is currently confined in discontinuous, isolated population clusters in Peloponnese, Fokida, Samos isl., Halkidiki and North-eastern Greece. The reduction was more distinct in Southern Greece, which used to be the jackal's main area 20 years ago. The current minimum size of the jackal population in Greece was estimated at 152-162 different territorial groups. The largest population cluster was found in Nestos – Vistonida area, NE Greece. In Southern Greece, the jackal is found in the Mediterranean maquis zone at altitudes below 600m asl. Some individuals were observed up to 1000m asl, but were considered exceptional. In Northern Greece the species was found in areas below 250m asl, while the highest population densities were found in thickets around wetlands up to 10m asl.

KEY WORDS : *Canis aureus*, Greece, status, acoustics, vocalization, howling response

INTRODUCTION

The jackal in Europe is distributed in small and scattered populations, mainly along the Mediterranean and Black Sea coast of the Balkan Peninsula (DEMETER & SPASSOV, 1993 ; KRYSTUFEK *et al*., 1997). In this area occurs only in Mediterranean-type scrubland and lowland wetlands (DEMETER & SPASSOV, 1993), and being on the top of the food chain it is an important indicator of these ecosystems.

The golden jackal has become by far the most rare canid species in Greece (GIANNATOS & IOANNIDIS, 1989; 1991; KARANDINOS & PARASCHI, 1992) as its population has been declining during the last three decades. The jackal is the only medium-sized carnivore in Greece that has suffered a rapid decline in its distribution and population numbers, and the exact causes for the species' reduction in Greece are generally unknown. No systematic survey has been carried out so far.

The legal status of the species is still obscure and undetermined. It is listed as "vulnerable" in the Red Data Book for Greek Vertebrates (KARANDINOS, 1992) but otherwise it is neither officially declared as a game species nor as a protected one. In general very little information is available on jackal ecology and conservation status in Europe.

In order to elaborate conservation measures for the species and develop an action plan for its conservation, WWF Greece completed a country-wide survey and mapping of the species' population status, distribution, and status changes during the last 25 years. This study summarises the first results of this project.

MATERIAL AND METHODS

Survey area

The survey was carried out between May 2000 and June 2001. The survey area included all localities in Greece with recent sightings, confirmed damage, or at least some (even doubtful) evidence of jackal presence. Selection of these areas was based on relevant information collected through questionnaires addressed to Forest Services, Hunting Associations, WWF Greece members, and personal interviews with local people, especially shepherds. After gathering and verifying all collected answers, a total of 264 possible areas of presence were identified. In each of these areas selected survey routes were drawn based on existing road networks, vegetation, and morphology. Calling stations were set along these routes in such a way as to cover completely each area of presence. Each station was located in a site with good visibility and acoustics, and usually – but depending on the terrain – at a high vantage point. Linear distance between successive trial calling stations was between 2-4 km, depending on the topography of the sampling area. Each station's co-ordinates were recorded by GPS.

Acoustic method

The current population status of the jackal in Greece was assessed by a calling survey method that combined acoustic and visual observations of jackals after stimulation with playback howls. Similar methods have been extensively used to survey social and vocal carnivores (MC CARLEY, 1975 ; HARRINGTON & MECH, 1982 ; CREEL & CREEL, 1996 ; JAEGER et al., 1996 ; MILLS et al., 2001).

A broadcasted group-yip howl by three to four jackals was used at each calling station. The howl was recorded on a mini disc and broadcasted using an Aiwa AMF 65 recorder wired to a 20-Watt caller with 15-Watt chip amplifier. The howls were played from the roof of a vehicle at night at the selected calling stations, always one hour after sunset on calm and dry nights. Windy or rainy nights, which could seriously disturb the observers' hearing capacity or animal responsiveness, were strongly avoided (Mc Carley, 1975 ; Jaeger et al., 1996). Each howl broadcast lasted for 30-sec and was followed by a 5-minute pause. This set of broadcast and pause was repeated six times, for an overall session time of ca. 30 minutes. The direction of the caller was changed every two to three howls, depending on the landscape structure and the direction of the wind. During and after each howl broadcast, two to three members of the field team recorded the direction and the possible number of the responding jackhals. It was assumed that each response-direction coincided with a territorial group.

In the event of an immediate response from close-quarters, high intensity spotlights (500,000-1,000,000 candle power) were used to survey the area for 360^0 around the calling station to locate approaching animals. When the response was heard from a great distance, or if no response at all was recorded, the area was surveyed after the 2^{nd} or 3^{rd} howl broadcast (i.e. 5-10 minutes from the beginning of a session), in order not to scare away possible approaching animals. Observation was facilitated by 7x50 binoculars. In locations with good visibility, approaching animals could be identified from more than 250m by their characteristic gait and shining eyes. In cases of approaching animals we counted all the animals in view.

It was assumed that only territorial groups of jackals were responding to the broadcast playbacks. Identification of different individuals howling in chorus within each group was not possible by hearing alone, especially in cases of groups of more than two animals.

Maximum human hearing distance on windless nights from a vantage point in open terrain with no background noise was determined at 1.8-2 km, whereas the maximum distance for attracting jackals was determined at 1.5 km. In order to experimentally test the maximum distance that the jackals could be heard with accuracy in a relatively open terrain, after the detection of a jackal group one of the observers stayed close to the animals, while the rest of the team drove to distances of 1.5 and 2 km. The jackal howls were broadcasted in both distances. After the jackals responded the two groups communicated to verify audibility. At both distances both the playbacks and the jackal howls were audible to all observers, but at the 2 km distance the broadcast was faint. Maximum audibility was achieved during the night, when it was silent and the animals forage in the open.

The attracting distance was tested in an open area where jackals had been previously located. After the stimulation howling, jackals were observed approaching from distances of 1.5 km down to 50 m from the calling station.

At each calling station the effective area for an audible response from the jackals was estimated to be between 7 and 12.5 km^2, depending on the different landscape topography of the surveyed area.

At each site the following parameters were also recorded to assess major features of the habitat and jackal-human interactions. 1) Altitude and the most dominant plant species within a 1km radius from the approximate location of the jackals during the point count survey. The radius was selected under the assumption that these locations were within the jackals' home range. 2) The distance from the nearest human settlement.

RESULTS

Population status

During the survey 264 possible areas of presence were visited and a positive jackal response was recorded in 131 (50%). The easternmost peninsula of Halkidiki (Mt. Athos) was not surveyed because a research permit was not issued in time. However, from personal observations we can verify that the species was present in almost all areas of the peninsula.

At the majority of calling stations (67%) the jackals responded within the first five minutes. In 45 cases it was possible to attract animals from the responding jackal group. The majority of sightings (85%) involved one to two animals. The largest group observed consisted of five individuals, but such a number was observed only once (Fig. 1). The minimum total number of groups found was 152-162 (Tab. 1).

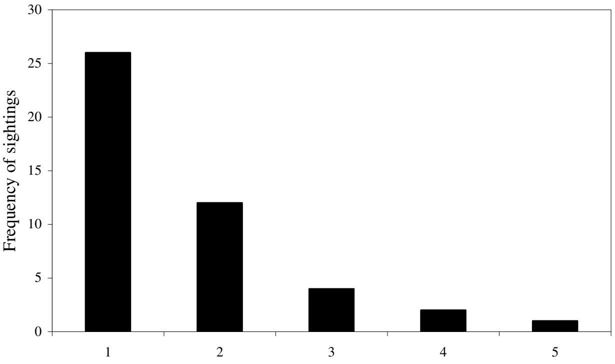


Fig. 1. – Frequency and number of approaching jackal individuals

According to records of the Ministry of Agriculture (Min of Agriculture, unpublished data), the decline of the jackal population started in the 70s and was even more intense in the early eighties. Even by 1980, the harvest was much reduced compared with those of the years 1974 to 1979 (Tab.1).

Information from local observers, verified by the present survey, showed that no jackal groups existed between Fokida and the southernmost jackal population in Northern Greece in Halkidiki. There was only one, but unconfirmed, report of the presence of one jackal group in Central Macedonian Province (Fig. 2).

Habitat types

Because of distinctive differences and similarities in the habitat types, the jackal distribution in Greece was divided in two sub-regions : Southern Greece (Peloponnese, Fokida, Samos) and Northern Greece (Halkidiki, Serres, Nestos-Vistonida, Evros) (Fig.2). Based on the predominant habitat types, the jackal presence areas were divided into two main categories : wetlands, mainly in Northern Greece (Fig. 3a), and other habitat types, mostly Mediterranean maquis (Fig. 3b).

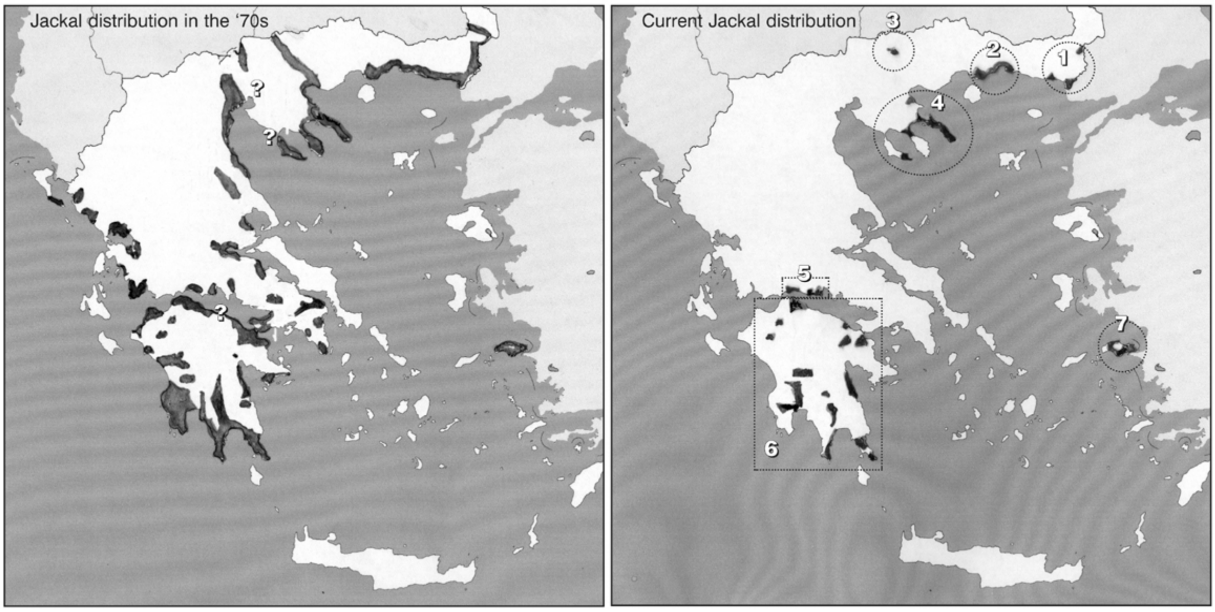


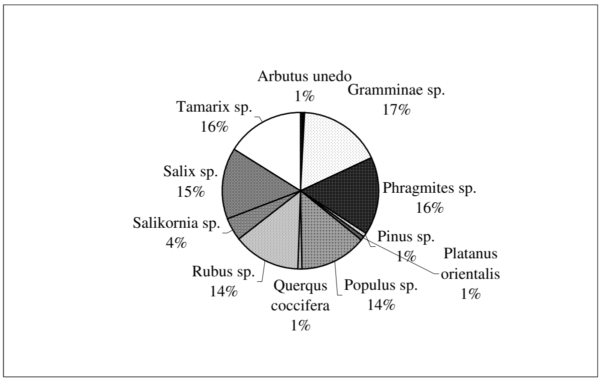
Fig. 2. – The golden jackal distribution in Greece in the 1970s and today. 1) Evros, 2) Vistonida-Nestos, 3) Serres, 4) Halkidiki, 5) Fokida, 6) Peloponnisos, 7) Samos

In Southern Greece, jackals were found in more mountainous habitats than in the North (Fig.4). The highest observed group in Northern Greece was in Halkidiki at 250m asl, while in the south (Peloponnese) jackals were observed even at 1050m asl. The largest population cluster in Greece (located in Nestos – Vistonida area) as well as other coastal wetland populations were found in areas at less than 10 m altitude.

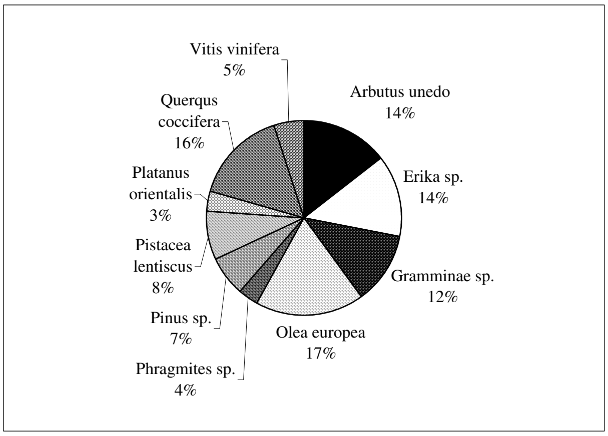
TABLE 1

Estimated minimum number of jackal territories in each area in Greece

AREA	**Number of jackals killed annually in the 1974 – 1979 period (min-max)**	**Number of jackals killed in1980**	**Minimum number of jackal group territories (2000 -2001 survey data)**
Peloponnese	517-1049	192	43 – 45
Fokida	1-8	5	9 –11
Samos	13 –96	0	12
Serres	14 – 63	52	1-2
Halkidiki	33-90	20	26
Vistonida- Nestos	53-122	16	53
Evros	27-74	1	8 – 12
Rest Of Greece	34 - 254	83	1?
TOTAL	**903 – 1332**	**369**	**152 – 162**



3a



3b

Fig. 3. – The most frequent plant species in the jackal habitats of Northern Greece (3a) and in Southern Greece (3b).

The highest jackal population densities were found in the wetlands of Northeastern Greece. If we set the effective area in each survey trial at 7 to 12.5 km^2 the jackal territory densities range from 0.08 to 0.5 groups/km^2. The highest densities were detected in wetland and riparian areas, namely in Vistonida – Nestos and in Mornos delta in Fokida, while the lowest were in Mediterranean maquis vegetation areas in Peloponnese.

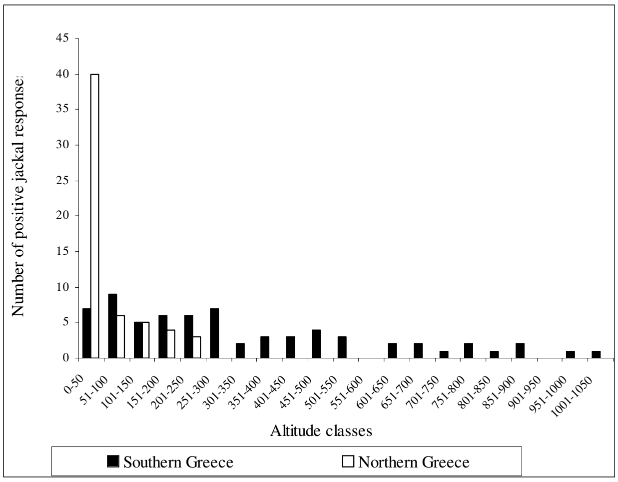


Fig. 4. – Observed jackal groups per altitude intervals

Jackals and humans

According to local shepherds, very little damage to livestock is recorded in marginal mountainous areas in Peloponnese, and what does occur is caused mostly by isolated roaming individuals. In Peloponnese, stray dogs and jackals are the only animals that could prey on small, hoofed livestock, since there are no wolves. The shepherds usually know which of the two canids is responsible for the losses. In areas with relatively large jackal populations no complaints about livestock damage were recorded.

The mean distance of the observed jackal groups from the nearest human settlement was found to be 2.61 km (Range : 0.1-4.5 km). (Fig.5).

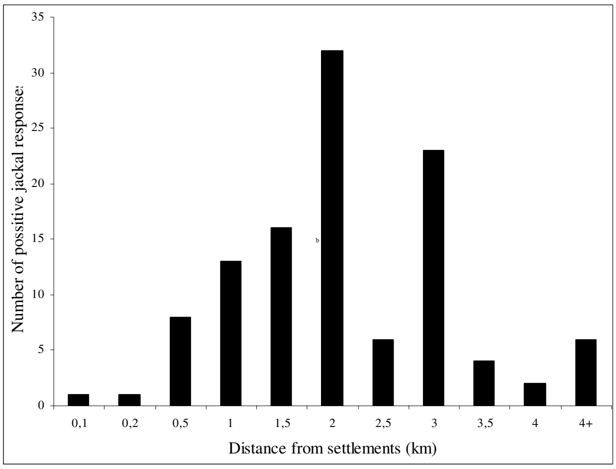


Fig. 5. – Jackal group sighting distances from nearest settlements

Jackals and other canids

Some observations :

- In three cases during the survey, wolves approached the jackal-calling stations at a quick trotting pace, presumably to chase off the jackals from the location.

- Dogs barked aggressively whenever jackal howling was heard, and at close quarters some became strongly agitated. In many cases dog groups (three to seven individuals) approached the calling station in a running manner, barking in a hostile way after hearing broadcast jackal howls. The reaction of unleashed dogs was to chase away the jackals instantly.

- Although no actual observations of close fox - jackal interactions were made during the survey, in our current study area in Fokida, foxes occurred permanently only on the fringes of the jackal territories. However, in the winter we have seen a few individual foxes within jackal territories, and in one case a fox approached about 250 m of a jackal group of four (Giannatos pers. obs.).

DISCUSSION

The results show a very sharp decline of the golden jackal population in South Peloponnese, where, according to the records of the Ministry of Agriculture and the results of our questionnaires and interviews, the jackal population was thriving in the 70s and 80s. The process of disappearance in Peloponnese is ongoing since local extinctions of jackals are still reported. The jackal population in Peloponnese is now estimated at close to 10% of the population level 20-25 years ago.

According to the survey data the jackal population in Samos Isl. has also declined during the last decade, and the species has become rare in parts of the island. However a rapid population recovery was observed in the island recently.

With the exception of Fokida prefecture, jackals have disappeared from all central and western Greece. The species still survives in isolated and mostly fragmented population clusters in a few locations in North-eastern Greece. In Halkidiki, the distribution of the jackal has also been reduced but not as sharply as in Peloponnese. In Evros prefecture the jackals remain only in a few isolated locations. There may be a source population in eastern Evros delta, near the borders with Turkey, but its status is unclear. The only area where the jackal population seems stable or even locally increasing is Nestos-Vistonida and the surrounding lagoons, which host the largest continuous jackal sub-population in Greece. A major threat to the jackal population in this area is the destruction of the coastal marshes due to the building of summerhouses.

The decline of the jackal can be partly attributed to the fact that all wild canid species (namely the jackal, the fox and the wolf) were considered pests during the ’70 and ’80s, and consequently legally persecuted by every possible means, including poisoning. This poisoning campaign had generally a short-term effect on most of the other canids involved : both foxes and wolves quickly recovered and reoccupied their areas soon after the ban of poisoning in 1980 (Min. of Agriculture). However, this was not the case for the golden jackal whose populations continued to decline alarmingly.

Preliminary data from the field indicate that the relationship of the jackal to other canid species was that of a competitor. Wolves usually dominated jackals, and jackals dominated foxes. The ranges of jackals and wolves in Central and Northern Greece were almost exclusive. According to Genov & Wassiliev (1989) and Krystufek & Tvrtkovic (1990) the wolf presence is a limiting factor for jackal distribution in the Balkan Peninsula. It seems that jackal population density is a factor that could greatly influence the presence of foxes. In our current study area in Fokida, foxes were very scarce in the main jackal territory. This is a high-density jackal area with few hiding places, very different from many other areas that have been surveyed in Greece. In Israel where jackals and foxes co-exist, the jackals may kill or displace foxes (Macdonald, 1987). In southern Peloponnese an increase of the fox population was observed in areas where the jackals have been decimated. No foxes existed in Samos island (Dimitropoulos et al., 1998).

Although jackal-induced damage and general disturbance to humans was minimal, the public attitude to the animal seemed to be from negative to indifferent. This is probably related to the official designation of the species as harmful in Greece until 1990. The jackals in Greece were found only in Mediterranean-type habitats and lowland wetlands, close to human settlements. This indicates possible dependance on human produced food. Jackals as opportunistic foragers have been known to subsists almost entirely on garbage and human waste (MacDonald, 1979). In conclusion, the existing jackal populations in Greece are discontinuous and clustered. The survival of these populations is dependent on the size of each cluster and the connectivity between them.

The applied survey method proved to be quick, easy and inexpensive. Jackal groups were detected even in areas with very thin presence, in marginal habitats, or even close to fierce competitors such as stray dogs. Absence of response to the acoustic stimuli cannot be translated to absence of jackals. However, the 30 min duration of the trial at each calling station seemed be enough to stimulate even the shyest animals. In two areas where the jackal group territories were known, there was an absolute accordance between the actual number of groups and the number recorded during the 2000 – 2001 acoustic survey (Giannatos, pers.obs.). The possibility for a lone animal, probably a free-ranging young, to respond is usually lower than that of one belonging to a family group. In known groups we noticed that sub-adults do not always vocalize (Giannatos, pers. obs.). It is also ossible that responsiveness of the animals could be uneven, since the large groups in high-density areas tend to respond more readily than small groups in low-density areas (Jaeger et al., 1996 ; Moehlman, 1981). The repetition of trials at certain periods of time will help us to understand the situation of the existing groups in different locations (M. Jaeger, pers. comm.). Jackals could become habituated to the sounds and thus not respond to the playbacks. We don't know how often the howls could be repeated while maintaining good results. In known locations in Samos the jackals did not respond when the playbacks were played two nights in a row. However, one known isolated group consisting of two sub-adults responded every time that the playbacks were played. More research is needed to establish the effective time and conditions for repeatability.

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The spatial distribution of anchovy and sardine in the northern Aegean Sea in relation to hydrographic regimes

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ABSTRACT. Acoustic survey data were combined with hydrological parameters with the aim of understanding the relationships between the spatial distribution of anchovy and sardine and environmental regimes. Acoustic and concurrent hydrological sampling was carried out in the Northern Aegean Sea (eastern Mediterranean) during June 1995 and June 1996. In order to examine hydrological parameter selection by anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*), cumulative distribution functions were estimated. Both species were significantly associated with areas of deeper surface and upper mixed layers, which implied an association of anchovy and sardine with anticyclones. Within the range of available temperatures and bottom depths, sardine further showed a significant affinity to warm as well as to shallow waters. These results are discussed in relation to species' life histories and existing knowledge of oceanographic features in the surveyed area.

KEY WORDS : anchovy, sardine, Northern Aegean Sea, spatial distribution, environmental variable selection.

INTRODUCTION

Small pelagic species comprise a very important part of the total world fisheries catch. About 25% of the total catch of the European pilchard (*Sardina pilchardus* (Walbaum, 1792)) and almost 90% of the total catch of the European anchovy (*Engraulis encrasicolus* (Linnaeus, 1758)) is taken in the Mediterranean Sea (Freon & Misund, 1999). To improve the understanding of the mechanisms that are responsible for the availability of these resources, there is a need to integrate environmental information with biological and fishery knowledge. Habitat selection affects the spatial distribution of the species and is often the outcome of trade-offs between different agents such as heredity, predation and availability of food (Freon & Misund, 1999).

Although the Northern Aegean Sea is the most important fishing ground for anchovy and sardine in the Eastern Mediterranean (Stergiou et al., 1997), published studies on their spatial distribution in the area are generally lacking and the linkage to hydrological regimes has never been studied. Previous investigations in the Northern Aegean Sea mainly focused on the ichthyoplankton distribution and abundance in relation to oceanographic conditions (Somarakis et al., 2002), the estimation of the size of the stocks using fisheries independent techniques (Machias & Somarakis 1997), and the analysis of fisheries landings data (Stergiou et al., 1997 and references therein). The present study attempts to relate the spatial distribution of anchovy and sardine to environmental conditions, combining data from concurrent hydroacoustic and hydrographic surveys carried out in June 1995 and June 1996 over the continental shelf.

MATERIAL AND METHODS

Acoustic data were collected during two surveys carried out on board the "R/V PHILIA" in June 1995 and June 1996. The study area covered the continental shelf and slope waters of the Thracian Sea, Strymonikos Gulf and Thermaikos Gulf (Fig. 1). The sampling scheme was based on 30 predetermined transects and the surveyed area was stratified into : Thracian Sea (Stratum I), Strymonikos Gulf (Stratum II) and Thermaikos Gulf (Stratum III). Stratum I covered 29%, stratum II 27% and stratum III 44% of the study area. (for details see Tsimenides et al., 1992).

The acoustic equipment used was a Biosonic Dual Beam 120 kHz V-Fin Echosounder (Model 120, 3° + 3°). The system was regularly calibrated using the standard sphere method (Foote, 1987). The echoes were processed using the software ESP v3 of Biosonics Inc. The speed of the vessel was 8 nautical miles (nm) per hour. Acoustic echoes were registered continuously along transects and were integrated over one nm, which served as the Elementary Distance Sampling Unit (EDSU). The sardine and anchovy echoes were discriminated from those of other fishes by the characteristic echogram shape and back-scattered energy of the schools (Giannoulaki et al., 1999). Information on fish schools was obtained by means of identification hauls made with a pelagic trawl (vertical opening : 10 m, codend : 10 mm) (Giannoulaki et al., 1999).

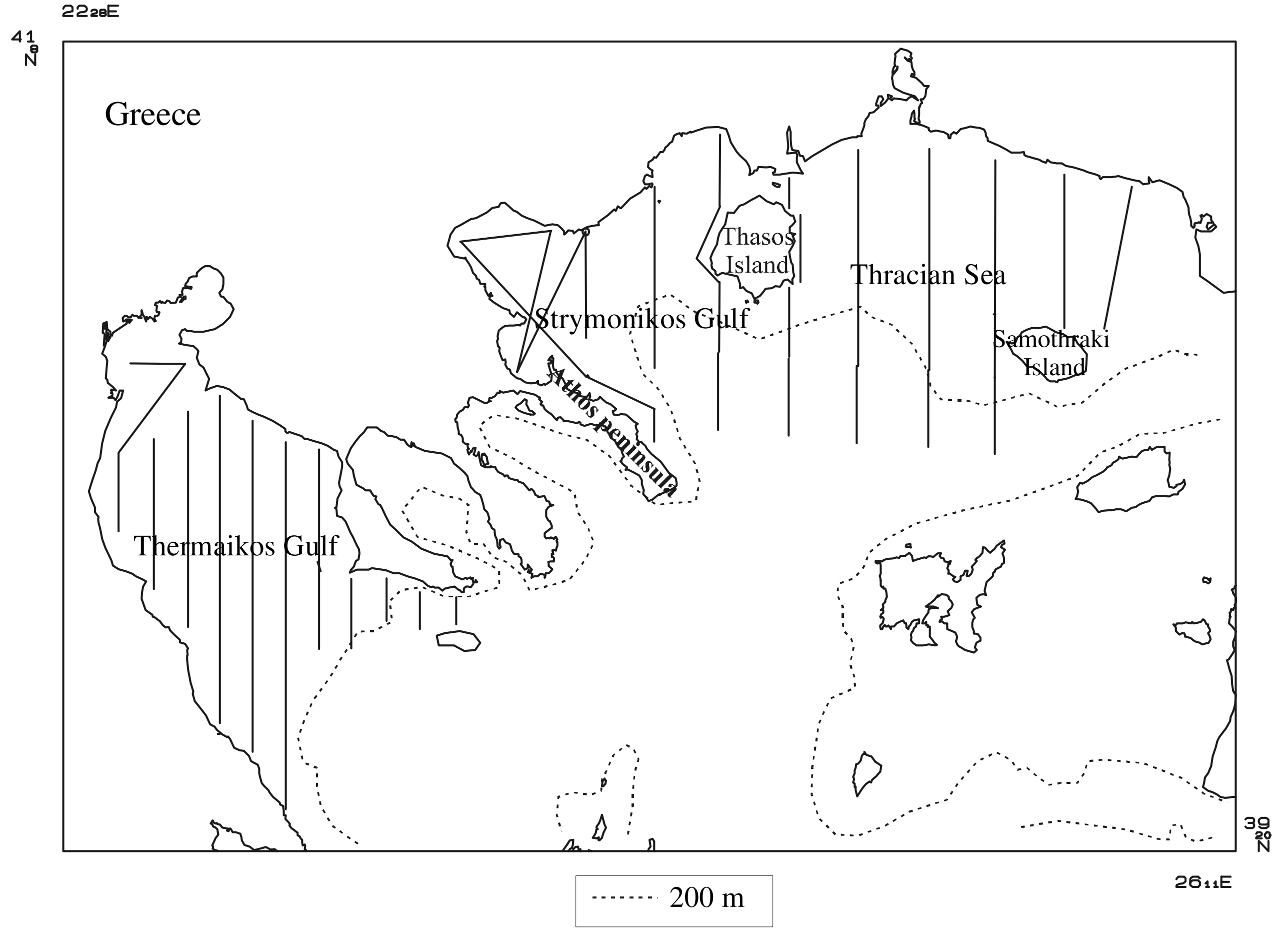

Fig. 1. – Map of the study area (Northern Aegean Sea) showing transects (lines) and toponyms mentioned in the text.

Hydrographic sampling was performed over a grid of 144 and 147 stations in 1995 and 1996, respectively. At each station vertical profiles of temperature and salinity were obtained with a SBE-19 Seacat internally recording CTD unit (Sea Bird Electronics). To study the association of fish with environmental factors, we calculated the depth and mean values for temperature and salinity of the following water column layers : (a) the surface mixed layer (SML) ; (b) the upper mixed layer (UML) and (c) the bottom layer (BL) (Laprise & Pepin 1995). In addition, (d) the mean temperature stratification (^{o}C m^{-1}) and (e) mean salinity stratification (psu m^{-1}) for the UML were calculated. The SML was defined as the homogeneous layer immediately below the sea surface where temperature was 1^{o}C less than that of surface waters (Laprise & Pepin 1995). The UML was the layer from the surface down to the depth where temperature was 1 ^{o}C higher than that of bottom waters. The BL was the layer from the end of the upper mixed layer down to the bottom or until 200m, wherever bottom depth was greater than 200 m. The breakdown of the water column into SML, UML and BL described better the well-stratified conditions at sea and provided a rough indication of the water circulation (e.g. UML depth was deeper in anticyclonic than in cyclonic areas).

We used the local regression model, LOESS (Cleveland 1979), in a predictive mode, to interpolate as a function of latitude and longitude, all the above-mentioned variables onto the anchovy and sardine locations (multiple R-squared >0.94). A neighbourhood of 40% of the data (span =0.4) was used here. The number of nearest-neighbours (i.e. size of the neighbourhood) usually expressed as percentage or span of the data points, is a smoothing parameter. LOESS models provide much flexibility because the model is fitted as a single smooth function of all the predictors.

The habitat selection of the two species was simplified by analysis of cumulative distribution functions (CDFs) following Perry & Smith (1994). We examined relationships between each species density (integrated echo per nautical mile) and each one of the hydrological variables, as well as bottom depth. The CDF (in %) for all variables f(t), were calculated as follows :

$$f(t)=100\cdot\frac{\sum_{h=1}^{L}\sum_{i=1}^{n_h}\frac{A_h}{n_h}I}{\sum_{h=1}^{L}\sum_{i=1}^{n_h}\frac{A_h}{n_h}} \quad \text{where } I=\begin{cases}1, & if\ x_{hi}<t\\ 0 & otherwise\end{cases}$$

and t is a level of each variable ; A_h is the area of stratum h ; n_h is the number of EDSU in stratum h ; x_{hi} is the value of the variable at the EDSU i in stratum h ; L is the number of strata. The CDF for anchovy or sardine integrated echo per mile, g(t), was calculated similarly :

$$g(t)=100\frac{\sum_{h=1}^{L}\sum_{i=1}^{n_h}\frac{A_h}{n_h}y_{hi}I}{\sum_{h=1}^{L}\sum_{i=1}^{n_h}\frac{A_h}{n_h}y_{hi}} \quad \text{where } I=\begin{cases}1, & if\ x_{hi}<t\\ 0 & otherwise\end{cases}$$

and y_{hi} is anchovy or sardine integrated echo in EDSU *i* in stratum *h*.

To examine variation in the parameters selection by anchovy or sardine, we compared CDFs of each variable, f(t), and anchovy or sardine echo in relation to the corresponding variable g(t). We calculated parameter

$$S=\sum_{t=1}^{t}\left[f(t)-g(t)\right]$$

for each variable. S compares average available variable to the average variable selected by anchovy or sardine. Positive values of S indicated that anchovy or sardine select high values within the ranges studied (SWAIN & KRAMER, 1995). We used a Kolmogorov-Smirnov type of statistic to test the significance of variable selection. The test statistic D was defined

$$D=\max\left|f(t)-g(t)\right|$$

(maximum absolute vertical distance) when f(t) and g(t) were the two functions compared. Significance was assessed using randomisation tests (PERRY & SMITH, 1994). All statistical inferences were based on a 0.05 significance level.

TABLE 1

Northern Aegean Sea. The hydrological characteristics of the water column in June 1995 and June 1996. Avg.: Average values, s.d.: standard deviation, Max: maximum value, Min: minimum value, SML: surface mixed layer, UML: upper mixed layer, BL: bottom layer (see text for layer definition).

		June 1995				**June 1996**			
	Layer	**Avg.**	**s.d.**	**Max**	**Min**	**Avg**	**s.d.**	**Max**	**Min**
Depth (m)	SML	9.15	1.86	12.51	5.08	8.23	2.05	11.63	4.61
	Uml	35.51	7.45	48.17	16.93	25.55	4.70	35.83	19.59
Mean Temperature (^{0}C)	Sml	24.30	0.58	25.06	23.01	21.93	0.86	24.47	20.00
	Uml	19.57	0.64	21.38	18.13	19.04	0.44	19.89	18.04
	Bl	14.38	0.41	15.47	13.74	12.86	0.24	13.58	12.31
Mean Salinity (psu)	Sml	34.66	1.11	36.07	32.46	33.89	1.19	35.33	31.05
	Uml	36.55	0.88	37.97	34.65	35.43	0.93	37.07	33.86
	Bl	38.52	0.22	39.01	37.75	38.24	0.22	38.64	37.67
Temperature stratification (^{o}Cm^{-1})	Uml	-0.31	0.07	-0.20	-0.62	-0.35	0.09	-0.22	-0.58
Salinity stratification (psu m^{-1})	UML	0.13	0.06	0.38	0.07	0.18	0.06	0.33	0.08

RESULTS

The water column in the North Aegean Sea presented typical spring-to-early summer conditions. It was generally well stratified during both surveys (SOMARAKIS et al., 2002). The upper water column as well as the bottom layer was generally warmer and more saline in 1995 than in 1996 (Table 1). Acoustic data were used to estimate the anchovy and sardine biomass in the area, which was similar for the two years (EPET, 1996[1] ; MACHIAS & SOMARAKIS, 1997).

Distribution and abundance maps of anchovy and sardine (Fig. 2) showed that, in the Thracian Sea, the main concentrations of both species generally occurred between the islands of Thasos and Samothraki. High numbers for both species were also recorded between the island of Thasos and the Athos peninsula (Strymonikos Gulf), however anchovy abundance was lower and fish distributed more inshore in Strymonikos Gulf during June 1996 when compared to June 1995 (Fig. 2d). In the Thermaikos Gulf, anchovy distribution consisted of two major groups, one in the inner and another one in the outer part of the Gulf, whereas the distribution of sardine comprised many small clusters (Fig. 2).

Analysis of the CDFs revealed positive associations of anchovy with SML depth, UML depth and BL temperature at a significant level (Table 2, Fig. 3). These results were indicative of a higher probability of occurrence for anchovy in water columns characterized by deeper surface and upper mixed layers. Anchovy affinity to warmer waters below the thermocline (BL) was marginally significant (p=0.049, Table 2). Sardine showed a strong positive relationship ($p << 0.01$) with SML depth, UML depth, SML temperature, UML temperature and BL temperature (Table 2, Fig. 3). Hence, in contrast to anchovy, sardine was clearly associated with warmer waters. Moreover sardine showed a negative relationship with bottom depth (Table 2, Fig. 3) indicating a selection for shallow waters. Salinity and stratification parameters did not exhibit statistically significant effects (Table 2).

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[1] EPET (1996). Development of Greek Fisheries. EPET 125, II/94, Final Report.

TABLE 2

Indices of parameter selection by species. S: index of parameter selection; D: test statistic; p-value: probability of statistical significance of parameter selection based on the randomization test described in the text. SML: surface mixed layer; UML: upper mixed layer; BL: bottom layer.

Parameters	Layer	Anchovy			Sardine		
		S	D	p-value	S	D	p-value
Bottom Depth (m)		-68.63	11.26	0.629	-123.33	8.75	0.018
Depth of SML (m)		117.23	20.06	0.016	69.52	12.10	0.004
Depth of UML (m)		103.48	18.78	0.035	93.88	11.58	0.006
Temperature (°C)	Sml	169.63	16.82	0.121	211.47	20.13	0.000
	Uml	43.91	8.92	0.853	74.23	12.87	0.000
	Bl	131.81	17.62	0.049	193.93	23.87	0.000
Salinity (psu)	Sml	-2.75	6.70	0.992	-20.37	7.90	0.058
	Uml	6.91	16.84	0.117	6.44	4.75	0.445
	Bl	-11.33	13.21	0.463	15.73	8.13	0.053
Temperature stratification (°C m^{-1})	Uml	-77.65	11.43	0.605	-54.24	6.41	0.170
Salinity stratification (psu m^{-1})	Uml	-80.20	12.69	0.550	-35.59	7.32	0.105

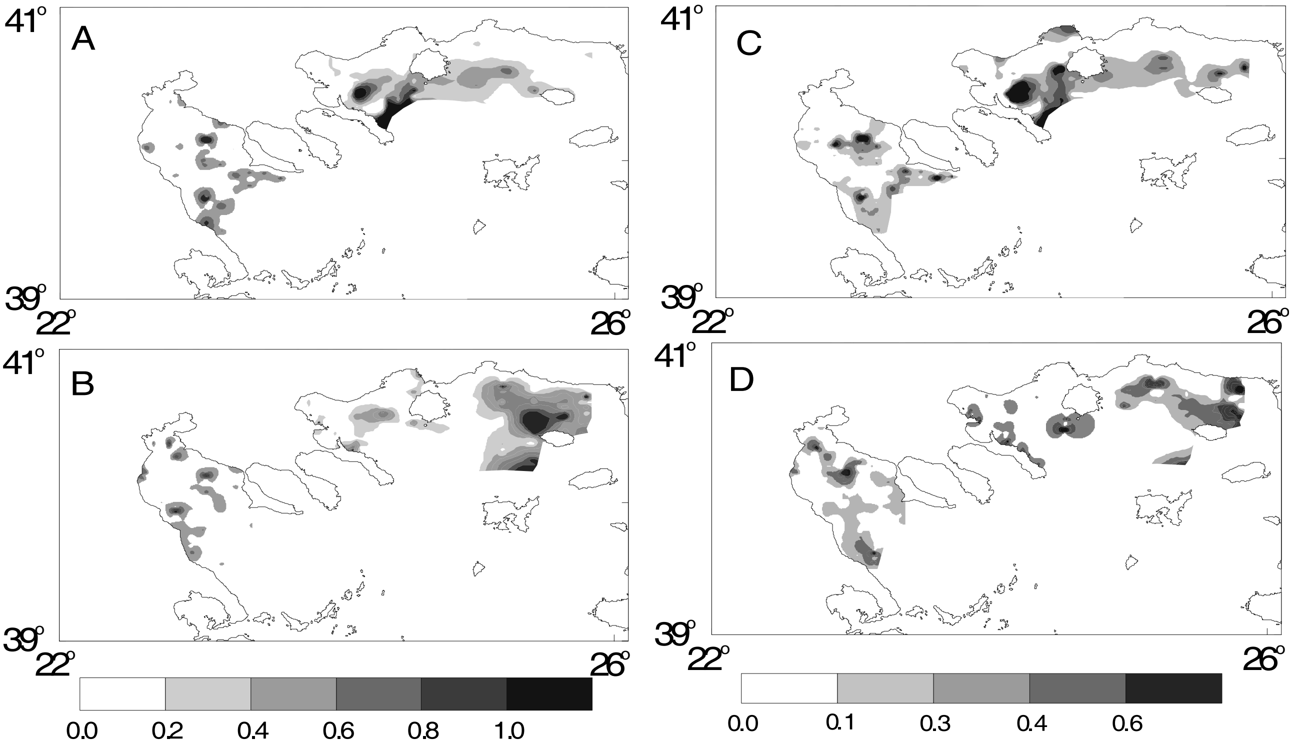

Fig. 2. – Contour maps of fish acoustic cross section (in md) in the Northern Aegean Sea. (A) Sardine distribution in June 1995, (B) Sardine distribution in June 1996, (C) Anchovy distribution in June 1995, and (D) Anchovy distribution in June 1996.

DISCUSSION

The present study showed a high concentration for both anchovy and sardine in the waters between the islands of Thasos and Samothraki, as well as the island of Thasos and the Athos peninsula. These areas were characterized by the presence of two anticyclonic systems : one in the Samothraki plateau (the Samothraki gyre) and another one in the Strymonikos Gulf (SOMARAKIS *et al.* 2002). These gyres are an almost permanent feature in the area during early summer and are coupled with a cyclonic system located south of the island of Thasos, the overall circulation being mainly determined by the presence of the Limnos-Imvros stream, which carries waters of Black Sea origin onto the Samothraki plateau (SOMARAKIS et al., 2002). Deeper surface and upper mixed layers characterize the anticyclonic gyres due to the tendency of isopycnals to move downward in down-welling areas in contrast to cyclonic (up-welling) areas where the isopycnals tend to move upwards (POND & PICKARD, 1983). The association of anchovy and sardine with anticyclones was shown by the significant relationships with deeper SMLs and UMLs (Table 2). These anticyclonic gyres are plankton retention areas and characterized by high concentrations of mesozooplankton (SOMARAKIS, 1999), i.e. high food availability for small pelagic fish. Such structures are also known to entrain fish eggs and larvae and restrict their dispersal (HEATH, 1992). Early summer is the spawning period of anchovy in Greek waters (SOMARAKIS, 1999), thus, selection by spawning adults of areas of favourable feeding conditions within gyres, would also be favourable for their spawn, because of retention and the reduced offshore dispersal (BLAXTER & HUNTER, 1982).

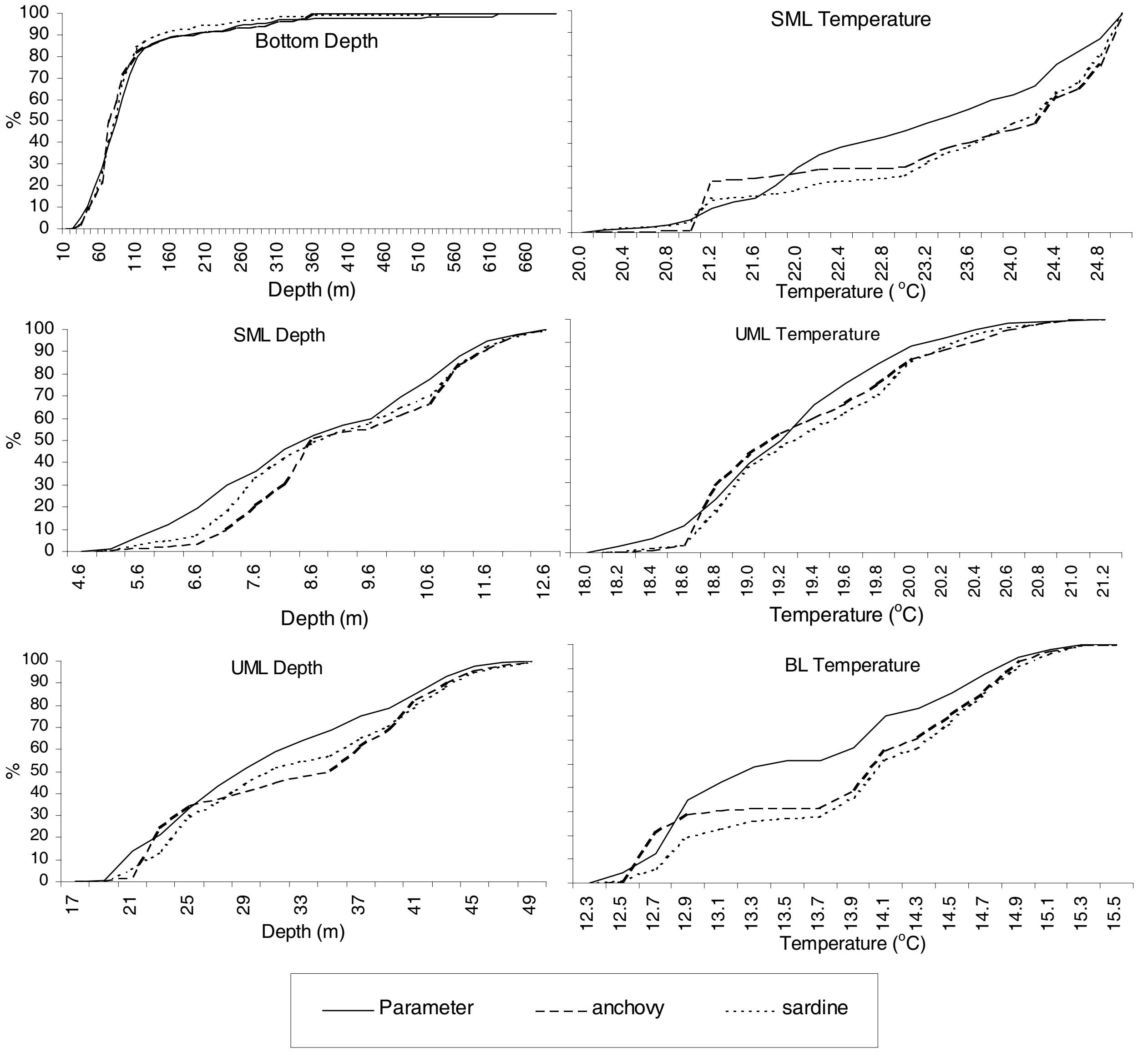

Fig. 3. – Cumulative distribution functions of bottom depth, significant hydrological parameters and anchovy/ sardine backscattering cross-section in relation to the available values of the parameters. SML : surface mixed layer ; UML : upper mixed layer ; BL : bottom layer.

In the Thermaikos Gulf, which is a semi-enclosed gulf, fish were generally distributed in many small clusters covering most parts of the gulf. The degree of enclosure of an area is significantly related to higher spatial patchiness for pelagic resources in the Greek seas, as has been shown by a recent study using geostatistical techniques (GIANNOULAKI et al., 2002).

Within the range of available temperatures, sardine was further selective for warm waters, which was not the case for anchovy. Sardine spawns during winter, whereas during summer it is characterised by fast somatic growth and fat deposition (SARDINE, 2001[2]). Temperature accelerates growth, within the natural thermal range experienced by the species in its habitat (URSIN, 1979). Hence sardine`s selection for warm waters is probably related to growth optimisation.

Another significant relationship for sardine was its affinity to shallow waters. Inshore waters are the preferred habitat for age-0 fish, which dominate the sardine population during early summer (SARDINE, 2001). Close association of sardine to shallow waters has also been reported for *Sardinops sagax* in the Southern Ben-

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[2] SARDINE 2001: Evaluation of the Southern Greek Sardine Stocks, No 98/039. Final Report.

guela up-welling region (Barange & Hampton, 1997) and *Sardina pilchardus pilchardus* in the Bay of Biscay (Scalabrin & Masse, 1993).

The present study is the first attempt to relate the spatial distribution of anchovy and sardine to hydrology in the Northern Aegean Sea. It highlights the significance of environmental regimes in determining population patterns in space. Further investigations on the spatial patterns of these planktivorous fish should address the effect of food availability, which controls both their growth and reproduction (Freon & Misund, 1999).

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PCBs and organochlorine pesticide residues in eggs of threatened colonial charadriiform species (Aves, Charadriiformes) from wetlands of international importance in northeastern Greece

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ABSTRACT. The levels of eight PCB congeners (IUPAC 8, 20, 28, 52, 101, 118, 138 and 180) and 13 organochlorine pesticides (α-HCH, β-HCH, Lindane, Heptachlor, Heptachlor epoxide, Aldrin, Dieldrin, Endrin, 2,4'-DDT, 2,4'-DDD, 4,4'-DDT 4,4'-DDD and 4,4'-DDE) were measured in eggs of Mediterranean gulls (*Larus melanocephalus*) (*Lm*), avocets (*Recurvirostra avosetta*) (*Ra*) and common terns (*Sterna hirundo*) (*Sh*) collected at the Evros Delta (*Lm*, *Ra*), Porto Lagos (*Lm*) and Axios Delta (*Lm*, *Sh*), north-eastern Greece in 1997. All pollutants were detected in all areas and species, with the exception of Dieldrin in the Mediterranean gull. Percent levels of higher chlorinated PCB congeners (IUPAC 118, 138 and 180) were greater than other compounds in all species and areas, probably due to their bioaccumulative properties. Only the median concentrations of PCB 28 differed significantly among areas in Mediterranean gull eggs. Significant differences between Mediterranean gulls and avocets (Evros) were found with regard to PCB 138 and PCB 180, whereas differences between Mediterranean gulls and common terns (Axios) were found in all PCBs except PCB 8 and PCB 20. These differences were due to the different diets of the species studied. Maximum pesticide concentrations in all samples were below 50 ppb, except for ß-HCH and 2,4'-DDD, both of which predominated among all compounds in all areas and species. The same trend has been found in other waterbird species in Greece, suggesting a particular pollution pattern in the region. Significant differences in the median concentrations of most pesticides were found among areas in the Mediterranean gull. Such differences were also found between Mediterranean gulls and avocets and between Mediterranean gulls and common terns, again due to different feeding habits. Our results suggest that, in the wetlands of northeastern Greece, agrochemical sources dominate over industrial pollution. Pollutants still persist in Greek wetlands, but their levels are too low to have any adverse biological effect on the species studied.

KEY WORDS : Polychlorinated biphenyls, organochlorine pesticides, *Larus melanocephalus*, *Recurvirostra avosetta*, *Sterna hirundo*, Greek wetlands.

INTRODUCTION

Polychlorinated biphenyls (PCBs) and organochlorine pesticides (hereafter pesticides) are two groups of substances that have different chemical structure and applications. PCBs were extensively used as plasticizers, as additives in hydraulic and dielectric fluids in industry and as fire retardants. Numerous organochlorine compounds have been used as pesticides. Nevertheless, both groups of chemicals have high toxicity and persistence in the environment. Studies have shown that some compounds of both groups can negatively affect wildlife reproduction and population levels and/or (particularly PCBs) cause various embryonic deformities and mortality (GILBERTSON et al., 1991 ; YAMASHITA et al., 1993 ; CUSTER et al., 1999). Some of these substances can also pose threats to humans, especially at high levels, but also due to background exposure (LONGNECKER et al., 1997). Due to their lipophilic structure, both groups tend to bioaccumulate along food chains, and thus reach greater concentrations in higher-level consumers (TANABE et al., 1987 ; HARDING et al., 1997).

In Greece, pesticides and PCBs were banned before the mid-seventies, but studies have indicated that both groups persist in the Greek environment (ALBANIS et al., 1994 ; KONSTANTINOU et al., 2000 ; GOUTNER et al., 2001). Monitoring and comparative studies in multiple areas using higher trophic level receptors are scarce. However, Greek wetlands are of particular interest for such studies, as they a) support in their vicinity considerable human populations, who consume local resources such as water and fish and b) they also provide refuge to internationally important populations of wildlife, especially birds.

The levels of organochlorines in seabird eggs reflect the diet of the female and pollutant levels in body reserves, thus constituting a useful indicator of environmental contamination (PEARCE et al., 1989). Waterbirds are top predators in aquatic environments, and, especially fish-eating species, are suitable bioindicators (SCHARENBERG, 1991). Nevertheless, due to the complexity of the food chains and particularities in the response of each species to these chemicals, pollution studies must continue.

The aims of this study were : a) to investigate the occurrence of PCBs and pesticides in the eggs of some threatened waterbirds that represent different links in the food chain of Greek wetlands ; b) to find out whether these chemicals occur in levels threatening the survival of these species ; c) to obtain indirect information about the pollution of these birds' habitats, especially as all wetlands where we collected data are of international importance and protected by the Ramsar Convention.

MATERIAL AND METHODS

This study was carried out in wetlands of northeastern Greece (Fig. 1). The Evros Delta, at the Greek-Turkish border, is the easternmost Greek wetland (40°47’N, 26°05’E), extending over 11,000 ha, and with a great a variety of habitats (Babalonas, 1980). The river Evros, originating in Bulgaria, is the border between Greece and Turkey for about 200 km and receives considerable amounts of transboundary pollution. Porto Lagos (40°01’ N, 25°08’ E), is an area in a wide wetland complex including the shallow, polluted, brackish Lake Vistonis and multifarious coastal lagoons. The Axios Delta (40°30’N, 22°53’E) is part of an extensive wetland complex, situated at the west coast of Thermaikos Gulf (Kazantzidis et. al., 1997). This river originates in the former Yugoslavia and suffers considerable pollution, probably being the most highly polluted water body of northeastern Greece (Fytianos et al., 1986). All three wetlands are of international importance and protected by the Ramsar convention.

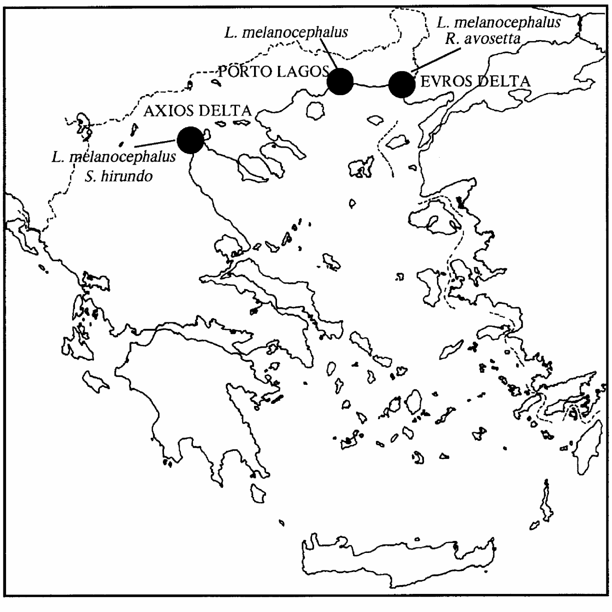

Fig. 1. – Map indicating the areas and species studied within the context of Greece.

Colonies were visited during the egg-laying period in April and May 1997. Under licence, we collected eggs of the Mediterranean gull (*Larus melanocephalus* Temminck 1820) (from the Evros and Axios Deltas and Porto Lagos), avocet (*Recusvirostra avosetta* L. 1758) (Evros Delta) and common tern (*Sterna hirundo* L. 1758) (Axios Delta) (Fig. 1). These species represent different links in the food chains of wetlands, as they have different diets. Eggs collected were either laid outside nests or from nests that were destroyed and abandoned by breeding birds due to flooding. Flooding may happen to these species' nests because they are made at close proximity to water. Eggs were opened in the laboratory on the day of collection and their contents were placed in chemically cleaned jars and deep frozen until analysis.

The following eight PCB congeners were analysed : PCB 8, 20, 28, 52, 101, 118, 138, 180. Of these congeners, five (PCB 28, 52, 101, 138, 180) belong to the group known as "target" or "indicator" PCBs (Bachour et al., 1998). The organochlorine pesticides analysed in this study were α-HCH, ß-HCH, Lindane, Heptachlor, Heptachlor epoxide, Aldrin, Dieldrin, Endrin, 2,4'-DDT, 2,4'-DDD, 4,4'-DDT 4,4'-DDD 4,4'-DDE.

PCB-standards were obtained from Dr. Ehrensdorfer GmbH laboratory in concentrations of 10 mg/ml. Supelco No. 4-9151 organochlorine pesticides mixture standard in isooctane was used in concentrations of mg/ml for the chromatographic analysis. All solvents used (hexane, acetone, petroleum ether), were pesticide residue analysis grade, purchased from Pestiscan (Labscan Ltd, Dublin, Ireland). Florisil (50-100 mesh) and sodium sulfate (pro-analysis) were from Merck (Darmstadt, Germany).

The analytical procedures and chromatographic conditions used have been described in detail in other recent papers of the authors (Konstantinou et al., 2000 ; Goutner et al., 2001). Here we provide a brief outline of the respective methods. An aliquot of 5-10 g of homogenized egg contents was extracted using sodium sulphate and petroleum ether (1 :1) mixture.The centrifuged supernatant was evaporated in a rotary evaporator to 10 ml and lipids were then removed using sulfuric acid. The clean-up was completed by adsorption chromatography, eluting the colorless layer through a chromatography glass column. All solvents used for packing the column were degassed in sonication bath. The purified sample was evaporated in a rotary evaporator to ca. 5 ml and in gentle N_2 stream at 35°C to ca. 0.5 ml. Then samples were stored in silanized vials in a refrigerator (-20°C). Mean recoveries and method detection limits for each congener and compound are given in Konstantinou et al. (2000).

A Shimadzu 14B gas chromatograph equipped with a Ni 63 electron capture detector (ECD) was used for the organochlorine residue analysis. Helium was used as the carrier and nitrogen as the make-up gas. Pure reference standard solutions were used for instrument calibration, recovery, quantification and confirmation. The confirmation of organochlorine residues was performed by using a GC-MSD, QP 5000 Shimadzu equipped with DB-5 capillary column.

Concentrations of pollutants were not normally distributed, thus the median of each pollutant, and the median total concentrations of PCBs (hereafter ΣPCBs) and pesticides (Σpesticides) were compared. We used the Mann-Whitney U test to compare concentrations between species in the Evros and Axios Deltas and Kruskal-Wallis χ^2 test to compare concentrations in Mediterranean gull eggs from the three areas. We calculated the ratio Σpesticides/

TABLE 1

PCB and organochlorine pesticide concentrations (ppb wet weight) in charadriiform eggs from Greek wetlands (< d. l.: below detection limits); n.s.: not significant

	EVROS DELTA (EV)										AXIOS DELTA (AD)										PORTO LAGOS (PL)				ALL WETLANDS	
	L. melanocephalus (N = 15)				R. avosetta (N = 20)				Statistics		*L. melanocephalus* (N = 15)				*S. hirundo* (N = 13)				Statistics		*L. melanocephalus* (N = 13)				L. melanocephalus	
	Mean	**Median**	**Min**	**Max**	**Mean**	**Median**	**Min**	**Max**	**Z**	**P**	**Mean**	**Median**	**Min**	**Max**	**Mean**	**Median**	**Min**	**Max**	**Z**	**P**	**Mean**	**Median**	**Min**	**Max**	**K-Wallis χ^2**	**P**
PCBs																										
PCB8	1	< d. l.	< d. l.	8	1	< d. l.	< d. l.	4	-0.22	n.s.	1	< d. l.	< d. l.	3	< d. l.	< d. l.	< d. l.	< d. l.	-2.50	n.s.	1	< d. l.	< d. l.	3	1.34	n.s.
PCB20	1	1	< d. l.	3	1	1	< d. l.	3	-0.03	n.s.	< d. l.	< d. l.	< d. l.	2	1	1	< d. l.	2	-1.33	n.s.	1	1	< d. l.	3	2.87	n.s.
PCB28	6	3	< d. l.	36	4	4	< d. l.	11	-0.83	n.s.	2	1	< d. l.	4	10	9	< d. l.	22	-3.16	0.002	2	2	< d. l.	6	6.59	0.037
PCB52	2	2	< d. l.	6	5	2	1	45	-1.00	n.s.	1	1	< d. l.	3	4	5	< d. l.	10	-2.83	0.005	2	2	< d. l.	3	0.72	n.s.
PCB101	1	1	< d. l.	5	2	2	1	3	-1.20	n.s.	2	1	< d. l.	9	7	6	4	12	-4.08	< 0.001	6	6	< d. l.	17	1.34	n.s.
PCB118	10	7	< d. l.	28	6	6	< d. l.	11	-0.90	n.s.	11	4	< d. l.	66	30	26	2	69	-3.30	< 0.001	7	< d. l.	< d. l.	41	2.57	n.s.
PCB138	26	20	7	115	6	5	3	14	-4.60	< 0.001	12	11	< d. l.	36	30	25	14	68	-3.52	< 0.001	21	21	< d. l.	42	4.54	n.s.
PCB180	10	8	1	33	1	1	< d. l.	3	-4.52	< 0.001	7	3	1	31	13	12	7	27	-3.06	0.002	5	4	< d. l.	16	8.97	n.s.
ΣPCBs	57	54	19	152	26	25	11	54	-3.60	< 0.001	35	32	4	132	95	85	52	173	-3.66	< 0.001	45	43	3	78	4.99	n.s.
Pesticides																										
Σ-BHC	1	< d. l.	< d. l.	7	< d. l.	< d. l.	< d. l.	1	-1.92	0.055	3	< d. l.	< d. l.	47	1	1	< d. l.	3	-3.49	< 0.001	< d. l.	< d. l.	< d. l.	1	0.19	n.s.
Σ-BHC	203	113	3	774	76	61	16	277	-2.63	0.008	85	85	< d. l.	149	122	127	24	243	-1.40	n.s.	76	84	22	115	2.94	n.s.
Lindane	1	< d. l.	< d. l.	9	1	< d. l.	< d. l.	2	-2.13	0.034	< d. l.	< d. l.	< d. l.	< d. l.	1	< d. l.	< d. l.	4	-3.52	< 0.001	< d. l.	< d. l.	< d. l.	1	4.21	n.s.
Aldrin	< d. l.	< d. l.	< d. l.	2	< d. l.	< d. l.	< d. l.	1	-0.18	n.s.	< d. l.	< d. l.	< d. l.	< d. l.	< d. l.	< d. l.	< d. l.	1	-0.23	n.s.	< d. l.	< d. l.	< d. l.	1	9.40	0.009
Dieldrin	< d. l.	< d. l.	< d. l.	< d. l.	1	< d. l.	< d. l.	20	-2.51	0.012	< d. l.	< d. l.	< d. l.	< d. l.	< d. l.	< d. l.	< d. l.	1	-2.27	0.023	< d. l.	< d. l.	< d. l.	< d. l.	-	-
Endrin	1	< d. l.	< d. l.	7	2	1	< d. l.	8	-1.95	0.051	1	1	< d. l.	6	2	2	< d. l.	4	-3.09	0.002	1	< d. l.	< d. l.	9	7.79	0.020
Heptachlor	< d. l.	< d. l.	< d. l.	3	< d. l.	< d. l.	< d. l.	1	-1.13	n.s.	< d. l.	< d. l.	< d. l.	2	< d. l.	< d. l.	< d. l.	1	-0.70	n.s.	< d. l.	< d. l.	< d. l.	1	3.64	n.s.
Heptachlor epox.	12	11	< d. l.	33	7	5	1	16	-2.53	0.011	7	3	1	49	12	12	6	19	-3.34	< 0.001	5	4	2	10	14.14	< 0.001
4,4'-DDE	2	2	< d. l.	7	1	1	< d. l.	5	-2.47	0.014	1	1	< d. l.	7	3	3	< d. l.	7	-2.33	0.020	2	1	< d. l.	8	9.34	0.009
2,4'-DDD	112	25	11	735	252	266	1	694	-2.83	0.005	186	76	9	711	342	350	105	700	-2.42	0.016	26	24	3	73	7.08	0.029
2,4'-DDT	1	1	< d. l.	4	1	1	< d. l.	6	-0.50	n.s.	1	< d. l.	< d. l.	3	1	1	< d. l.	2	-0.02	n.s.	1	< d. l.	< d. l.	4	9.55	0.009
4,4'-DDD	< d. l.	< d. l.	< d. l.	1	3	2	1	11	-5.06	< 0.001	< d. l.	< d. l.	< d. l.	< d. l.	1	< d. l.	< d. l.	8	-0.86	n.s.	1	< d. l.	< d. l.	3	1.57	n.s.
4,4'-DDT	2	< d. l.	< d. l.	11	5	3	< d. l.	44	-2.64	0.008	1	< d. l.	< d. l.	9	4	5	< d. l.	7	-3.27	0.001	2	< d. l.	< d. l.	7	2.18	n.s.
ΣOCs/ΣPCBs	8	4	1	33	16	13	1	44	-2.27	0.023	16	10	1	57	5	5	4	9	-1.73	n.s.	6	3	1	43	11.68	0.003

/ΣPCBs in samples as a measure of agrochemical vs. industrial pollution (Fossi et al., 1984 ; Pastor et al., 1995b) and then we compared the median values as previously specified. Separate cluster analyses for PCB and pesticide percentage levels were used to evaluate differences in pollution patterns among the areas studied. As linkage rule we used the “single linkage”, where the distance between two clusters is determined by the distance of the two closest objects (nearest neighbors) in the different clusters. This rule will string objects together to form clusters, and the resulting clusters tend to represent long chains. As distance measure we used the “Euclidean distance” that is the geometric distance in the multidimensional space. Euclidean distances are computed from raw data, and this has certain advantages, as the distance between any two objects is not affected by the addition of new objects, which may be outliers, to the analysis (Statistica, 1999).

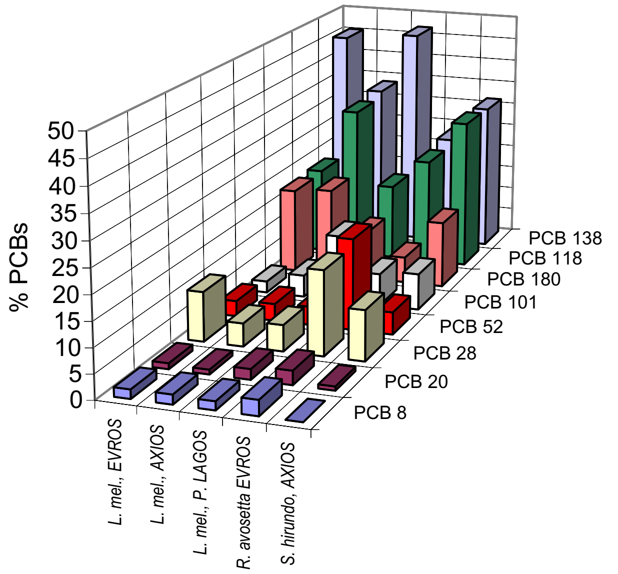

Fig. 2. – Fingerprint of PCB congeners (% of total concentration in each egg sample) detected in the charadriiform species studied in three Greek wetlands.

RESULTS

Polychlorinated biphenyls

With the exception of PCB 8, which was not detected in common tern eggs in the Axios Delta, all other congeners analysed were detected in all species’ eggs. In the Evros Delta significant differences were found only in the median concentrations of PCB congeners 138 and 180 between Mediterranean gull and avocet egg samples, due to higher concentrations in the gull eggs (Table 1). In contrast, in the Axios Delta, the median concentrations of all congeners, except 8 and 20, were significantly different between Mediterranean gull and common tern egg samples. In this case, the concentrations of all congeners were higher in the common tern. The only congener with concentrations differing significantly among Mediterranean gull eggs from the three wetlands was PCB 28, showing highest levels in the Evros Delta. Of eight congeners analysed, the maximum levels of PCB 8, 28, 52, 138 and 180 were found in the Evros Delta. The maximum levels of PCB 118 were found in the Axios Delta, whereas of congeners 20 and 101 at Porto Lagos.

The proportions of congeners with a higher substitution pattern (118 and above) predominated in all species and areas, but some of the “lower” congeners occurred in relatively high concentrations, mostly in avocet eggs less so in common tern and Mediterranean gull eggs, resulting in characteristic fingerprints (Fig. 2).

Cluster analysis separated the pollution pattern of avocet eggs from all other samples. Another group included both species sampled in the Axios Delta, while a third joined the pollution patterns of Mediterranean gulls from the Evros Delta and Porto Lagos (Fig. 3).

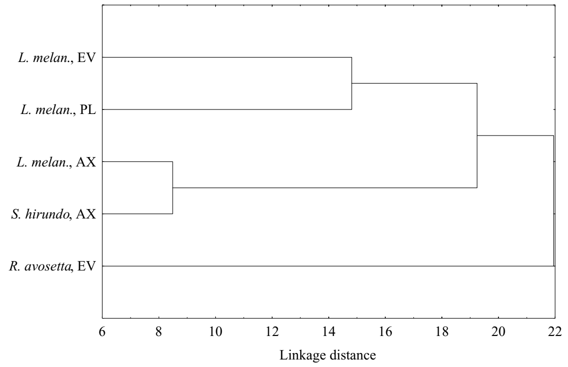

Fig. 3. – Cluster indicating the PCB pollution patterns of the species studied in the three wetlands. Euclidean distance measures and single linkage rule were used.

Organochlorine pesticides

Of the 13 compounds analysed in bird eggs, Dieldrin was below detection limits in Mediterranean gulls in all wetlands, but was detectable in the other two species. Median concentrations of most compounds (except Aldrin, Heptachlor and 2,4'-DDT) differed significantly between Mediterranean gulls and avocets in the Evros Delta (Table 1). Notably, of all samples, the maximum concentrations of Dieldrin, 2,4'-DDT, 4,4'-DDD and 4,4'-DDT were found in avocets. In the Axios Delta, the median concentrations of most compounds (except ß-HCH, Aldrin, Heptachlor 2,4'-DDT and 4,4'-DDD) were significantly different between Mediterranean gulls and common terns. The median concentrations of Aldrin, Endrin, Heptachlor epoxide, 4,4'-DDE, 2,4'-DDD and 2,4'-DDT differed significantly among Mediterranean gull eggs from the three different wetlands (Table 1). The maximum concentrations of six organochlorines, namely ß-HCH, Lindane, Aldrin, Heptachlor, 2,4'-DDD and 4,4'-DDT, were found in the Evros Delta, whereas maximum concentrations of α-HCH and Heptachlor epoxide were found in the Axios Delta, and maximum concentrations of Endrin, 4,4'-DDE, 2,4'-DDT and 4,4'-DDD were measured at Porto Lagos.

Of all compounds, the proportions of ß-HCH and 2,4'-DDD clearly predominated in all areas and in all three species studied, resulting in a characteristic fingerprint. In addition, levels of Heptachlor epoxide were higher than Heptachlor (Fig. 4).

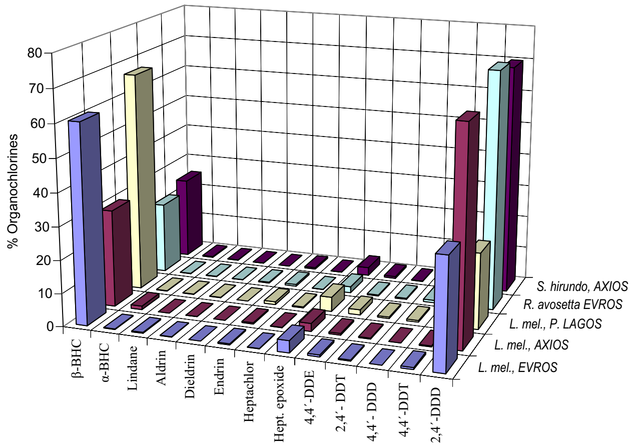

Fig. 4. – Fingerprint of organochlorine pesticides (% of total concentration in each egg sample) detected in the charadriiform species studied in three Greek wetlands.

Cluster analysis distinguished two groups : one joined the pollution patterns of Mediterranean gulls from the Evros Delta and Porto Lagos, while the other connected common terns and avocets, which were separate from the Mediterranean gulls of the Axios Delta (Fig. 5).

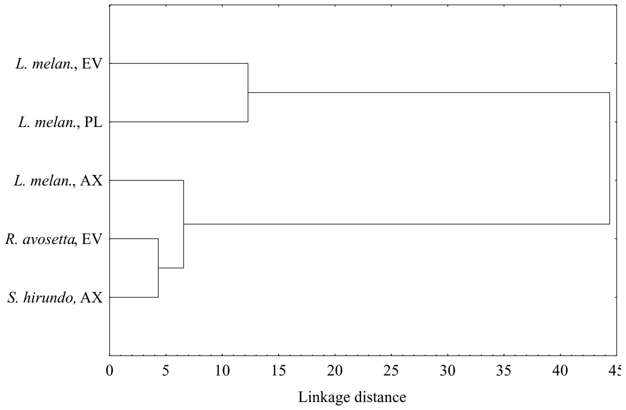

Fig. 5. – Cluster indicating the organochlorine pollution patterns of the species studied in the three wetlands. Eucledian distance measures and single linkage rule were used.

The medians of the ratio Spesticides/SPCBs varied from 2.62 (Mediterranean gull, P. Lagos) to 13.49 (avocet, Evros Delta). The difference of the medians of this ratio was significant between Mediterranean gulls and avocets and also among Mediterranean gulls from all areas (Table 1). Spearman Rank Correlations between Σpesticides and ΣPCBs for Mediterranean gulls (pairs between areas), for Mediterranean gull and avocet, and Mediterranean gull and common tern were all statistically insignificant.

DISCUSSION

Of PCBs detected in our samples, some mono- and di-ortho coplanar congeners such as 28, 118, 138, 180 were the most elevated in all species and areas. These congeners exhibit considerable bioaccumulation patterns and are persistent in the environment because of their substitution pattern (Metcalfe & Metcalfe, 1997). Congeners 118, 138, 180 have also been found in high concentrations in larids' eggs in other areas of the Mediterranean (Focardi et al., 1988 ; Pastor et al., 1995b).

The differences in median congener concentrations detected between Mediterranean gulls and avocets in the Evros Delta, and especially between Mediterranean gulls and common terns in the Axios Delta, were probably due to the different feeding habits of the species involved. Avocets are lower in the food chain than larids feeding mainly on invertebrates (Goutner, 1985 ; Focardi et al., 1988 ; Denker et al., 1994). The common tern is mainly piscivorous, whereas the Mediterranean gull's diet varies greatly among years and areas. It is mainly composed of insects and fish (Goutner, 1986), but may also include considerable amounts of plant material (Goutner, 1994). The similarity in PCB pollution of Mediterranean gull eggs from all study areas suggests dietary similarities during the study.

The pattern of pollution found by the cluster analysis, that is the grouping of the Axios Delta samples as a distinct cluster from that of the Mediterranean gull samples from the eastern part of the study area, together, may suggest different historical patterns of management regime of PCBs in the areas studied. The sources of PCB pollution at the Axios Delta have been transboundary and of municipal origin (Larsen & Fytianos, 1989), while the other areas' pollutant sources are unknown at present.

To compare the PCB levels found in this study with results of other studies, we multiplied by two the sum of PCB concentrations in the eggs of the three species sampled (Dirksen et al., 1995). In the avocet, the mean (median) concentration multiplied by two was 51 (50) ppb, in the common tern 189 (170) ppb, and in the Mediterranean gull 114 (109) ppb. In the Great Lakes' Herring Gulls (*Larus argentatus* Pontoppidan 1763), concentrations that have been associated with reduced hatching success are generally higher than 70 ppm (Gilman et al., 1977 ; Weseloh et al., 1979). In the Great Lakes' Double-crested Cormorants, *Phalacrocorax auritus* (Lesson 1831), total PCB means of c. 4 to 7 ppm were associated with live-deformities (hard tissue malformations, Yamashita et al., 1993), whereas in Massachusets, USA, total PCB means of 1.4-6.0 ppm were not associated with adverse biological effects in the common tern (Nisbet & Reynolds, 1984). Consequently, the contaminant levels found in this study seem to pose no threat to the populations of the waterbirds studied.

Although pesticides (with the exception of Lindane) were banned in Greece in 1972 (Albanis et al., 1994), most of them were detected in egg samples in our areas, though in low levels. The occurrence of pesticides in bird eggs seems also to be dependent on their feeding habits (Fasola et al., 1987). Nevertheless, the differences in median concentrations we detected between species in the same area or in the same species among areas, can only in part be attributed to different feeding habits. We suppose that Dieldrin and probably the other drins found in avocet and common tern eggs are accumulated during wintering or migration, as these species follow the eastern flyway to African wintering quarters. In the Axios Delta, drins were also found in eggs of other distant migrants, such as the little tern (*Sterna albifrons* Pallas 1764) and the Squacco heron (*Ardeola ralloides* Scopoli 1769) (ALBANIS et al., 1996 ; GOUTNER et al., 1997).

The elevated amounts of 2,4'-DDD in comparison to 4,4'-DDE are probably due to its presence in zooplankton and in the water column. Zooplankton possibly acquires DDTs from sediments or from the water column, where the DDD form constitutes the major fraction of DDTs (STRANBERG et al., 1998). Elevated 2,4'-DDD levels may indicate that this compound was a major constituent in a technical mixture used in the region. An important finding is that the characteristic similarity of pesticide fingerprints in all areas and species was also found in previous studies in Greece involving the cormorant, (*Phalacrocorax carbo* (L. 1758) and Audouin's gull (*Larus audouinii* Payraudeau 1826) (KONSTANTINOU et al., 2000 ; GOUTNER et al., 2001). These suggest a particular pattern of organochlorine pesticide pollution in Greece.

The higher levels of ß-HCH in all egg samples were probably due to the relatively high stability of this compound against metabolism (OXYNOS et al., 1993). Lindane is still used as seed and soil insecticide in various cultivations. Lindane levels were lower than those reported in waterbids in other studies, but ß-HCH levels (where analysed) were generally higher (FOSSI et al., 1984 ; FASOLA et al., 1998). Lindane is not harmful to birds, in contrast to Heptachlor and especially its metabolite Heptachlor epoxide, which are lethal for birds in concentrations ≤9 ppm (BLUS et al., 1985). Concentrations found in our egg samples did not seem to pose any threat to the birds studied. DDE is a compound that can lower the breeding productivity of waterbird populations by reducing eggshell thickness (BLUS, 1984 ; CUSTER et al., 1999). Levels of DDE that can affect eggshell thickness in the common tern are beyond 4 ppm (WESELOH et al., 1989). For the American avocet (*R. americana* J. F. Gmelin 1789), the presumptive adverse threshold of DDE in eggs is 3-8 ppm (ROBINSON et al., 1997). Thus, it seems that the DDE levels we found in our study are too low to be harmful for the birds involved.

The median ratio of Σpesticides/ΣPCBs was > 1 in the samples from all areas, denoting a dominance of agrochemical over industrial pollution in northeastern Greece. Similar results have been found in other studies in Greece and in the eastern Mediterranean and Black Sea regions (FOSSI et al., 1984 ; PASTOR et al., 1995a ; GOUTNER et al., 2001).

CONCLUSIONS

The most heavily polluted wetland area studied was the Evros Delta, where maximum concentrations of most pollutants were found in birds' eggs. Pollution patterns reflected the birds' different positions in the food chain. Levels of both pollutant groups were of the lowest reported, being rather a normal follow up of the ban of these substances in the mid-seventies, and were too low to have adverse effects on birds. The higher agrochemical pollution reflects the underdevelopment of industry in the region. The occurrence of compounds such as drins may reflect differences in bioaccumulation patterns due to different migration routes and/or wintering grounds of some species. Predominance of ß-HCH and 2,4-DDD' in all species' eggs and also in others studied in Greece (*P. carbo, L. audouinii*), suggests a particular pattern of agrochemical pollution in this region.

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The diet of nestlings of three Ardeidae species (Aves, Ciconiiformes) in the Axios Delta, Greece

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ABSTRACT. The diets of the little egret (*Egretta garzetta*), the night heron (*Nycticorax nycticorax*) and the squacco heron (*Ardeola ralloides)* were studied by analyzing nestling regurgitations collected during five breeding seasons (1988-1990 and 1994-1995) at a heronry in the Axios Delta (Northern Greece). In total, 267 regurgitations from little egrets, 247 from night herons and 19 from squacco herons (only in 1995) were collected and analyzed. Each prey item was identified to the lowest possible taxon. The dry mass of each prey taxon was also estimated from oven-dried prey specimens collected in the field.

At least 58 different prey taxa were identified among 5,108 items found in little egret regurgitations, at least 45 taxa among 2,373 items regurgitated by night herons and 12 taxa among 277 items from squacco herons regurgitations. Differences were detected between the three ardeid species in the proportion of each prey category. Little egret nestlings were mainly fed fish (39.6% by number) and insects (32.0%), but amphibians and fish were the most important groups by biomass (44.9% and 32.9% respectively). The proportions of prey categories varied significantly between years ($\chi^2_{12} = 922.91$, $p < 0.001$). The night heron nestlings were mainly fed insects and the crustacean *Triops cancriformis*, although the dry mass of the latter contributed little to the consumed biomass (4.0% compared to the 37.9% of insects). Small mammals and reptiles were included in the diet of the young night herons, while the fish they ate were much bigger than those consumed by little egret nestlings. The proportions of the night herons' main prey categories varied significantly between years ($\chi^2_{24} = 598.67$, $p < 0.001$). Squacco heron chicks were fed mainly insects (50.9%) and amphibians (31.8%), the latter being more important by biomass (73.6%). In a cluster analysis, diet of young little egrets and night herons showed greater similarity from 1988 to 1990 than between 1994 and 1995, suggesting temporal changes in prey use. Study years tended to group separately for each species, but those of the little egret were more scattered in the cluster than the night heron's, thus reflecting greater prey use variability. The diet of the squacco heron was similar to that of the little egret when prey type frequencies were considered, but closer to the night heron's by dry mass. The dry mass differed significantly between the species ($\chi^2 = 87.39$, $p < 0.001$, Kruskal-Wallis test). This dietary segregation may be a mechanism that reduces competition among these ardeid species, especially when prey is limited.

KEY WORDS : Ardeidae, diet, Axios, little egret, night heron, squacco heron

INTRODUCTION

The little egret (*Egretta garzetta* Linnaeus, 1766), the night heron (*Nycticorax nycticorax* Linnaeus, 1758) and the squacco heron (*Ardeola ralloides* Scopoli, 1769) breed in a multi-species colony in the Axios Delta. These ardeid species share certain foraging habitats, such as freshwater marshes and rice fields, but exploit them in different proportions (FASOLA, 1994). The little egret exploits all aquatic habitats in the Axios Delta, including salt marshes and the seashore, whereas the other two herons forage only in freshwater habitats. Thus, although the three sympatric species may be considered generalists, they seem to be separated ecologically by their selection of different prey type or size.

The diet of the three study species is poorly known in Greece. Studies concerning the diet of the little egret are available from Kerkini Lake (TSACHALIDIS, 1990) and the Axios Delta (FASOLA 1994 ; KAZANTZIDIS et al., 1996 ; KAZANTZIDIS, 1998). The diet of the night heron has been studied at the Kerkini Lake (BIRTSAS, 2002), while the squacco heron data presented here are the first published for Greece. The diet of the three ardeid species has been studied in more detail in other Mediterranean countries : France (VALVERDE, 1956 ; HAFNER, 1977 ; VOISIN, 1991), Italy (MOLTONI, 1936 ; FASOLA et al., 1981, FASOLA et al., 1993 ; FASOLA, 1994), Spain (GONZALES-MARTIN & GONZALES-SOLIS, 1990 ; PEREZ et. al., 1991 ; MARTINEZ et. al., 1992) and Israel (ASHKENAZI and YOM-TOV, 1996). Although, the diet of various herons has often been studied in the western Palearctic multiyear studies comparing the diet of sympatric species are generally scarce. The objectives of this study were to describe the diets of these three ardeid species, and to compare them between species and years. For the squacco heron we have data from 1995 only, and are therefore unable to present a comparison between years.

MATERIAL AND METHODS

The study was carried out in the Axios Delta, northern Greece (40° 30' N, 22° 53' E), part of a large wetland complex situated in the western part of Thermaikos Gulf (N. Aegean Sea). It extends over 68.7 km^2 and comprises estuarine and deltaic areas, with a variety of natural and man-made habitats such as salt and fresh water marshes, ricefields, vegetated islets, river banks, tamarisk shrubland, and sandy shores (ATHANASSIOU, unpublished data). This wetland complex is of international importance according to the Ramsar convention, and a Special Protected Area.

The heron colony where the regurgitations were collected is located in a riverine forest of Tamarisks (*Tamarix* spp.), Willows (*Salix* spp.) and Alders (*Alnus glutinosa*), on an island near the mouth of the River Axios. This colony is the second biggest in Greece in terms of both number of breeding pairs and number of species (KAZANTZIDIS, 1998). Other breeding species were great cormorants (*Phalacrocorax carbo* Linnaeus, 1758), pygmy cormorants (*Phalacrocorax pygmaeus* Pallas, 1773), spoonbills (*Platalea leucorodia* Linnaeus, 1758) and glossy ibises (*Plegadis falcinellus* Linnaeus, 1766*)*. The total breeding population of the colony ranged, in recent years from 1,100 to 2,000 pairs (KAZANTZIDIS, 1998).

Heron diet was studied by analyzing nestling regurgitations collected during the breeding seasons of 1988-1990 and 1994-1995 (squacco heron data were collected only in 1995). Regurgitations were collected throughout each nestling period, on a weekly basis, from April until early July. After collection, the regurgitations were refrigerated until analysis. In order to estimate the quantitative contribution of each prey type, the dry mass of each prey taxon was measured. Samples from each prey type were collected during the nestling period from the main feeding habitats (ricefields, irrigation canals, salt- and freshwater marshes). Dry mass was measured by weighing each prey taxon dried in an electric oven for 48 hours at approximately 70°C. Intact items found in the regurgitations were also used for the estimation of their dry mass.

In order to compare the frequencies of items from the different prey categories between years, we used Chi-square tests. We used Mann-Whitney U-tests and Kruskal-Wallis χ^2 tests to compare median prey dry mass between the study species. In order to identify the diet similarities or differences between the three study species and the years of the study, a cluster analysis was applied to the proportions of main prey categories in each study species X year combination.

RESULTS

We collected 533 regurgitations in total (267 from little egrets, 247 from night herons and 19 from squacco herons). In these we identified 7,758 prey items with a total dry mass of 3,207 g belonging to 74 different taxa (Appendix 1).

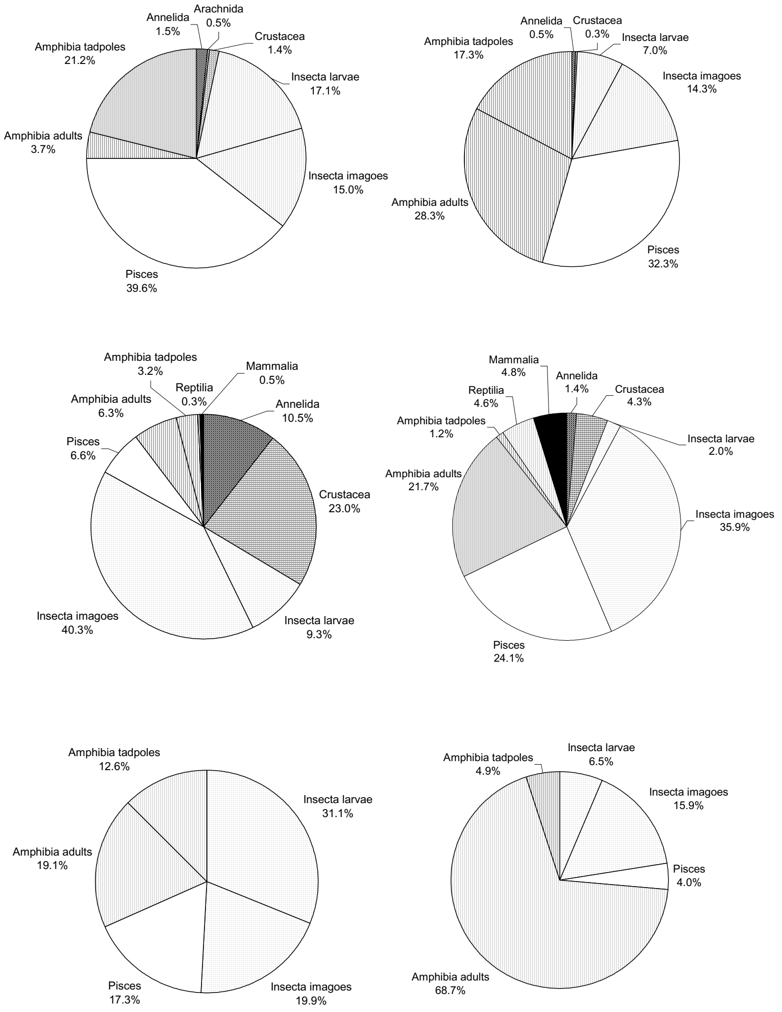

Fig. 1. – The diets of nestlings of the little egret (top), night heron (middle) and squacco heron (bottom) by number (left) and by dry mass (right) of the main prey categories.

Little egret

At least 58 different taxa were identified among 5,108 prey items (1,499 g dry mass). By number, fish were the most important prey category (39.6%), followed by insects (32.1%) and amphibians (24.9%) (Fig.1). From a total of 22 fish species identified, *Aphanius fasciatus*, *Gambusia affinis* and *Gasterosteus aculeatus* represented 85.5% of all items. Of at least 27 species of insects, the majority were larvae of Odonata, Dytiscidae and Hydrophilidae (94.3% of all insect larvae). Among imagoes, *Gryllotalpa gryllotalpa* and *Zygoptera* spp. (Odonata) prevailed, making up 72.2% of all items. Tadpoles predominated among amphibians (85.0%), while the adults were mainly *Rana ridibunda* and *Hyla arborea*. annelids (*Lumbricus terrestris*), arachnids (mainly *Argyroneta aquatica*) and crustaceans (Gammaridae and the phyllopod *Triops cancriformis*) contributed less to the diet and were not present in all study years (Figs 1-2).

By dry mass, amphibians and fish were the most important food resources (45.6% and 32.3%, respectively, of the total dry mass) (Fig. 1). Each of the other prey categories contributed less than 1% (Fig. 1). The average dry mass of all prey items was 0.29g ± 0.72 (Table 1).

TABLE 1

The average dry mass (± SD) of the main prey categories consumed by the three ardeid species

Prey type	Little Egret	Night Heron	Squacco Heron	Kruskal-Wallis χ^2 [1]
Insects	0.20 ± 0.26	0.50 ± 0.31	0.27 ± 0.29	379.4
Fish	0.24 ± 0.96	2.37 ± 5.43	0.14 ± 0.13	221.5
Amphibians	0.53 ± 0.69	1.56 ± 0.93	1.43 ± 0.97	337.2
Others	0.03 ± 0.04	0.11 ± 0.01	0	-17.38[2]
Total	0.29 ± 0.72	0.65 ± 1.7	0.62 ± 0.81	87.39

1. $p < 0.0001$ in all cases.
2. Mann-Whitney U-test was applied. Annelids, crustaceans and arachnids only are included.

Diet composition differed between years (χ^2_{12} = 922.91, $p<0.001$). Within the main prey categories, the differences were also significant (fish : χ^2_4 = 598.72, $p<0.001$; insects : χ^2_4 = 369.65, $p < 0.001$; amphibians : χ^2_4 = 159.6, $p<0.001$) (Fig. 2).

Night heron

At least 45 different taxa were found among 2,373 prey items (1,537 g dry mass). Insects (at least 22 taxa) were by far the most numerous prey (49.6%), followed by crustaceans (exclusively *T. cancriformis*) (23.1%), amphibians (9.5%) and fish (6.6%). Annelids (*Lumbricidae*) also contributed in relatively high proportion (10.5% by number), although they appeared only in three out of five study years (Figs 1-2). Reptiles (*Natrix natrix* and *Emys orbicularis*) and mammals (*Arvicola terrestis, Microtus arvalis*, *Rattus* spp.) were also found in low proportions (Figs 1-2). The majority of insects were imagoes (81.3% of all insect items), predominantly *G. gryllotalpa* (77.8% of all imagoes and 31.3% of all prey items). Amphibians were mainly adult *R. ridibunda* (66.7%). Of 13 fish species found in the regurgitations, *Leuciscus cephalus*, *Carassius auratus* and *Lepomis gibbosus* were the most numerous (58.3% of all fish items). By dry mass, insects were the most important category (37.9%), followed by fish (24.1%) and adult amphibians (21.7%) (Fig. 1). The average dry mass of all prey items was 0.65 g ± 1.7 (Table 1).

Diet composition differed between years, both considering all prey types (χ^2_{24} = 598.67, $p<0.001$), and within each of the main prey categories (fish : χ^2_4 = 41.45, $p<0.05$; insects : χ^2_4 = 184.36, $p<0.001$; amphibians : χ^2_4 = 102.48, $p<0.001$). The number of mammals and reptiles did not differ between years (χ^2_4 = 8.07, p = 0.089 and χ^2_4 = 2.56, p = 0.633, respectively) (Fig. 2).

Squacco heron

The 277 prey items found (171 g dry mass) belonged to at least 12 different taxa. By number insects (eight species and 50.9% of all prey items) were the most important prey category, followed by amphibians (31.8%) and fish (17.3%) (Fig. 1). The majority of insects (61.0%) were larvae (mainly Odonata, Dytiscidae and Hydrophilidae), while imagoes were mainly *G. gryllotalpa* (65.5% of all imagoes). Amphibians were mainly adults of *R. ridibunda* (60.2% of all amphibians). Of the three fish species found, *G. affinis* was the most numerous (81.3%).

By dry mass, *R. ridibunda* was the most important prey taxon (68.7% of the total dry mass), followed by *G. gryllotalpa* (15.9%), whereas fish represented only 4.0% of the total (Fig. 1). The average dry mass of all prey items was 0.62g ± 0.81 (Table 1).

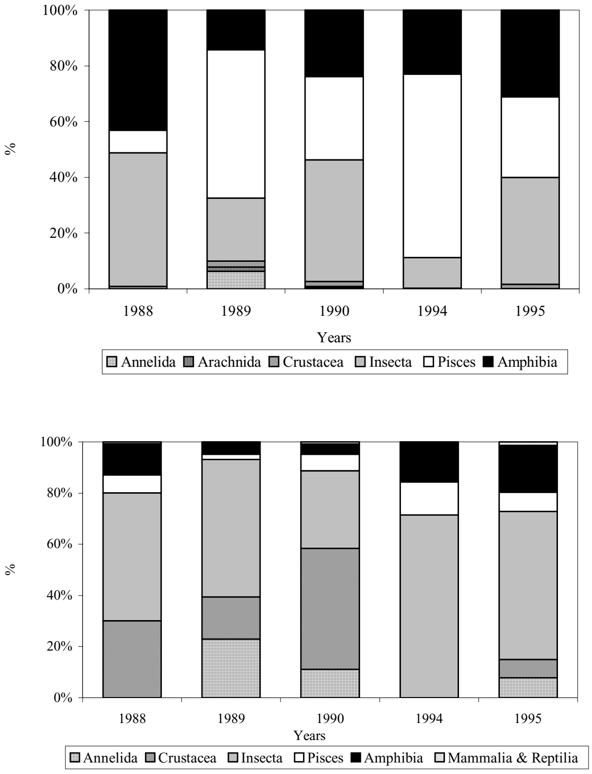

Fig. 2. – The yearly composition of the diet (by number of the main prey categories) of the little egrets (top) and night herons (bottom).

Interspecific comparison

The little egret had a more diverse diet than the other two species, and preyed mainly upon small-sized prey. Both fish and amphibians (mainly tadpoles) eaten by little egrets were small-sized (average dry masses of 0.24g ± 0.96, and 0.21g ± 0.69 respectively).

The median prey dry mass differed significantly between the three ardeid species as a result of the smaller average dry mass of prey of the little egret (Table 1).

The night herons took insects, fish and amphibians of larger size than those taken by the other two species (Table 1). In addition, night herons fed on large prey such as reptiles and mammals, which were absent from the diet of the little egret and the squacco heron (Fig. 1, Appendix 1). Crustaceans (*T. cancriformis*) were also absent from the diet of these two species while they were common in the night heron's diet. This difference may be due to the absence of *T. cancriformis* from the foraging areas during the nestling period of the little egret and the squacco heron, but its availability to night herons, which start breeding at least two weeks earlier than the other two species (Fasola et al., 1981, Kazantzidis et al., 1997).

Of 74 different taxa identified in the nestlings' regurgitations, 37 were common to the three ardeid species while only four (namely *R. ridibunda*, Dytiscidae and Hydrophilidae larvae, and *G. gryllotalpa*) participated in proportions of more than 10% of all prey items in the diets of all three ardeid species.

The diets of the squacco heron and the little egret shared 11 species in common (Fig. 3, Appendix 1), while a higher resemblance was found between the diets of the little egret and the night heron (31 common species or taxa). Only nine species or taxa were common to the squacco and the night herons' diets.

Inter-year comparison

Differences between years were detected, and the diets of both the little egret and the night heron showed greater similarity from 1988 to 1990 than between 1994 and 1995, suggesting temporal changes in prey use (Figs 2-3). Study years tended to group separately for each species, but those of the little egret were more scattered in the cluster, indicating a greater prey use variability (Fig. 3).

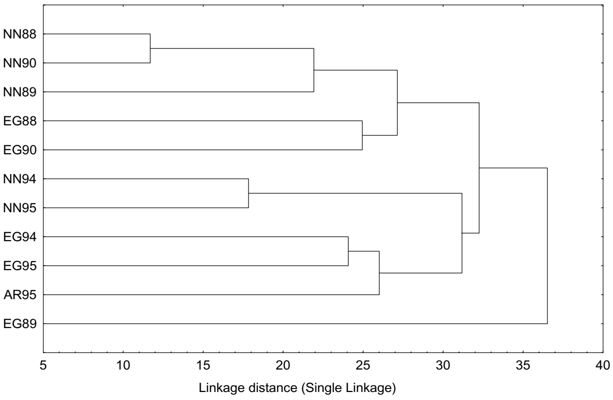

Fig. 3. – Comparison of the diet (by prey categories) between the three ardeid species and study years (EG : little egret, NN : night heron, AR : squacco heron).

DISCUSSION

The three ardeid species considered in this study had distinctive diets. Little egrets took a wide variety of prey types and fed mainly on small-sized fish, insects and tadpoles. Similar findings have also been reported from Kerkini Lake (Tsachalidis, 1990) although the size of fish there was larger (up to 9.3 cm) and *T. cancriformis* contributed to the diet in a higher proportion (up to 8.1%). In the Camargue, S. France, freshwater fish also predominated in the diet of little egrets' nestlings (Hafner, 1977 ; Kazantzidis et al., 1996). In Italy the contribution of fish to the diet was smaller, but still significant (28.07%) (Fasola et al., 1981). Generally, although differences have been detected even among different colonies of the same area, fish seems to be the most important prey for the little egret (Voisin, 1991).

Night herons fed heavily on insects (especially *G. gryllotalpa*), which were the most important prey category by both number and dry mass. *T. cancriformis* and annelids were present in only some years of the study. Fish and amphibians were not common (both less than 10% of all prey items). These findings differ from those of all other studies of this species' diet conducted in Greece and in other Mediterranean countries. Birtsas (2002) reported that in Kerkini Lake the nestlings' diet consisted mainly of fish (86.5%) and amphibians (12.1%), while insects represented only 1.5% of all prey items. Similarly, fish was the night heron's major food type (93.7%) in Extremadura, Spain, (Perez et al., 1991), in Israel (Ashkenazi & Yom-tov, 1996) and in Serbia (Laszlo 1986). Furthermore, Fasola et al. (1981, 1993) and Fasola (1994) reported that in various Italian colonies, fish (Cyprinidae) or amphibians dominated the diet, while insects were found in very low proportions. In the Camargue, night herons feed mostly on fish and coleopteran larvae (Valverde, 1956 ; Hafner, 1977). The great geographical variability in the night heron's diet probably reflects differences in prey availability in each breeding area and a great flexibility in prey use by this species.

The diet of the squacco heron at the Axios Delta is similar to that reported by Moltoni (1936), Cramp & Simmons (1977), Hafner (1977), Hancock & Kushlan (1984), Laszlo (1986) and Voisin (1991). In all of the above studies, insects or amphibians predominated by number, although amphibians or fish had greater dry mass. Differences between colonies were found in Italy (Fasola et al., 1993 ; Fasola 1994), where fish (Cyprinidae) was the most frequent prey type in two out of three heronries, whereas insects participated in small proportions in all three colonies.

Dietary differences between the years of our study also indicate that these ardeid species are opportunistic foragers, changing their diet from one year to the next according to prey abundance and availability. For example, crustaceans, which were taken by both the little egret and the night heron, were completely absent in 1994 from both species' diet, suggesting a decrease of crustacean population in that year. Where studies of more than one year are available, they report temporal differences. In 1970, little egrets in the Camargue preyed mainly on insects, while in 1971 fish and crustaceans were more frequent (more than 50%) (Hafner 1977). In the same study, no differences were detected in the proportions of prey types in the night and squacco herons.

The differences in prey taken by the three study species reflect mainly differences in their foraging habitats and distribution of prey. Little egrets were foraging in all available feeding habitats (Kazantzidis & Goutner, 1996), which may account for the high prey variation reported in this study. Night and squacco herons avoid open habitats and forage mainly in fresh water marshes and occasionally in ricefields, thus limiting the range of prey types they can capture. The differences in prey dry mass also indicate a dietary segregation between the ardeid species.

In conclusion, there is a dietary segregation between the three ardeid species with regard to both relative frequencies and dry mass of prey types. There is a partitioning of food resources by foraging habitats and/or choice of prey. This resource partitioning may be a mechanism that reduces competition among the species, especially when prey is limited.

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APPENDIX 1

The prey species (number of items) identified in the nestling regurgitations of the three ardeid species

Species	***Egretta garzetta***	***Nycticorax nycticorax***	***Ardeola ralloides***
Prey type			
INVERTEBRATES			
ANNELIDA			
Oligochaeta			
Lumbricidae	-	68	-
Lumbricus terrestris	79	149	
Allolopophora spp.	-	3	-
Eisenia foetida	-	30	-
ARTHROPODA			
Chelicerata			
Argyroneta aquatica	9	-	-
Pholcus phalangioides	1	-	-
Unidentified Arachnida	14	-	-
Crustacea			
Phillopoda			
Triops cancriformis	36	547	-
Amphipoda			
Gammaridae	32	-	-
Talitridae	2	-	-
Decapoda			
Palaemonidae	3	-	-
Insecta			
Odonata			
Larvae	328	31	35
Imagoes			
Zygoptera	276	22	5
Platycnemis spp.	2	-	-
Anisoptera	9	18	-
Aeshnidae	46	-	7
Libellulidae	30	-	-
Unidentified Odonata			
Orthoptera			
Acrididae	3	8	2
Tetrigidae	1	-	-
Tettigoniidae	3	-	-
Gryllotalpidae			
Gryllotalpa gryllotalpa	276	744	36
Unidentified Orthoptera	-	1	-
Dictyoptera - Mantodea	1	-	-
Hemiptera - Heteroptera			
Naucoridae	2	1	-
Llyocoris cimicoides	8	-	-
Notonectidae			
Notonecta glauca	5	-	-
Gerridae			
Gerris lacustris	9	-	-
Aquarius najas	1	-	-
Scutelleridae			
Eurygaster maura	1	-	-
Lygaeidae	-	2	-
Unidentified Hemiptera	7	5	2
Diptera			
Cyclorrhapha			
Tachinidae	1	-	-
Calliphoridae	1	-	-
Syrphidae	18	2	-
Brachycera			
Stratiomyidae imagoes	7	1	3
Stratiomyidae larvae	25	26	-
Tabanidae larvae	-	-	1
Unidentified Diptera	5	2	-
Hymenoptera	3	3	-
Apocrita	2	1	-
Formicidae	-	1	-
Coleoptera			
Carabidae	-	15	-
Amara aenea	-	2	-
Scarabaeidae	1	5	-
Elateridae imagoes	1	2	-
Elateridae larvae	-	2	-
Coccinellidae	-	16	-
Coccinella 7-punctata	2	14	-
Propylea 14-punctata	-	1	-
Chrysomelidae	1	2	-
Leptinotarsa decemlineata	-	1	-
Dytiscidae imagoes	22	37	-
Dytiscidae larvae	275	82	31
Lybius spp.	-	2	-
Hydrophilidae imagoes	2	15	-
Laccobius spp.	2	-	-
Laccobius sinuatus	-	1	-
Hydrophilus piceus	-	1	-
Hydrophilidae larvae	218	75	-
Hydrophilus piceus	25	2	19
Heteroceridae			
Heterocerus flexuosus	-	1	-
Unidentified Coleoptera	16	32	-
VERTEBRATES			
Pisces			
Cyprinidae	2	2	-
Leuciscus cephalus	5	17	-
Cyprinus carpio	4	-	-
Pseudorasbora parva	1	2	-
Rutilus rutilus	8	8	1
Carassius auratus	7	15	-
Phoxinus phoxinus	4	1	-
Rhodeus sericeus	18	-	1
Alburnus alburnus	2	2	-
Cobitidae			
Cobitis spp.	3	-	-
Cobitis taenia	2	-	-
Gasterosteidae			
Gasterosteus aculeatus	150	-	-
Poeciliidae			
Gambusia affinis	567	-	39
Centrarchidae			
Lepomis gibbosus	2	12	-
Gobiidae			
Gobius spp.	21	-	-
Knipowitschia caucasica	2	-	-
Pomatoschistus spp.	3	1	-
Clupeidae			
Sardina pilchardus	1	-	-
Atherinidae			
Atherina spp.	68	6	-
Atherina boyeri	24	1	-
Cyprinodontidae			
Aphanius fasciatus	1013	6	-
Mugilidae	5	-	-
Liza saliens	2	-	-
Blenniidae			
Blennius pavo	8	-	-
Pleuronectidae			
Platichthys flesus	1	-	-
Soleidae			
Solea solea	4	-	-
Exocoetidae	-	2	-
Unidentified fish	95	81	7
Amphibia			
Rana ridibunda	158	95	52
Hyla arborea	9	1	-
Rana spp. adults	24	54	1
Rana spp. tadpoles	1084	75	35
Reptilia			
Natrix natrix	-	6	-
Emys orbicularis	-	1	-
Mammalia			
Arvicola terrestris	-	1	-
Microtus arvalis	-	2	-
Rattus spp.	-	2	-
Unidentified mammals	-	7	-
TOTAL	5108	2373	277

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SHORT NOTE

Seasonal variation in abundance of *Corophium orientale* (Crustacea : Amphipoda) in Monolimni lagoon (Evros Delta, North Aegean Sea)

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KEY WORDS. Amphipods, *Corophium orientale*, abundance, seasonal variation, Aegean sea

Amphipods of the genus *Corophium* are frequently important components of inshore ecosystems. *Corophium orientale Schellenberg*, 1928 is a common and frequently abundant inhabitant of Mediterranean lagoons and coastal brackish environments; nevertheless, its population dynamics have not yet been studied. The present study describes the monthly variation in population density of the amphipod *C. orientale* in the two parts of Monolimni lagoon, Evros Delta, N. Aegean Sea. This variation is discussed in relation to the life cycle of the species and to some abiotic and biotic factors.

Monolimni (or Paloukia) lagoon, occupying an area of about 115 ha, communicates with the sea mainly through an opening 15m wide. Between February 1998 and February 1999 macroalgae were occasionally observed in both parts of the lagoon (the southern and northern ones), while a meadow of *Ruppia maritima* occurred in the innermost northern one. During the aforementioned period monthly samples of benthic macrofauna were collected at the stations I_1 and B_2 located in the southern and northern part of Monolimni lagoon, respectively (1). For this study all *Corophium orientale* specimens were separated from the remaining macrofauna and counted.

Further examination of *C. orientale* specimens was used for the description of the life cycle of this species (2). The structure of the macrobenthic assemblages in these stations throughout the period February 1998 to February 1999, as well as the monthly variation in several water and sediment parameters were also described (1). Table I shows the fluctuations of all these environmental parameters over the sampling period.

In station I_1, population density of *Corophium orientale* was low in February – April, increased in May – July and peaked in August (Fig. 1). It decreased in September – October ; after October, density gradually decreased until the last sampling (Fig. 1). In station B_2, the abundance of *C. orientale* was low in February – March 1998, increased from April onwards and peaked in June (Fig. 1). It decreased in July – August. Density increased again in September, while after September it varied at relatively lower levels (Fig. 1). Density of *C. orientale* showed a significant seasonal variation in both stations (Kruskal – Wallis one – way analysis of variance : H=22.398, DF=3, P<0.001 in station I_1 ; H=9.152, DF=3, P<0.05 in station B_2) being lowest in spring in both stations and highest in summer in station I_1 and in autumn in station B_2. During spring density of the two populations did not differ significantly (Mann – Whitney U – test) ; however, density in station I_1 was significantly higher than that in station B_2 mainly in summer (P<0.001), but also in autumn and winter (P<0.01).

Fig. 1. – Monthly variation in population density (mean ± standard error) of *Corophium orientale* in station I_1 and station B_2 in Monolimni lagoon, Evros Delta.

We tested for significant correlations (Spearman's Rank correlation coefficient ρ) between the monthly variation in population density of *C. orientale* and that in (a) several physicochemical parameters of the water and sediment, and (b) the abundance of the constant co-occurring macrofaunal taxa [*Ventrosia maritima* (Milaschewitch, 1916), *Streblospio shrubsolii* (Buchanan, 1890), *Hediste diversicolor* (Muller, 1776), *Gammarus aequicauda* (Martynov, 1931), *Abra ovata* (Philippi, 1836) in both stations, as well as Cumacea in station I_1 and *Cerastoderma glaucum* (Poiret, 1789), Chironomidae larvae and Tubificidae in station B_2]. In station I_1, there was a significant positive correlation between density of *C. orientale* and salinity (Table 1) ; salinity had a value of about 0.3 psu in spring, 1.2 – 5.6 psu in summer, 3 – 4 psu in autumn and 0.5 – 1.5 psu in winter. A significant negative correlation was found between *C. orientale* abundance and dissolved O_2 and also O_2 saturation (Table 1), since these parameters had higher values during the colder period of the year, when the amphipod abundance was more or less low. The correlations of *C. orientale* density with those of the constant macrobenthic taxa were not significant. In station B_2, no significant correlation was found between *C. orientale* abundance and any one of the abiotic parameters (Table 1) ; there was a positive correlation with the abundance of the bivalve *A. ovata* (ρ=0.736, P<0.01) and the amphipod *G. aequicauda* (ρ=0.648, P<0.05), which showed similar trends in seasonal variation.

TABLE 1

The range of several physicochemical parameters of water and sediment and Spearman's rank correlation coefficient (ρ) values between density of *Corophium orientale* and these physicochemical parameters throughout the sampling period in stations I_1 and B_2 in Monolimni Lagoon, Evros Delta (*: P<0.05; **: P<0.01; ns: not significant; n=13; a: n=12; b: n=11).

		Station I_1		**Station B_2**	
	Variable	**Variable Range**	ρ	**Variable Range**	ρ
Water	Depth (cm)	50 - 85	-0.048 ns	30 – 55	0.599 ns b
	Salinity (psu)	0.3 – 5.6	0.810 **	0.3 – 5.7	0.377 ns
	Dissolved O_2 (mg l^{-1})	6.05 – 14.7	-0.706 * b	9.78 – 18.0	-0.400 ns b
	O_2 saturation (%)	74 – 122	-0.645 * b	101 – 220	-0.064 ns b
	pH	7.4 – 9.1	-0.349 ns	7.45 – 9.32	0.069 ns
	Transparency (cm)	35 – 65	0.019 ns	15 – 55	0.046 ns a
	Temperature (°C)	1.8 – 26.7	0.516 ns	4.2 – 28.5	0.126 ns
Sediment	Temperature 1cm (°C)	2.1 – 26.6	0.512 ns	3.7 – 27.0	0.190 ns
	Temperature 5cm (°C)	1.9 – 26.5	0.512 ns	3.5 – 28.6	0.176 ns
	Median diameter (µm)	143 – 176	-0.108 ns	94 – 129	-0.033 ns
	Organic matter (%)	0.15 – 1.73	0.525 ns	0.48 – 2.20	0.538 ns

Salinity was the only examined parameter that essentially showed an association with the density of *C. orientale*. Extremely low salinities coincided with decreases in abundance in winter and with low abundances in spring. Nevertheless, the increase in population density during late spring at salinities of 0.3 – 0.4 psu indicates that this amphipod is highly tolerant to extremely low salinities ; particularly, it appears to be more tolerant than other brackish water *Corophium* species, such as *C. volutator* and *C. insidiosum* (3, 4).

In station I_1 breeding of *C. orientale* peaked in March, June and September, and a spring, a summer and an overwintering cohort were produced showing a life span of about 4, 5 and 8 – 9 months, respectively (2). Therefore, population density increased during late spring and summer following the recruitment of the spring and summer cohorts, while it decreased after summer mainly or partly due to the die – off initially of the spring cohort and afterwards of the summer one. A similar increase in density during the main reproductive period has been also reported for other *Corophium* populations (e.g. 5, 6). Breeding of various *Corophium* species occurs mainly from mid or late spring to autumn in northern brackish habitats, while in more southerly ones the breeding period is usually wider (e.g. 7, 8). Comparison of the monthly variation in abundance of *C. orientale* in the two parts of Monolimni lagoon revealed a striking difference during summer. In station B_2 breeding of *C. orientale* peaked in April and then, in September ; a lack of large individuals observed in summer possibly contributed to that hiatus in reproduction (2). That lack should be attributed to a size – selective predation probably by shorebirds (*Tringa totanus, Calidris* spp.), which gather especially in that part of the lagoon during summer. As a consequence, recruitment occurred only during late spring and early autumn, two discrete generations, a spring and an overwintering one, were produced (2) and population density decreased in July. Predation by migratory shorebirds (*Callidris pusilla*) has been considered itself responsible for a similar decline in densities of *Corophium volutator* during summer in intertidal mudflats of the Bay of Fundy, Canada (9, 10). In addition, the major part of the *C. orientale* population may have temporarily emigrated from station B_2 during August, when dense vegetation of *Ruppia maritima* and high temperatures occurred, in order to avoid some unfavorable conditions such as low oxygen concentrations at night. Under experimental conditions an emigration of *Corophium volutator* from sediments associated with low oxygen saturation has been observed (11).

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Allozyme variation in populations of the karyotypically polymorphic vole *Microtus* (*Terricola*) *thomasi* (Mammalia, Rodentia) from Greece

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ABSTRACT. Five distinct karyotypic forms of the vole *Microtus (Terricola) thomasi* are known in Greece so far : the earlier described forms *"thomasi"* (2n=44, FN=44) and *"atticus"* (2n=44, FN=46), and the more recently discovered ones with a)2n=41,42, FN=42,43,44, b)2n=40, FN=42, and c)2n=38, FN=40. The present study gives information on genetic relationships between vole populations belonging to the different karyotypic forms, based on allozyme variation. Eighteen loci were typed on cellulose acetate plates in 102 voles collected from six localities of mainland Greece, and the allelic data obtained were analysed using the biostatistical program BIOSYS-1. Populations studied show high intra- and interpopulation electrophoretic variability. A UPGMA dendrogram revealed clear separation of the *"atticus"* karyotype population from all others. Among the latter, two main groups exist : one including the population with the typical *"thomasi"* karyotype and another comprising all populations with polymorphic karyotypes. The clustering of the six populations studied is in agreement with karyological data given in recent literature.

KEY WORDS : Allozymes, voles, *Microtus (Terricola) thomasi*, Greece, karyotype variation

INTRODUCTION

Voles of the genus *Microtus* (subgenus *Terricola*) of the Arvicolidae family are represented in Greece by three species; *Microtus* (*Terricola*) *subterraneus*, *M. (T.) felteni*, and *M.(T.) thomasi* (Mitcell-Jones et al., 1999). *Microtus* (*Terricola*) *thomasi* Barrett-Hamilton, 1903, is endemic to the SW Balkan peninsula; in Greece it is distributed in the mainland (except Thrace and Eastern and Central Macedonia) and on the Evvoia island. It can be found from sea level up to an altitude of 1700 m.

Extensive karyological investigations (Giagia & Ondrias 1973; Giagia 1985; Giagia-Athanasopoulou et al., 1995; Giagia-Athanasopoulou & Stamatopoulos, 1997) have shown that *M.* (*T.*) *thomasi* occurs as several different karyotypic forms in Greece. Table 1 shows these forms, their geographical distribution and the way each has evolved from another. Discovery of this karyotypic polymorphism triggered interest in the study of its possible role in the speciation process (King 1993; Searle 1993; Fraguedakis-Tsolis et al. 1997).

Some morphological and ethological studies indicate that the *"thomasi"* and *"atticus"* karyotypic forms can be regarded as two different species (Miller 1910; Miller 1912; Kratochvil 1971; Petrov & Zivcović 1972; Stamatopoulos & Ondrias 1986), whereas other morphological, behavioural, immunological and biochemical studies suggest these two forms are conspecifics (Niethammer 1974; Corbet 1978; Petrov & Zivcović 1979; Niethammer & Krapp 1982; Nikoletopoulos et al. 1992; Petrov 1992; Tsekoura et. al. 2002). In support of the latter opinion, no reproductive isolation was observed between these two forms under laboratory conditions (Giagia-Athanasopoulou & Stamatopoulos unpublished data).

The present study aims to clarify the genetic relationships between some of the Greek *M.*(*T.*) *thomasi* populations representing all known karyotypic forms.

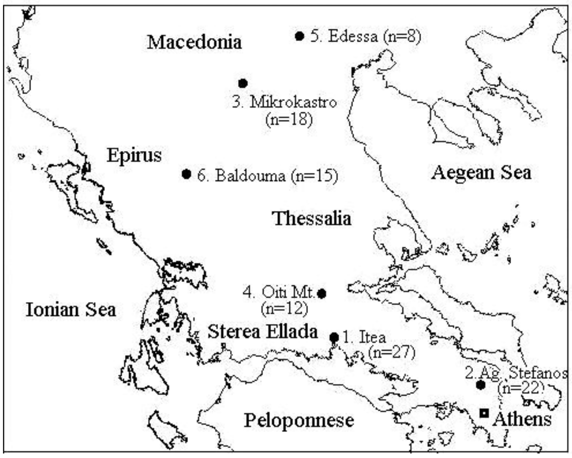

Fig. 1. – Map of Greece showing sampling localities of the present study and numbers of individuals collected from each locality.

MATERIAL AND METHODS

102 individuals of *M.(T.) thomasi* were collected from six localities of mainland Greece taking care that each of the populations belonged to one of the six known karyotypic forms (Table 1, Fig. 1). All individuals were live-trapped between September 1995 and May 2001, and each was karyotypically analysed by Giagia-Athanasopoulou (personal communication).

TABLE 1

The six known karyotypic forms of *Microtus (Terricola) thomasi*, their distribution in Greece and the populations that represent these forms in the present study (2n=diploid chromosome number, FN=fundamental number, n=number of individuals) (karyotypic data were obtained from Giagia & Ondrias 1973; Giagia 1985; Giagia-Athanasopoulou et al. 1995; Giagia-Athanasopoulou & Stamatopoulos 1997)

Karyotypic form	**Karyotype**	**Distribution**	**Populations**
"thomasi"	2n=44, FN=44	Parts of Central Greece and the central part of South Peloponnese	Itea (Fokida pref., Sterea Ellada) (n=27)
Pericentric inversion of the X chromosome			
"atticus"	2n=44, FN=46	Parts of Central Greece and the largest part of Peloponnese	Ag. Stefanos (Attiki pref., Sterea Ellada) (n=22)
Tandem fusion between the X chromosome and a small acrocentric autosome			
"subalpine"	2n=42, FN=42	Parts of Pindos mountain range, as well as areas of eastern Epirus and Western Macedonia	Mikrokastro (Kozani pref., Macedonia) (n=18)
Robertsonian centric fusion of an autosome			
"Rb-subalpine"	2n=40, FN=42	Epirus and mountainous Central Greece	Oiti Mt. (Fthiotida pref., Sterea Ellada) (n=12)
Unnamed	2n=41,42, FN=42,43,44	A small area around Baldouma village, pref. of Ioannina (Epirus)	Baldouma (Ioannina pref., Epirus) (n=15)
Unnamed	2n=38, FN=40	A zone along the Greek-FYROM borders (Central-West Macedonia)	Edessa (Pella pref., Macedonia) (n=8)

TABLE 2

The enzymes and loci analyzed, their code numbers, the tissues they were extracted from and the buffers used (Buffers : A = 25mM Tris - 190mM glycine - pH 8.5, B = 40mM Tris - 10mM citrate - pH 7.6, C = 40mM phosphate - pH 6.3).

Enzyme	Tissue	Locus	E.C. number	**Buffer**
Aconitase	Heart	Aco-1	4.2.1.3.	B
Adenosine deaminase	Spleen	Ada-1	3.5.4.4.	A
Adenylate kinase	Heart	Ak-1	2.7.4.3.	B
Creatine kinase	Heart	Ck-1	2.7.3.2.	B
Glutamate oxaloacetate transaminase	Kidney	Got-1,2	2.6.1.1.	C
Glucose dehydrogenase	Kidney	Gpd-1	1.1.1.47.	A
Glucose phosphate isomerase	Kidney	Gpi-1	5.3.1.9.	A
Isocitrate dehydrogenase	Kidney	Idh-1,2	1.1.1.42.	B
Lactate dehydrogenase	Kidney	Ldh-1,2	1.1.1.27.	A
Malic enzyme	Liver	Mod-1	1.1.1.40.	B
Malate dehydrogenase	Kidney	Mor-1,2	1.1.1.37.	B
Mannose phosphate isomerase	Kidney	Mpi-1	5.3.1.8.	A
Nucleoside phosphorylase	Kidney	Np-1	2.4.2.1.	A
Phosphoglucomutase	Kidney	Pgm-1	2.7.5.1.	A

After the animals were humanely killed, their heart, liver, spleen and kidneys were removed and placed in a deep-freezer (-75° C). Skulls and skins of the specimens are deposited in the collections of the Zoological Museum of Patra University.

The tissues were homogenized and used for the electrophoretic analysis of 14 enzymes coded by 18 loci (Table 2) on prepared cellulose acetate plates (Helena Laboratories). The electrophoretic procedure was carried out according to Tsekoura et al. (2002), following methods developed for other small mammals (Searle 1985; Fraguedakis-Tsolis et al. 1997; Hauffe et al. 2002).

The allelic data obtained were analysed using BIOSYS-1 (Swofford & Selander 1981).

RESULTS

Of the 18 loci examined, 13 (72.2%) were found polymorphic. Three of these 13 loci (*Gpi-1*, *Mpi-1, Idh-1*) were polymorphic in only one of the six populations (Ag. Stefanos) while another locus (*Np-1*) was polymorphic in all six populations. Each monomorphic locus was fixed for the same allele in all populations (Table 3).

The mean values of the expected (He) and observed (Ho) heterozygosity, the percentages of polymorphic loci (P%), and the mean number of alleles per locus (A) for each of the examined populations are also shown in Table 3. Itea is the population with the most polymorphic loci (50.00%) and also shows the highest mean number of alleles per locus (1.56), whereas Edessa and Baldouma are the least polymorphic populations both with 22.22% of loci polymorphic and 1.22 alleles per locus. Low values of heterozygosity characterize all six poplulations.

This excess of homozygotes is also revealed by the values of the F_{IS}, F_{IT} and F_{ST} indices (Wright 1951 ; Nei 1977) (Table 4). Indeed, although the genetic loci *Gpi-1*, *Idh-1* and *Ldh-1* present negative values of the fixation index F_{IS} and the locus *Idh-1* also presents a negative value of F_{IT}, these values are very small in contrast with the high positive values obtained for all the other cases ; this strong general tendency of the *F*-statistics for positive values is theoretically known to indicate a deficiency of heterozygotes. The mean value of the fixation index F_{ST} of all polymorphic loci reveals that the genetic differentiation among the six populations is responsible for 51.6% of the total genetic variability, whereas intrapopulation polymorphism is the cause of the remaining 48.4% of this variability (Wright 1951).

The values of Rogers' genetic similarity varied from 0.614 (Ag. Stefanos and Edessa) to 0.964 (Oiti Mt. and Edessa), while those of Nei's genetic distance varied from

TABLE 3

The allelic frequencies for all polymorphic loci, the mean values of expected (He) and observed (Ho) heterozygosity, the percentage of polymorphic genetic loci (P%) and the mean number of alleles per locus (A) of each studied population (n = number of individuals collected) (Populations: 1.Itea, 2.Ag. Stefanos, 3.Mikrokastro, 4.Oiti Mt., 5.Edessa, 6.Baldouma).

Genetic loci		**Populations**					
		1	**2**	**3**	**4**	**5**	**6**
Ada-1	a	0.685	0.000	0.806	0.708	1.000	1.000
	b	0.315	1.000	0.194	0.292	0.000	0.000
Got-1	a	0.889	0.500	0.000	0.000	0.000	0.000
	b	0.111	0.500	1.000	1.000	1.000	1.000
Got-2	a	0.648	0.500	0.000	0.000	0.000	0.000
	b	0.352	0.500	1.000	1.000	1.000	1.000
Gpd-1	a	0.333	0.568	1.000	1.000	1.000	1.000
	b	0.667	0.432	0.000	0.000	0.000	0.000
Gpi-1	b	0.000	0.886	0.000	0.000	0.000	0.000
	c	1.000	0.114	1.000	1.000	1.000	1.000
Idh-1	a	1.000	0.909	1.000	1.000	1.000	1.000
	b	0.000	0.000	0.000	0.000	0.000	0.000
	c	0.000	0.091	0.000	0.000	0.000	0.000
Ldh-1	a	1.000	1.000	0.472	0.083	0.125	0.933
	b	0.000	0.000	0.528	0.917	0.875	0.067
Ldh-2	a	0.241	1.000	0.722	0.167	0.250	0.967
	b	0.759	0.000	0.278	0.833	0.750	0.033
Mod-1	a	0.500	0.000	0.194	0.375	0.571	1.000
	b	0.500	1.000	0.806	0.625	0.429	0.000
Mor-1	a	0.926	0.955	1.000	1.000	1.000	0.700
	b	0.076	0.045	0.000	0.000	0.000	0.300
Mor-2	a	0.130	0.000	0.056	0.000	0.000	0.000
	b	0.870	1.000	0.944	1.000	1.000	1.000
Mpi-1	a	0.000	0.409	0.000	0.000	0.000	0.000
	b	1.000	0.591	1.000	1.000	1.000	1.000
Np-1	a	0.481	0.955	0.222	0.042	0.063	0.133
	b	0.481	0.045	0.750	0.917	0.938	0.867
	c	0.037	0.000	0.028	0.000	0.000	0.000
	d	0.000	0.000	0.000	0.042	0.000	0.000
n		27	22	18	12	8	15
He		0.187	0.143	0.115	0.085	0.071	0.048
Ho		0.053	0.035	0.080	0.051	0.071	0.048
P%		50.00	44.44	33.33	27.78	22.22	22.22
A		1.56	1.44	1.39	1.33	1.22	1.22

0.004 (Oiti Mt. and Edessa) to 0.374 (Ag. Stefanos and Edessa) (Table 5).

The UPGMA dendrogram of the genetic relationships between the six populations, resulting from the Nei's distance values, is shown in Fig. 2. It demonstrates a clear separation of the Ag. Stefanos population, with the rest of the examined populations being divided into two groups: one including the Itea population and another one comprising all the others. The population of Baldouma branches next, while the other populations form two branches : one of them involves the Mikrokastro population, and the other the populations of Oiti Mt. and Edessa.

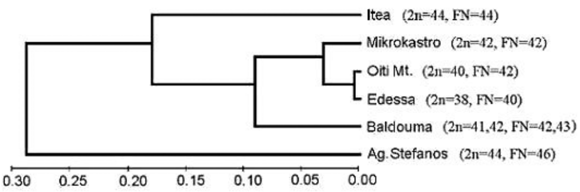

Fig. 2. – UPGMA dendrogram of genetic relationships among the six populations, based on Nei's unbiased genetic distances.

TABLE 4

The values of F_{IS} ,F_{IT} and F_{ST} fixation indices of all polymorphic loci

Locus	F_{IS}	F_{IT}	F_{ST}
Ada-1	0.576	0.805	0.541
Got-1	1.000	1.000	0.673
Got-2	0.961	0.980	0.485
Gpd-1	0.775	0.883	0.479
Gpi-1	-0.128	0.850	0.867
Idh-1	-0.100	-0.015	0.077
Ldh-1	-0.056	0.635	0.654
Ldh-2	0.830	0.915	0.499
Mod-1	0.321	0.593	0.401
Mor-1	0.689	0.744	0.175
Mor-2	0.328	0.381	0.079
Mpi-1	1.000	1.000	0.366
Np-1	0.286	0.605	0.447
Mean	0.545	0.780	0.516

DISCUSSION

The percentage of polymorphic loci (72.2%) of the populations studied is quite high compared to those calculated by GRAF (1982), which varied from 27.3% to 42.1%, for a number of arvicolid species not including *M.* (*T.*) *thomasi*. That author also calculated a mean value of the percentage of heterozygosity per locus for the Arvicolidae family (4.3% ± 2.5%), which he considered relatively high compared to other mammals. Our values vary from 3.0% (Baldouma) to 8.0% (Mikrokastro) and are similar to those of Graf. Therefore, we could conclude that the populations examined in the present study are characterized by a pronounced genetic variability.

The *F*-statistics reveal a general excess of homozygotes in the populations examined (F_{IS},F_{IT} >0), evincing the tendency of most polymorphic loci to stabilize some of the alleles, perhaps resulting from a population subdivision into smaller units (tribes, families), a fact that has also been confirmed for other species of this genus (NYGREN & RASMUSON 1980). The presence of loci that exhibit negative values of F_{IS} and F_{IT} (*Gpi-1*, *Idh-1*, *Ldh-1*), could be due to positive selection of heterozygotes.

TABLE 5

Values of Rogers' genetic similarity (below diagonal) and Nei's unbiased genetic distance (above diagonal) between the six populations studied.

Population	**Itea (2n=44, FN=44)**	**Ag. Stefanos (2n=44, FN=46)**	**Mikrokastro (2n=42, FN=42)**	**Oiti Mt. (2n=40, FN=42)**	**Edessa (2n=38, FN=40)**	**Baldouma (2n=41,42, FN=42,43)**
Itea (2n=44, FN=44)	-	0.193	0.162	0.186	0.184	0.182
Ag. Stefanos (2n=44, FN=46)	0.738	-	0.225	0.337	0.374	0.309
Mikrokastro (2n=42, FN=42)	0.775	0.698	-	0.030	0.030	0.063
Oiti Mt. (2n=40, FN=42)	0.779	0.634	0.919	-	0.004	0.119
Edessa (2n=38, FN=40)	0.771	0.614	0.910	0.964	-	0.086
Baldouma (2n=41,42, FN=42,43)	0.748	0.667	0.880	0.836	0.871	-

The mean value of the fixation index F_{ST} (0.516) reveals that the populations studied present about equal inter- and intrapopulation genetic variability.

Moreover, Graf (1982) calculated mean Nei's genetic distances for different taxonomic levels within the family Arvicolidae. However, a recent study on Greek populations of *M.(T.) thomasi* showed that their genetic distances do not agree with those given by Graf for the population level, and appear to be much greater (Tsekoura et al. 2002). This conclusion is also verified by our results, suggesting that *M.(T.) thomasi* exhibits an intraspecific variability much higher compared to other European *Microtus* species. Therefore, it appears that Graf's conclusions should be revised to include the case of *M. (T.) thomasi*, which does not seem to follow Graf's pattern. Nonetheless, it is worth mentioning that, as has also been indicated in Tsekoura et al. (2002), our results show that the population of Ag. Stefanos presents the highest genetic distances from all the other populations.

The UPGMA dendrogram (Fig. 2) indicates a clear separation of the *"atticus"* karyotype population (Ag. Stefanos) from all others. Among the latter ones, consisting of two main groups, the population with the original *"thomasi"* karyotype (Itea) separates from all populations with polymorphic karyotypes. With the exception of the Ag. Stefanos population, this clustering is in agreement with the pattern of karyotype evolution within *Microtus thomasi* in the area of Greece, as indicated in Table 1. The genetic differentiation of the population of Ag. Stefanos which has a derived karyotype ("*atticus*", 2n=44, FN=46), is possibly due to particular environmental conditions that prevailed in this sampling area alone (intensive urbanization and other human activities). This area was selected because it is the closest available to the *terra typica* of the originally described vole taxon *Pitymys atticus* Miller, 1910, from which later the "*atticus"* karyotype was firstly described (Giagia & Ondrias 1973 ; Giagia 1985).

Within the cluster of the polymorphic karyotypes, the population of Baldouma (2n=41,42, FN=42,43) separates from the others, which form two groups : one composed of the population of Mikrokastro (2n=42, FN=42-*"subalpine"*) and another composed of the populations of Oiti Mt. (2n=40, FN=42-*"Rb-subalpine"*) and Edessa (2n=38, FN=40). The Edessa population karyotype, as already mentioned, is closely related to the *"Rb-subalpine"* one (Giagia-Athanasopoulou & Stamatopoulos 1997), which, in turn, has emerged from the *"subalpine"* type (Giagia-Athanasopoulou et al. 1995). The Baldouma population can be regarded as a hybrid one, because it consists of individuals with the *"subalpine"* karyotype (2n=42, FN=42) and hybrids with 2n=41, FN=43, resulting from crosses of *"Rb-subalpine"* (2n=40, FN=42) individuals with 2n=42, FN=44 ones, the latter not being included in our sample (Table 1) (Giagia-Athanasopoulou & Stamatopoulos 1997). Therefore, this population is expected to have intermediate karyotypic characteristics between the populations of Mikrokastro and Oiti Mt.. Our results confirm this point, since the population of Baldouma exhibits similar values of genetic distance from both these two populations (Table 5, Fig. 2).

The results of the electrophoretic analysis and the clustering of the populations examined agree to a large extent with the karyological data. This correspondence encourages us to make further attempts to clarify genetic relationships among the Greek populations of this species. Our main approach will concern more electrophoretic and other molecular studies of populations belonging to the already known karyotypic forms and any as yet undiscovered ones.

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Neogene/Quaternary mammalian migrations in Eastern Mediterranean

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ABSTRACT. Palaeogeographic and climatic changes in the Eastern Mediterranean during the Neogene/Quaternary led to extended mammalian migrations and faunal exchanges between Eurasia and Africa. At the same time, the Beringian landbridge was activated several times, and American faunal elements entered Eurasia. It appears that the main factor affecting migration potential and faunal changes/exchanges during the Neogene was palaeogeography, while after the early Pliocene migrations were mainly controlled by climatic changes. Several mammalian migrations can be distinguished, but the most important was that of the middle Orleanian at about 17.0-18.0 Ma when Africa and Eurasia were connected after a long separation and a great number of African faunal elements entered Eurasia and vice versa. Some more important faunal changes also occurred : 1. at ~5.5 Ma, marking the beginning of the Pliocene, 2. at ~ 2.0-1.8 Ma, marking the beginning of the Pleistocene, and 3. at ~1.0 Ma, defining the early/middle Pleistocene boundary and the establishment of modern mammal fauna. During the Pleistocene, oscillation of glacial and inter-glacial periods caused an alternation of cold-steppic faunas with temperate ones in the Eastern Mediterranean. Endemic late Pleistocene mammalian faunas developed in the Mediterranean islands after their isolation ; "dwarf" elephants, cervids and hippos occurred, as well as giant rodents.

KEY WORDS : Eastern Mediterranean, Neogene/Quaternary, Mammalia, migration, faunal changes, paleobiogeography.

INTRODUCTION

The Eastern Mediterranean is regarded as an important domain for mammal exchanges between Asia, Europe and Africa during the Neogene/Quaternary. The enlarged area of the Eastern Mediterranean includes the Balkan Peninsula, the Aegean Sea, Asia Minor and the Middle East. In this geographic region migration pathways between the three continents crossed. The number of localities for mammal fossils found in the Eastern Mediterranean is quite significant, providing a good base for further comparisons and discussion. The geological age of the faunas and the palaeogeography of the area are already well known from previous and essential works. However, the scarcity of the fossil record and the limited dating of several sites is a great disadvantage to reconstruct the palaeobiogeography.

The main Neogene/Quaternary mammalian migration waves between Eurasia and Africa are associated with important mammal turnovers, climatic and tectonic changes and in some cases also include mammalian forms arrived from America via the Beringian landbridge. The present article combines available data from the mentioned region and neighbouring ones, in order to extract the main migrations, the time spans during which they occurred and the palaeogeographic conditions under which they took place. Our work also focuses on the arrival of some important taxa into Greece and their significance in establishing the evolution of Greek faunas.

MIGRATION FACTORS

The migration of a mammal depends upon various factors. The most important are topographic/physicogeographic and climatic parameters. Geographic barriers, such as high mountain chains and/or sea channels are restrictive for the migration of mammals. Knowledge of the palaeogeography (global or regional) during the various geological periods is essential to extrapolation of migration waves and faunal turnovers. Climatic conditions and the palaeoenvironment of the origin and arrival areas also control migration potential. Animals adapted to warm climatic conditions cannot occupy cool areas and vice versa.

The size of an animal and the migration distance are positively related. A large-sized animal can cover a long migration distance during its life-span, while a micromammal (e.g. a rodent) usually needs more generations in order to cover the same distance or to pass a significant topographical barrier. In this case evolution and migration can be simultaneous.

The study of past migrations presupposes a good knowledge of taxonomy and age of the fossils. The taxonomic determination of the mammalian fossils is an important factor for establishing mammal migration and distribution. Differences in the definition of a "biological" and "palaeontological" taxon make the taxonomic determination of fossils more delicate. Geologic timing is another important factor. The age of mammalian faunas is determined either biochronologically (based on the faunal composition and its evolutionary stage) or radiometrically if possible. Magnetostratigraphy also provides good age resolution, but the method has not been extensively used in continental mammal-bearing deposits. During the last 30 years new methods were developped allowing quite precise age determination for the fossil mammalian faunas providing a good base for comparisons.

GEOTECTONIC BACKGROUND

It is generally accepted that during the entire Neogene/Quaternary there was a continuous connection between Europe and Asia, in the north Caspian region. The South European area and especially its eastern part was definitely formed during this period, by alpine orogenesis, extending the terrestrial communication between Asia and Europe. The following Quaternary tectonism and eustatic movements did not change dramatically the geography of the area, but were mainly of local significance. Neogene was also a time of important geotectonic events that allowed successive connections between Eurasia and Africa, creating great opportunities for faunal exchanges between these continents. The most important Neogene/Quaternary palaeogeographic changes are schematically given in the palaeomaps of Steininger & Rögl (1985) and Rögl (1999), used as background for our work. Geological time is mainly expressed by the system of Mammal Biozones of Mein (1990, 1999), which permits definition and recognition of small time-units and correlation between neighboring areas (Fig. 1).

AGENIAN-EARLY ORLEANIAN MIGRATION (23.8-18.0 MA)

During the Oligocene/Miocene boundary a deep trough between Arabian and Iranian plates, known as Tethyan Seaway (Fig. 2A), allowed communication of the Mediterranean with the Atlantic and the Indo-Pacific Oceans. The closure of the Tethyan Seaway was gradual, starting at ~19.0 Ma, and continuing until the end of MN 3 at ~18.0 Ma (Rögl, 1999). At the same time, Asia communicated with America through the Beringian landbridge and an important immigrant, the equid *Anchitherium*, invaded Asia. It rapidly dispersed to Europe as it is known from MN 3 of the Iberian Peninsula (Mein, 1990). *Anchitherium* is unknown in the Balkan Peninsula, while it appeared in MN 6 of Asia Minor (Forsten, 1990 ; Now 2002). Its absence from the Balkans could suggest that the area was not connected with Asia Minor, or more likely, that it has not yet been found there. Some inner-Eurasian faunal exchanges have also been recognized. In W. Europe the suids *Hyotherium* appeared in MN 1 and *Xenohyus* in MN 2 (Made, 1990), and the anthracothere *Brachyodus* in MN 3 (Mein, 1990). The MN 1-3 faunas are very rare in the Eastern Mediterranean. However, the presence of *Brachyodus* is recorded in the locality of Kalimeriani, Greece (Melentis, 1966). The sole specimen of *Brachyodus* cannot give a precise age for the locality, but an MN 3-4 age was suggested (Bonis & Koufos, 1999). The first spalacid *Debruijnia* is known from MN 3 of Asia Minor, while it was also found in Aliveri, Greece, dated at the base of MN 4 (de Bruijn *et al.*, 1992). These data suggest an early connection of Asia Minor with the Balkan Peninsula at the end of MN 3. During that time the Northern Aegean was a continental domain with low relief (Dermitzakis & Papanikolaou, 1981).

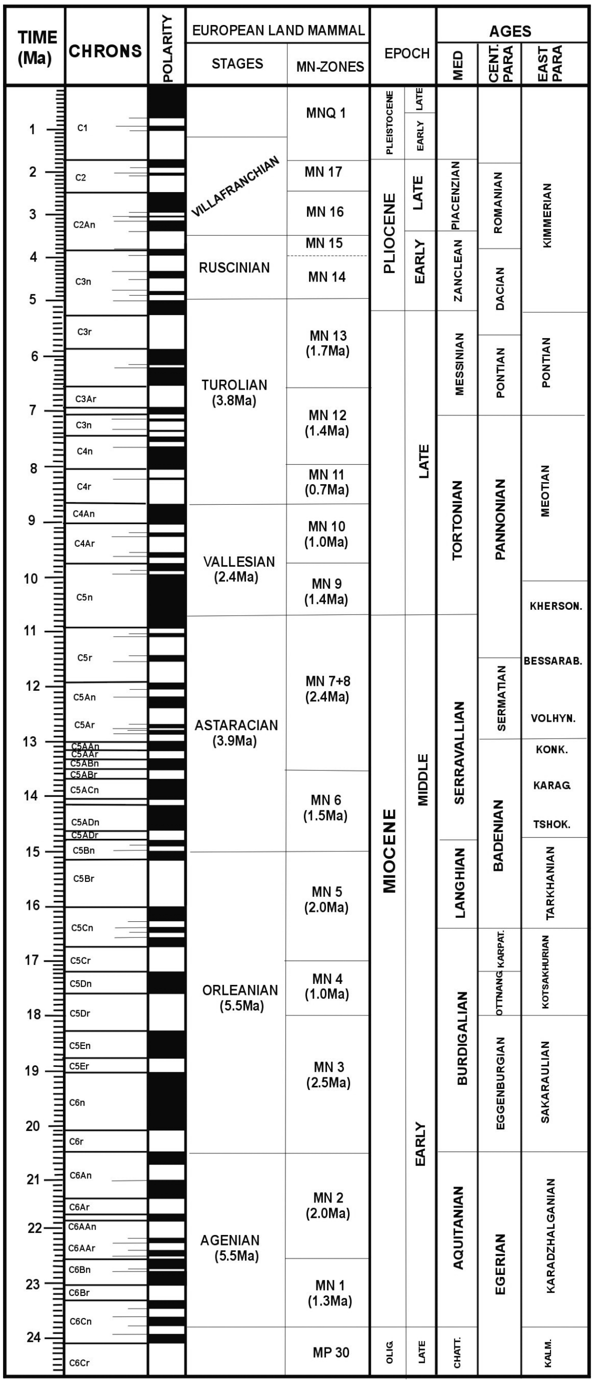


Fig. 1. – Chronologoical table for Neogene/Quaternary with the European land mammal stages and MN-Zones. According to Mein (1990), Steininger *et al.* (1990) and Steininger (1999).

MIDDLE ORLEANIAN MIGRATION (18.0-17.0 MA)

The Arabian and Anatolian plates collided at the end of MN 3 (middle Orleanian) re-establishing communication between Africa and Eurasia (Fig. 2B). The landbridge connecting the two continents is known as "*Gomphoth-*

erium-landbridge” (Rögl, 1999 ; Agusti *et al.*, 2001). The closure of the Tethyan Seaway probably provided an earlier connection with Asia as *Pliohyrax*, originating from Africa, was found in India at the end of MN 3 (Pickford, 1986). Its presence in the Eastern Mediterranean is reported later in the locality of Pasalar, Turkey, dated to MN 6 (Now, 2002). This earlier connection is also confirmed by the recent trace of a primitive deinothere *Prodeinotherium* in Lesvos island, Greece. Its dental morphology and the absolute age of the sediments including it, suggest an age of >18.4 Ma (Koufos *et al.*, 2003). This means that before the final closure of the Tethyan Seaway, there were some early short or temporary landbridges connecting Africa and Eurasia (before 18.0 Ma), allowing the entrance of some mammals. The Indopacific Seaway to the Eastern Paratethys was closed too. The western part of Paratethys was also closed and thus it became an isolated basin with endemic fauna and reduced salinity (Rögl, 1999). The Balkan Peninsula was completely connected with Asia Minor (Fig. 2C) except for some lakes or lagoons in the northern Aegean area (Dermitzakis & Papanikolaou, 1981).

A great number of African taxa migrated to Eurasia through the “*Gomphotherium*-landbridge”, while a simultaneous migration is also traced from Eurasia to Africa. The fauna of Negev in Israel, dated to MN 3, corresponds to the first exchange between them as it includes a mixed fauna with African (*Prodeinotherium, Gomphotherium, Anasipora, Dorcatherium, Kenyalagomys, Megapedetes*) and Asian (*Eotragus, Listriodon,* Rhinocerotidae) elements (Tchernov *et al.*, 1987 ; Agusti *et al.* 2001 ; Pickford 2001). Recent radiometric data suggest an age of ~20.7 Ma for this event (Rögl, 1999). The first African immigrants were the proboscideans ; the gomphotheres and the deinotheres, arriving in India (Bugti Fauna) at ~18.3 Ma (Barry *et al.*, 1985 ; Tassy, 1990) and in Eastern Mediterranean at ~18.4 Ma (Koufos *et al.*, in press). The proboscideans rapidly dispersed in W. Europe as they were found in the Iberian Peninsula at the beginning of MN 4, ~ 18.0 Ma (Tassy, 1990).

Several Asian taxa, such as the bovid *Eotragus*, the suid *Bunolistriodon*, the nimravid *Prosansanosmilus* and the rodents *Megacricetodon, Democricetodon, Cricetodon, Eumyarion* e.t.c. migrated also to Europe and/or to Africa (Agusti *et al.*, 2001 and literature listed). The subfamily Democricetodontinae appeared in Asia Minor during the early Miocene (MN 1-2) and then migrated to Africa and Asia (MN 3), as well as to America through the Beringian landbridge (MN 3-4). During MN 4 the subfamily appeared in the Balkans and Western Europe (Theocharopoulos, 1999).

Many Asian and African immigrants arrived in Greece too. The genera *Megacricetodon, Democricetodon* and *Karydomys* are recognized in Aliveri (early MN 4), Karydia and near Komotini (upper MN 4) (Theocharopoulos, 1999). The first carnivores (*Palaeogale, Euboictis*) appeared in Aliveri, Evia dated at the base of MN 4 (de Bruijn *et al.*, 1992). The genus *Euboictis* has possibly a southern Asian origin and the connection of Asia Minor with Europe allowed its migration to the Balkans and Central Europe during MN 4 (Schmidt-Kittler, 1999).

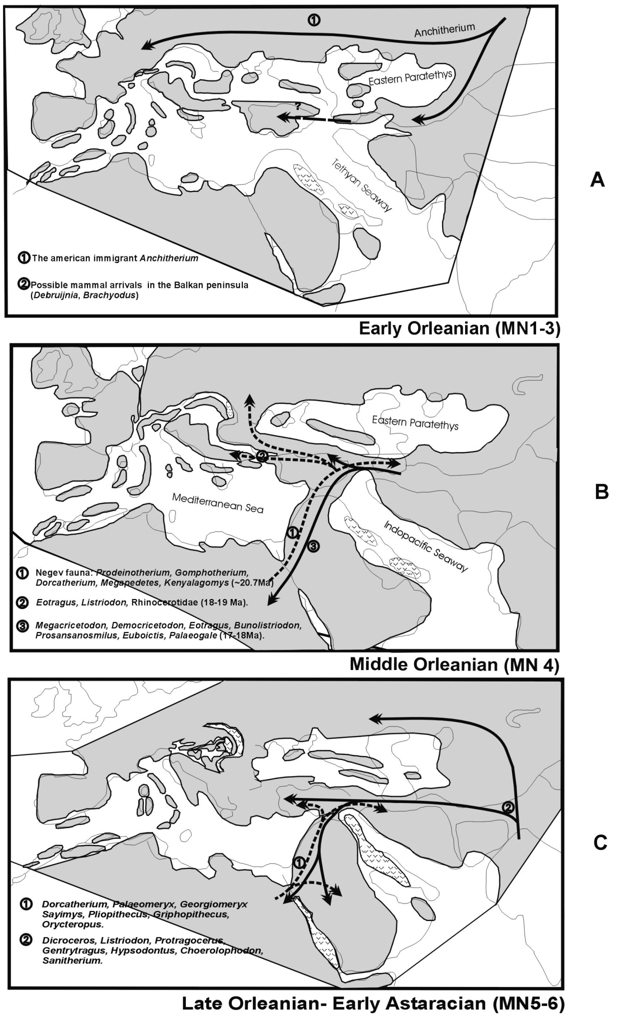


Fig. 2. – Palaeogeographic map of Mediterranean region with the main mammalian migration pathways and arrivals in Eastern Mediterranean.
a) Agenian-early Orleanian (MN 1-3)
b) Middle Orleanian (MN 4)
c) Late Orleanian-Early Astaracian (MN 5-6)
Palaeogeographic maps from Rögl (1999).

LATE ORLEANIAN-ASTARACIAN MIGRATIONS (17.0-10.7 MA)

A succession of short-term sea level oscillations during this time interval caused several changes to the palaeogeography of the Eastern Mediterranean. There is evidence of a late Orleanian transgression, re-opening the Tethyan Seaway (Rögl, 1999). Thus, the landbridge between Africa and Eurasia was active for short periods allowing faunal migrations between the two continents (Figs 2C, 3A). However, such short-term connections between the continents are not confirmed by mammal evidence. In any case three migration waves can be recognized at this time :

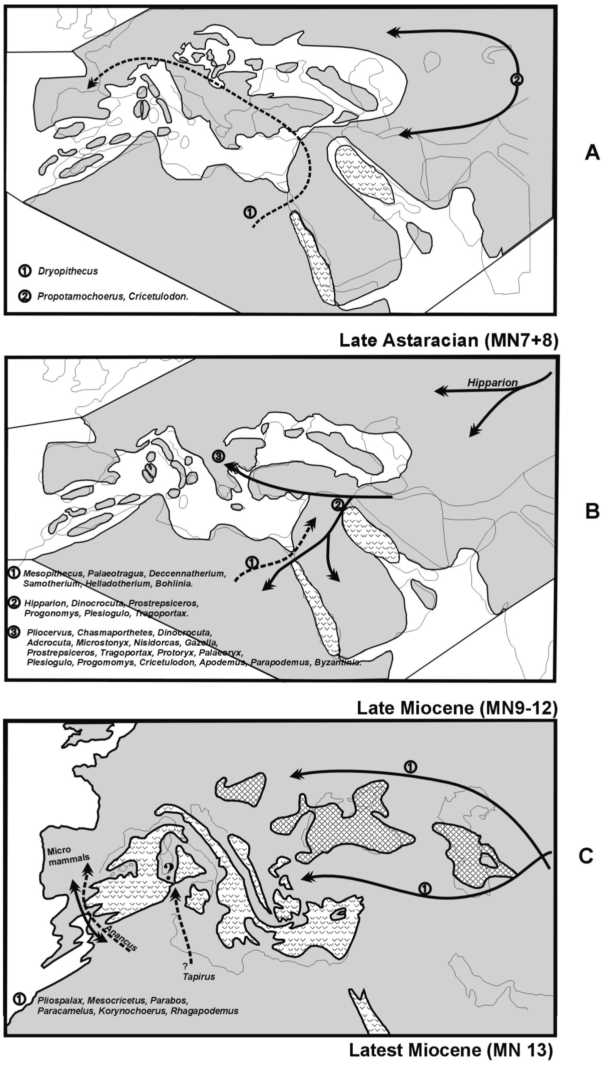


Fig. 3. – Palaeogeographic map of Mediterranean region with the main mammalian migration pathways and arrivals in Eastern Mediterranean.
a) Late Astaracian (MN 7+8)
b) Late Miocene (MN 9-12)
c) Latest Miocene (MN 13)
Palaeogeographic maps from Rögl (1999) and Steiniger & Rögl (1985).

a. During the late Orleanian, MN 5 (17.0-15.0 Ma) a migration wave from Africa arrived in the Eastern Mediterranean. The Greek fauna of Antonios, Chalkidiki dated to MN 4/5 at ~17.0 Ma (Koufos & Syrides, 1997) fits quite well with it. The Antonios fauna includes a small-sized *Dorcatherium* very close to the small-sized African form described by Pickford (2001). The giraffid *Palaeomeryx* is another African element present in Antonios fauna. The sanitheres known from MN 3 of Africa migrated to Asia (Pickford, 1984) at the end of MN 3. In the Eastern Mediterranean they appeared firstly in Antonios fauna. These data indicate a short-term mammal invasion, may be before the re-opening of the Tethyan Seaway. The locality of Thymiana, Chios Island, Greece includes strong evidences of a migration from Africa during this time span. The locality is dated to MN 5 or to 15.5 Ma according to magnetostratigraphic data (Kondopoulou *et al.*, 1993 ; de Bonis *et al.*, 1998). The giraffid *Georgiomeryx*, the tragulid *Dorcatherium,* and the ctenodactylid *Sayimys* indicate African origin confirming the above-mentioned connection. The proboscidean *Choerolophodon,* appeared firstly in Chios island coming probably from Asia since it was already present in the Bugti fauna, India, dated to MN 3, or ~18.3 Ma (Tassy, 1990). However, the most important arrival was that of the primates, originating from Africa and invading Eurasia during MN 5. The first primates with the genus *Pliopithecus* are known from the localities of Elgg (Switzerland) and Pontlevoy-Thenay (France) dated to MN 5, and they existed until the end of Vallesian (Andrews *et al.*, 1996).

b. A second migration wave from Africa during early Astaracian, MN 6 (15.0-13.5 Ma) brought several immigrants into Eurasia and the Eastern Mediterranean (Fig. 2C). The most important new element was the hominoid *Griphopithecus* of African affinities. It was recognized in the Turkish localities of Pasalar and Candir, as well as in Neudorf-Sandberg, Slovakia, all dated to MN 6. The Eur-Asian *Griphopithecus* is related to the African *Kenyapithecus* known from Maboko, East Africa dated to MN 4 (Andrews *et al.,* 1996). The arrival of the aardwark *Orycteropus* in the Eastern Mediterranean is also referred to this wave. The genus has African origin and its oldest remains out of Africa are those from Pasalar, Turkey dated to MN 6 (Fortelius, 1990). During MN 6 some asian elements also entered into Europe, such as the hyracoid *Pliohyrax*, the cervid *Dicroceros* and the suid *Listriodon* (Thenius, 1952 ; Made, 1990). The hyracoids originated from Africa and entered into the indian subcontinent at the end of MN 3. *Pliohyrax* dispersed eastwards in MN 6, appeared in the Eastern Mediterranean locality of Pasalar Turkey, dated to MN 6 (Fortelius, 1990). Several asian bovids (*Protragocerus, Tethytragus* and *Hypsodontus)* known from MN 5 of Asia Minor and Chios island migrated to Africa.

c. A third migration wave from Africa seems to have taken place, mainly in MN 8, but the poorly known late Astaracian, MN 7+8 (13.5-10.7 Ma), faunas of the Eastern Mediterranean do not allow detailed conclusions. The most important appearance was that of the hominoid *Dryopithecus* in Europe at about 12.5 Ma ago (Fig. 3A). The Asian suid *Propotamochoerus* entered Europe at that time (Made, 1999). The genus *Cricetulodon* arrived in the area at the end of MN 7+8 and it is known from Turkey and Greece (Koufos, 2003). The genus is known from MN 3 of W-C Europe where it persisted until MN 7+8 (Agusti *et al.* 2001 ; Now, 2002). According to Rögl (1999) during the late Astaracian there was a seaway between Paratethys and Mediterranean, prohibiting the migrations. These data suggest that at the end of MN 7+8 the connection between Europe and Asia was fully established.

LATE MIOCENE MIGRATION (10.7-6.7 MA)

The arrival of *Hipparion* in Eurasia from America, known as *Hipparion*-datum is a major event used extensively in biostratigraphy and biochronology as a marker of the beginning of the late Miocene (MN 9). A strong sea level drop around 11.0 Ma re-opened the Beringian landbridge (HAQ *et al.*, 1988) and some North-American mammals entered Eurasia. However, there are different opinions about the age of *Hipparion*-datum in Europe. The available faunal and magnetostratigraphic data from Spain suggest an age of 11.1 Ma (GARCES *et al.*, 1997). In the Eastern Mediterranean recent magnetostratigraphic data from Turkey suggest an age of 10.7 Ma (KAPPELMAN *et al.*, 2003). Similar dating is also proposed for the *Hipparion*-datum in Pakistan 10.7 Ma (PILBEAM *et al.*, 1996). Thus, the beginning of late Miocene (arrival of *Hipparion*) must be considered at 10.7 in the Eastern Mediterranean, at the moment. The hipparionine horses immediately entered Africa and dispersed rapidly to the whole continent, remaining until the beginning of the Pleistocene.

During the late Miocene there was a short landbridge between Africa and Eurasia (Fig. 3B), while the Red-Sea was more or less formed (RÖGL, 1999). This landbridge allowed faunal exchanges with the most important arrival being that of the cercopithecid *Mesopithecus.* The genus is very well known in Greece (Pikerni, Axios valley, Maramena), but it is also known in Bulgaria, Former Yugoslavian Republic of Macedonia (FYROM), Afghanistan, and Iran. Its first appearance in the Eastern Mediterranean was recorded in Axios valley, Greece at ~8.2 Ma (KOUFOS, in press.). The giraffids are well represented by several genera, such as *Palaeotragus, Bohlinia, Samotherium, Helladotherium* (Fig. 3B). The different climatic and environmental conditions between South-Eastern and Central-Western Europe did not allow to these large-sized mammals to pass into the occidental part. Only the small-sized *Palaeotragus* migrated to W.-C. Europe.

However, the most important arrivals during the late Miocene were those from Asia. The invasion of *Hipparion* into Eastern Mediterranean was accompanied by the arrival of several Asian mammal immigrants such as the large hyaena *Dinocrocuta*, the ictitheres and the extensively known hyaena *Adcrocuta.* The suid *Microstonyx* appeared in the Eastern Mediterranean at the end of MN 10 or more precisely at ~9.0 Ma (KOSTOPOULOS, 1994 ; KOUFOS, 2000). The carnivores *Plesiogulo* and *Chasmaporthetes* entered Eastern Mediterranean from Asia and were found in the Greek localities of Vathylakkos and Ravin des Zouaves-5, dated at ~7.5 Ma and 8.2 Ma respectively (SEN *et al.,* 2000). The Asian bovid association, arriving at the same time, included many genera, such as *Tragoportax, Gazella, Prostrepsiceros*, *Nisidorcas*, *Protoryx*, *Palaeoryx*, but most of them did not pass to the west of Europe. Among the small mammals invading the area the genus *Progonomys*, of Asian origin, arrived in the Eastern Mediterranean at ~ 10.1 Ma (KAPPELMAN *et al.*, 2003). There is a clear diachrony in its distribution as it is known from Pakistan at 12.3 Ma and from Spain at 9.64-9.74 Ma (PILBEAM *et al.*, 1996 ; AGUSTI *et al.,* 1997). The rodent *Parapodemus* is known from MN 12 of the Eastern Mediterranean, and arrived in the area from the north. Other rodents are the genera *Byzantinia*, *Occitanomys,* and *Apodemus,* all of Asian origin (AGUSTI *et al.,* 2001; KOUFOS, 2003). Thus, an extended bioprovince of savannah character was established from the Balkans to Iran-Afganistan, named Creco-Iranian Province (BONIS *et al.*, 1993).

During this time-span a significant number of hominoids appeared, representing a local European evolution. BEGUN (2001) proposed that *Dryopithecus*, after its appearance to Europe, evolved and then, during the late Miocene dispersed to the whole of Eurasia, giving rise to various forms, while at the end of the Miocene it re-entered Africa. The genera, *Dryopithecus* in W-C. Europe, *Oreopithecus* in Italy, *Ankarapithecus* in Turkey, *Sivapithecus* in India and *Lufengpithecus* in China are representatives of the late Miocene group of hominoids. In Greece the hominoid primate *Ouranopithecus macedoniensis* with an age from 9.0-9.6 Ma was found in the localities Ravin de la Pluie and Xirochori of Axios valley and Nikiti 1, in Chalkidiki (DE BONIS & KOUFOS, 1999 ; KOUFOS, 1993, 1995). *Ouranopithecus* is of special interest as it has strong relationships with the Plio-Pleistocene hominines (DE BONIS & KOUFOS, 2001).

LATEST MIOCENE MIGRATION (6.7-5.3 MA)

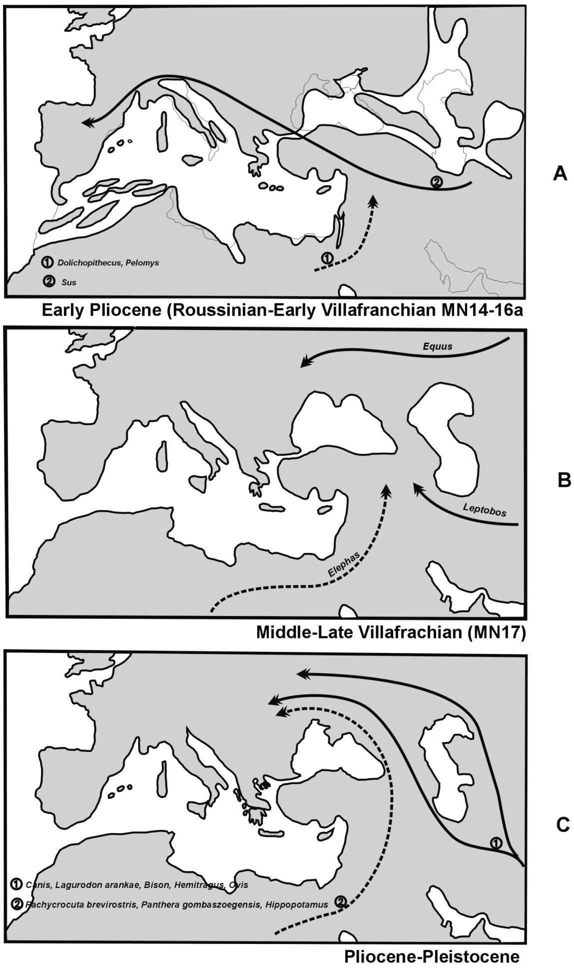
Although basin re-organization around the Mediterranean provoked several regional phenomena of isolation already during the middle Late Miocene (late Tortonian, MN 12 ; KRIJGSMAN *et al.,* 2000), accumulated data from Spain, Italy, Sicily, Gavdos, Crete and Cyprus suggest that a major isochronous palaeoenvironmental change at 6.8-6.7 Ma affected the entire Mediterranean (KRIJGSMAN *et al.*, 2002). This age marks the beginning of MN 13 zone, characterized by an important mammal turnover (AGUSTI *et al.,* 2001). It seems that at 6.1 Ma an ephemeral landbridge between Africa and Europe already existed in the Gibraltar area, caused by the emergence of the Betics intamontane basins, allowed the first terrestrial faunal exchange between these two lands across the Iberian peninsula (GARCES *et al.*, 1998). At 5.9 Ma a climatic trend towards increased aridity and continentality combined with the continuous tectonic convergence between Africa and Europe and the uplift of the Spanish and NW African mountain chains, caused the closure of the Iberian and Rifian Seaways and the definitive isolation of the Mediterranean basin from the Atlantic ocean (STEININGER & RÖGL, 1985 ; PARTRIDGE, 1997 ; DINARES-TURELL *et al.*, 1999). Conditions of high evaporation in the Mediterranean led to a significant sea level drop (more than 200m according to deltaic deposits) and the deposition of thick evaporitic beds, starting at 5.96 Ma (KRIJGSMAN *et al.*, 2002). More or less at the same time the Beringian landbridge was re-activated as a result of a global regression, allowing several mammalian taxa to invade Eurasia from N. America (*Alilepus*, ancestor of Leporidae). The Central Paratethys was divided in two intermountain basins : the Dacian Basin in Romania and the Pannonian Basin in Hungary. Sea temperatures in the Mediterranean for that period apparently showed strong fluctuations, with short warm and cold seasons. The relative fall of humidity and temperature in the continent allowed expansion around the Mediterranean of hard-leaved evergreen forests, but the peri-Mediterranean flora was not dramatically changed (SUC, 1986 ; SUC *et al.,* 1995)

These important physiogeographic transformations provided new migration pathways for mammals, and allowed more rapid and easy faunal exchanges between Africa and Europe. The main way between Africa and Eurasia in the Middle East remained open, as the Saharo-Arabic channel was not a significant obstacle for large mammals. However, the supposed connection between Africa and Europe across Tunis-Sicily or Sardinia-Corsica-Tuscuny was no longer sustainable, since the faunal data from this area indicate a high endemism, plausibly suggesting an insular palaeoprovince (BERNOR *et al.*, 2001). The exchange of mammals between the Iberian Peninsula and Africa is fully substantiated by the study of micromammals (THOMAS *et al.*, 1982, AGUSTI *et al.*, 2001). The communication of the Mediterranean with the Atlantic Ocean by the Gibraltar Seaway became re-established at the end of the Miocene, at about 5.3 Ma. An extensive transgression raised the sea level, and the Mediterranea filled again. Climatic conditions were also changed, being less dry. The presence of tragulids and cervids in the Greek fauna of Dytiko, Macedonia, dated to latest Miocene, is strong evidence for an increase of humidity in the Eastern Mediterranean (DE BONIS *et al.,* 1992). The end of the Miocene is characterized by the disappearance of several mammalian taxa including mastodonts (*Choerolophodon)*, carnivores (*Adcrocuta, Thalassictis*), suids (*Microstonyx*), giraffids (*Bohlinia*, *Samotherium, Helladotherium*), bovids (*Tragoportax, Prostrepsiceros, Protoryx, Palaeoryx*), cervids (*Procapreolus*), micromammals (*Parapodemus*). This extinction probably resulted from the change in palaeoecological conditions. Few taxa adapted to the newly established environment and entered to Pliocene, e.g. *Gazella*.

The extinction, however, left free ecological space, and new steppic immigrants, mainly from Asia, arrived and dispersed in the Eastern Mediterranean : *Pliospalax, Promimomys, Rhagapodemus*, *Mesocricetus, Parabos, Korynochoerus*, *Nyctereutes*, belong to these immigrants and characterize the beginning of the Pliocene. The earlier camelid *Paracamelus* was previously considered as belonging to this migration wave, but new data confirm an even earlier invasion. Moreover, forest dwellers, possibly of African origin, also arrived. *Tapirus arvernensis* appeared firstly in Italy in MN 13-14 (NOW 2002). The mastodont *Anancus,* an African immigrant already mentioned from MN 12 of the Iberian Peninsula, dispersed eastwards and occurred in the Balkans and the Black Sea in MN 14 (Greece, Hungary, Romania, Ukraine). Two Greek faunas (Maramena and Silata) correspond to this transitional period. Their mammal association includes young elements such as the suid *Korynochoerus* and the rodents *Rhagapodemus, Mesocricetus, Apodemus* and *Micromys* together with Miocene genera such as *Choerolophodon, Tragoportax, Samotherium* and *Pliocervus.* Both faunas have been dated to the Miocene/Pliocene boundary (SCHMIDT-KITTLER *et al.,* 1995, VASSILIADOU *et al.*, 2003).

EARLY-MIDDLE PLIOCENE MIGRATION (5.3-2.5 MA)

The main palaeogeography of the Mediterranean region changed slightly after the beginning of the Pliocene, being more or less similar to the recent one (Fig. 4A). The uplift of the Alpine chain separated Northern-Central from Southern Europe distinguishing their biotopes. The Black Sea was restricted more or less at its present limits, while the Caspian Sea formed a larger marine/submarine system ; communication between these two basins was possible, but not certain. The continuous northward drift of the Arabian plate allowed definitive opening of the Red Sea, but the African-Middle East migration pathway remained active. Climatic conditions changed to more warm and wet. This is clear from the extended Pliocene lignitic deposits in Greece, Turkey, FYROM and Bulgaria. The great percentage of Desmaninae in the Greek mammalian faunas of this period (Spilia 1, Kardia) confirms this opinion (VAN DER MEULEN &VAN KOLFSCHOTTEN, 1986).



Early Pliocene (Roussinian-Early Villafranchian MN14-16a

Middle-Late Villafrachian (MN17)

Pliocene-Pleistocene

Fig. 4. – Palaeogeographic map of Mediterranean region with the main mammalian migration pathways and arrivals in Eastern Mediterranean.
a) Early-Middle Pliocene (MN 14-16a)
b) Middle-Late Villafranchian (MN 17)
c) Pliocene-Pleistocene
Palaeogeographic maps from STEINIGER & RÖGL (1985).

Pliocene fossil mammal records in the Eastern Mediterranean are, however, scarce. Between 5.3 Ma and ~3.5 Ma ago several new forms arrived in Europe. The cercopithecid *Dolichopithecus* and the rodent *Pelomys* arrived from Africa via the Middle East. The former appeared in the Eastern Mediterranean in the Greek locality of Megalo Emvolon, dated to the base of MN 15 (Koufos & Kostopoulos, 1997). The rodent *Pelomys* arrived earlier at the beginning of the Pliocene, found in the Greek locality of Maritses, Rhodes (de Bruijn *et al.,* 1992). Several carnivores, cervids, bovids and rodents migrated to Europe, mainly from Asia. The cervids differentiated rapidly and gave rise to several genera, occupying a significant number of mainly forest ecological niches. The suid *Sus,* most possibly of southern Asian origin, made its first appearance in the Greek locality of Kessani dated to the base of MN 14 (Koufos & Kostopoulos, 1997). It rapidly dispersed to the whole of Europe as it is known from MN 14 of Italy, France and Spain (Now, 2002). Later, it was found in the localities of Apolakkia, Rhodes and Megalo Emvolon dated to MN 15 (Koufos & Kostopoulos, 1997). These types of mammalian faunas were partly changed at ~3.2 Ma because of a worldwide climatic cooling, causing a renewal of the mammal communities. Early Villafranchian (3.2 – 2.6 Ma) faunas are, however, poorly known in the Eastern Mediterranean.

THE MIDDLE-LATE VILLAFRANCHIAN FAUNAL TURNOVER (2.6-2.0 MA)

Since the main morphotectonic structures of the peri-Mediterranean region were completely developed, the palaeogeography of the area did not change. Migration and dispersion of the mammals were mainly affected by climatic fluctuations. At ~2.6 Ma (Middle Villafranchian, MN16) a climatic deterioration allowed a more arid phase, which characterized the rest of this period until 1.8 Ma ago. This time-span correlates to the development in the Mediterranean region of the steppic floras characterized by *Artemisia* and *Ephedra* (Suc, 1986 ; Suc *et al.,* 1995), and probably to the first major cool event of the northern hemisphere (Turner, 1995 ; Blum, 1997). The character of the mammalian faunas became more steppic, especially in Southeastern Europe. Nevertheless, the palaeoecological conditions changed gradually westwards delaying their presence in the Western Mediterranean. Therefore, during this time interval the palaeoecological conditions appeared to be more arid in the Eastern than in the Western Mediterranean. The middle Villafranchian faunas from Greece, Turkey and neighboring areas already had a more open/dry character than the isochronous faunas from Southwestern Europe as confirmed by the persistence of *Gazella*, giraffids e.t.c. (Kostopoulos & Sen, 1999 ; Kostopoulos & Koufos, 2000).

The most important arrivals in the Eastern Mediterranean and the whole of Europe are referred to the genera *Elephas*, *Leptobos* and *Equus*, known as *E-L-E event*. The genus *Equus* migrated earlier to Asia from N. America via the Beringian landbridge, but it arrived in the Eastern Mediterranean at the beginning of middle Villafranchian, c.a ~2.6 Ma (Azzaroli, 1990 ; Koufos, 2001). Its possible first appearance in the Eastern Mediterranean has been traced in Damatria, Rhodes Island, Greece. The fauna of Damatria is poor, but a dating to the upper part of early Villafranchian (MN 16b) is possible for it (Koufos, 2001). This age corresponds to ~2.6 Ma and fits quite well with the abovementioned first appearance of *Equus* in Europe. The genus dispersed rapidly throughout Europe, as it is traced in Spain at the same time. *Elephas* arrived from Africa following the Middle East pathway. *Leptobos* is an immigrant from Southern Asia and firstly appeared in the Eastern Mediterranean in the locality of Damatria. At the same time the second dispersal event of arvicolids appeared (Steininger & Rögl, 1985). During MN 16 several cervids of Asian origin adapted to local conditions providing new species or even genera. From the beginning of MN 17 three cervids *Croizetoceros*, *Eucladoceros* and "*Cervus*" / "*Pseudodama"* appeared in the Eastern Mediterranean. The mountain bovid *Gallogoral* and the slender antelope *Gazellospira*, both possibly of Asian origin, migrated to the Eastern Mediterranean and they were noted at several Greek localities (Koufos & Kostopoulos, 1997). Early ovibovines also appeared during this time (Spassov, 2000 ; Athanassiou, 2002). In the Eastern Mediterranean and the Black Sea a possible descendant of the late Miocene Palaeotraginae, the giraffid *Mitilanotherium,* is also present (Koufos & Kostopoulos, 1997 ; Kostopoulos & Athanassiou, in press). Incidentally, the presence of giraffids in W. Europe seems to be underestimated. New data from Spain justify the occurrence of late Pliocene giraffids in this area too (Arribas *et al*., 2001 and pers. obs.).

EARLY PLEISTOCENE MIGRATION (2.0-1.0 MA)

The climatic alternations and their effects on the sea level are the crucial factors of faunal changes during this period, which is characterized by a rapid renewal of the mammalian fauna at ~2.0-1.8 Ma (Kostopoulos & Koufos, 2000). The palaeogeography of the Eastern Mediterranean is similar to the recent one (Fig. 4C). During a short time span from 2.0-1.8 Ma several taxa enter Europe via the Balkan Peninsula and the Middle East (Spassov, 2000 ; Kostopoulos *et al.,* 2002). Between them the canid *Canis,* the rodent *Lagurodon,* the bovids *Bison, Hemitragus* and *Ovis* are Asian immigrants arrived in the Eastern Mediterranean at the beginning of the Pleistocene. The carnivores *Pachycrocuta brevirostris* and *Panthera gombaszoegensis,* as well as *Hippopotamus,* all of African origin, arrived in the area through the Middle East. All these immigrants replaced the typical Villafranchian faunas of the Eastern Mediterranean and Europe. Several old taxa (*Nyctereutes*, *Pliohyaena, Gallogoral, Procamptoceras, Leptobos, Gazellospira, Gazella, Sus strozzii, Mitilanotherium, Croizetoceros* e.t.c) disappeared and were replaced by new ones. This faunal change is well recorded in the Greek locality of Gerakarou and the Bulgarian locality of Slivnitsa, both dated at the end of the Pliocene (Koufos & Kostopoulos, 1997 ; Spassov, 1997). From the beginning of the Pleistocene (~1.8 Ma) new immigrants, especially from Asia, penetrated further : the characteristic steppic rodent *Allophaiomys pliocaenicus* dispersed in the whole peri-Mediterranean area. The bovids *Pontoceros, Praeovibos, Soergelia* and the cervid *Praemegaceros* arrived in the Eastern Mediterranean and then dispersed to Europe (Azzaroli, 1983 ; Kostopoulos *et al.,* 2002). These migration waves are closely related to the expansion of the steppe towards the southwest, including some northern and possibly cooler inhabitants.

MIDDLE-LATE PLEISTOCENE MIGRATION (<1.0 MA)

During the early Pleistocene a large steppic belt was established along Eurasia and N. America. At the beginning of the middle Pleistocene wet climatic conditions allowed an increase of humidity and rehabilitation of the forestrial cover. For the next one million years the climatic conditions are characterized by a cyclicity with alternation of cold and temperate periods, establishing the oscillations of the Pleistocene glaciations (AZZAROLI, 1983 ; SUC, 1986 ; TURNER, 1995). During this period no important arrivals are mentioned. Steppic and cold steppic forms of North Asian and American origin such as the bovids *Praeovibos, Ovibos, Soergelia* and the cervid *Rangifer*, as well as temperate dwellers such as the elephant *Palaeoloxodon,* the rhino *Dicerorhinus* and the large bovid *Bubalus* arrived in the Eastern Mediterranean and then dispersed almost throughout Europe. The expansion of their biomes depended on the alternation of the glacial/interglacial periods. In Southern Europe the so-called "Mediterranean biosystem" was established. The most important migrations followed a N-S and *vice versa* direction, caused by expansion of the glacial cover. However, the uplifted Alpine chain is a significant barrier for most of the mammalian taxa. The Southern European fauna is only affected by the paroxysmal phases of the central European N-S migrations. Cold steppic faunal elements such as *Mammuthus* and the wooly rhino *Coelodonta* are occasionally present there, while temperate dwellers predominated. Both cold and temperate taxa are known from the middle-late Pleistocene of Greece (MELENTIS, 1961 ; MARINOS, 1965).

On the contrary, the Mediterranean islands show a completely different faunal pattern from middle-late Pleistocene. The isolation of the islands due to tectonic movements or/and sea level fluctuations, allowed the development of special endemic faunas. The absence of predators and the dramatic reduction of the living space gave rise to an evolutionary process known as insular endemism. The body mass of the island mammals, adapted progressively to the new conditions, reduced or increased accordingly to their initial size (insular "nanism" in elephants, hippos or "gigantism" in rodents). Several islands in the Eastern Mediterranean (Rhodes, Carpathos, Tilos, Crete, Cyprus e.t.c.) include poor mammalian communities of endemic character with small-sized elephants, hippos and cervids (DERMITZAKIS & SONDAAR, 1978 ; KOTSAKIS *et al.,* 1979 ;).

CONCLUSION

During the Neogene/Quaternary several mammalian migrations and faunal changes have been recognized in the Eastern Mediterranean. The recognized main migrations of this period are : a) the middle Orleanian (18.0-17.0 Ma), b) the late Miocene (10.7-6.7 Ma), and c) the middle Viffafranchian (~2.6 Ma) one. At the same time smaller migration waves from Africa and Asia allowed the entrance of various mammalian taxa into Europe. Two important faunal changes have been recognized : a) the latest Miocene faunal change, which marks the beginning of the Pliocene, and b) the latest Pliocene change, marking the beginning of the Pleistocene. Known but less significant faunal changes are important for the division of the various stages into smaller time-spans. The migrations and faunal changes of the Neogene are mainly due to palaeogeographic re-organization of the Mediterranean area during the Pliocene and Pleistocene. When the Mediterranean acquired its final palaeogeography and structure, climatic changes became the main factor controlling mammalian migrations. Since the study of Neogene/ Quaternary faunas of the peri- Mediterranean region continues new data become available to confirm or modify our ideas.

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Effect of fishing on community structure of demersal fish assemblages

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ABSTRACT. Seasonal experimental trawl surveys (fall 1991-winter 1993) carried out in the Thracian Sea and Thermaikos Gulf (N. E. Mediterranean, Greece). In this area, fishing pressure is very high, since approximately 50% of the Greek otter trawl fleet operates here, producing more than 57% of the total demersal landings. From a total of 285 bottom trawls sampled at depths between 16-420 m, 157 fish species were caught. Indices of diversity, richness, evenness, dominance and ABC plots were used to assess spatial structure, seasonal changes and diversity of the demersal fish assemblages. In general, species diversity, richness and evenness decreased with water depth, with the highest values at depths <100 m. Dominance increased with depth, getting its maximum at depths >200 m. The effect of depth on the diversity patterns observed was always significant, while no seasonal trends were detected. Commercially important species were dominant in the shallowest zone, while non-commercial species predominated at depths below 200 m. At intermediate depths (30-200 m) almost 50% of the total catches comprised of non-commercially important fish species. The abundance/biomass comparison method proved a useful tool for assessing the impact of stresses on fish populations since it revealed moderate disturbance on fish communities at those depths where fishing pressure is the highest.

KEY WORDS : Community structure, diversity, ABC method, fishing effects, North Eastern Mediterranean

INTRODUCTION

The reductions of catch rates and mean size of individuals is well documented in world fisheries (PITCHER, 1996, PAULY *et al.* 1998). Consequently, new approaches to the study of exploited populations have been suggested, including the study of the fish assemblage structure in relation to environmental variables, and the characterization of seasonal changes to improve management practices (i.e. GISLASON *et al.* 2000). As pointed out by CADDY & SHARP (1988) this type of study is a necessary step towards understanding the dynamics of multispecies stocks. Such work can then be extended to find general patterns, which may be associated with particular environmental conditions and fishing effort.

Information on soft-bottom fish assemblages is particularly scarce in the Eastern Mediterranean region where demersal fish are heavily exploited as principal targets or as by-catch. In Greek waters, demersal fishes of the continental shelf and slope are subjected to an intensive fishery carried out by trawl, gillnet and longline fleets. Gillnets and longlines catch a small number of species, whereas the trawl fleet exploits a multi-species fishery targeting several demersal and benthic species. The results of experimental trawl fishing in the Greek seas indicate that commercially important demersal and inshore stocks suffer from growth over-fishing. As a result, commercial catches consist mainly of young immature individuals and a variety of non-commercial species that are discarded (STERGIOU *et al.*, 1997).

In the present study, trawl catch data obtained seasonally, between fall 1991 and winter 1993, from the continental shelf and the upper slope of the Thracian sea were analysed to investigate the structure of the demersal fish community. The main objective was to identify aspects of community structure that are most likely to reveal evidence of anthropogenic impact due to exploitation.

MATERIALS AND METHODS

Sampling procedure

A total of 285 hauls were taken during 8 experimental bottom trawl survey cruises on a seasonal basis (fall 1991-winter 1993) in the Thracian Sea and Thermaikos Gulf from standard depth stations between 16-420 m. Sampling stations were selected on a depth-stratified random decision and the otter trawl used (foot-rope length : 65.7 m, headline height : 1.5 m) was equipped with a cod-end bag liner of 16 mm stretched mesh size. Samples were collected during daylight between 08:00 and 17:00 hours. The duration of each trawl (bottom time) was 30-60 min and the trawling speed fluctuated from 2.5 to 3.0 knots depending on the depth and the nature of the substrate. The catch from each haul was sorted and identified to species level, and each species was enumerated and weighed separately on board. Since all hauls were carried out using the commercial trawl vessel ('Ioannis Rossos') and the same fishing gear, it was assumed that gear selectivity was constant. Those species regarded as pelagic or semi-pelagic in behaviour were excluded from the analyses since they had not been quantitatively sampled (i.e. *Scomber* sp., *Trachurus* sp., *Sardina pilchardus*, *Engraulis encrasicolus*).

Data analysis

Species abundance and biomass were calculated for each haul after standardization of the data to a 1 hour tow. Cluster analysis (group average) employing the Bray-Curtis similarity index (Field *et al*., 1982) was performed to the standardized abundance values of the species using the PRIMER algorithms, Plymouth Marine Laboratory (Clarke, 1993). In order to normalize the data and avoid skew a square root transformation was applied to the abundance data prior to cluster analysis (Field *et al*., 1982). Multidimensional scaling (MDS) ordination analysis was also performed with the same configuration as in cluster analysis with respect to similarity index and transformation. The typifying and discriminating species of each group of stations were determined using the SIMPER procedure (Clarke, 1993). This procedure indicates the average contribution of each species to the similarity (typifying species) and dissimilarity (discriminating species) between groups of samples. Variation in species relative abundance and biomass was also examined by using the graphical representations of species cumulative frequency distributions (*k*-dominance curves, Lambshead *et al*., 1983). Relative abundance and biomass of demersal species were superimposed using the *ABC* method of Warwick (1986) to provide information on the size of the most dominant species. The ecological parameters number of species (*S*), species diversity (Shannon-Wiener index, Hurlbert, 1978), richness (Margalef, 1968), dominance (Simpson's index, Krebs, 1989) and evenness (Pielou, 1966) were calculated for each of the station-groups defined by cluster analysis.

RESULTS

A total of 157 species belonging to 60 families were collected from 285 trawl stations at depths ranging from 16 to 420 m. On the basis of classification and ordination of the 285 hauls, in terms of species abundance, 4 major station-groups (I to IV) were distinguished, reflecting depth-related differences in demersal fish assemblages associated with the continental shelf and the upper slope (Fig. 1). Group I included stations from intermediate depth (30-90 m), while group II comprised all the deepest stations from the continental shelf (100-190 m). Group III consisted entirely of the shallow stations (16-28 m). All stations from the upper slope (200-420 m) were classified in group IV. Species dominated in each group are presented in Table 1. However, a relatively small number of species contributed most to the similarity of each group, but their relative abundances varied between adjacent groups (i.e. Groups I-III) (Table 1).

Table 1. Dominant fish species in the Thracian Sea and Thermaikos Gulf, based on abundance rank for each station group identified by cluster analysis. Densities (%N) are averaged over all samples in each group. % Cum: average contribution to the similarity in each group. C indicates commercially important species. SD : Standard Deviation

Group III (16-28 m) average similarity: 67.8 SD: 4.9	**% N**	**% Cum.**		**Group I (30-90 m) average similarity: 73.8 SD: 7.1**	**% N**	**% Cum.**	
Arnoglossus laterna	13.55	12.37	C	*Serranus hepatus*	17.36	7.85	
Serranus hepatus	8.75	23.29		*Trisopterus minutus capelanus*	17.59	15.12	C
Diplodus annularis	4.24	32.27		*Mullus barbatus*	7.44	21.29	C
Gobius niger	6.74	40.72		*Arnoglossus laterna*	10.12	27.00	C
Mullus barbatus	30.75	48.11	C	*Merluccius merluccius*	3.21	32.08	C
Trisopterus minutus capelanus	1.21	53.63	C	*Spicara flexuosa*	6.92	37.10	
Spicara flexuosa	5.43	59.14		*Lepidotrigla cavillone*	2.75	41.71	
Trigla lucerna	1.61	64.48	C	*Cepola rubescens*	2.34	46.23	
Merlangius merlangus euxinus	3.54	69.45	C	*Deltentosteus quadrimaculatus*	5.35	50.73	
Scorpaena notata	0.45	74.15	C	*Callionymus maculatus*	3.40	55.06	
Merluccius merluccius	0.76	78.50	C	*Scyliorhinus canicula*	2.45	58.74	
Gobius paganellus	4.45	82.18		*Citharus linguatula*	1.67	62.33	C
Solea vulgaris	4.45	85.36	C	*Lophius budegassa*	0.90	65.76	C
Cepola rubescens	0.65	88.03		*Serranus cabrilla*	0.84	68.74	
				Symphurus ligulatus	0.58	71.51	
				Gaidropsarus sp.	0.42	74.05	
				Raja clavata	0.15	76.18	C
				Arnoglossus thori	0.75	78.27	C
Group II (100-190 m) average similarity: 73.6 SD=4.4	**% N**	**% Cum.**		**Group IV (200-420 m) average similarity: 72.3 SD: 7.8**	**% N**	**% Cum.**	
Trisopterus minutus capelanus	27.74	10.17	C	*Hymenocephalus italicus*	14.71	11.03	
Merluccius merluccius	10.16	18.29	C	*Gadiculus argenteus argenteus*	24.52	21.95	
Argentina sphyraena	2.04	23.95		*Lepidorhombus boscii*	5.30	31.81	C
Lophius budegassa	2.26	29.31	C	*Micromesistius poutassou*	26.42	40.85	C
Lepidorhombus boscii	1.38	34.50	C	*Coelorhynchus coelorhynchus*	2.41	47.97	
Arnoglossus laterna	2.46	39.37	C	*Phycis blennoides*	1.06	54.59	C
Scyliorhinus canicula	2.18	44.11		*Lophius budegassa*	1.14	61.12	C
Lepidotrigla cavillone	4.05	48.77		*Argentina sphyraena*	14.07	67.63	
Callionymus maculatus	2.54	53.41		*Merluccius merluccius*	6.88	74.03	C
Cepola rubescens	1.59	57.88		*Galeus melastomus*	0.50	78.95	
Serranus hepatus	6.99	62.10		*Trigla lyra*	0.37	82.62	C
Capros aper	0.88	66.07		*Capros aper*	0.16	86.12	
Phycis blennoides	0.31	69.75	C				
Aspitrigla cuculus	1.68	73.02	C				
Trigla lyra	0.33	76.27	C				
Mullus barbatus	4.53	79.52	C				

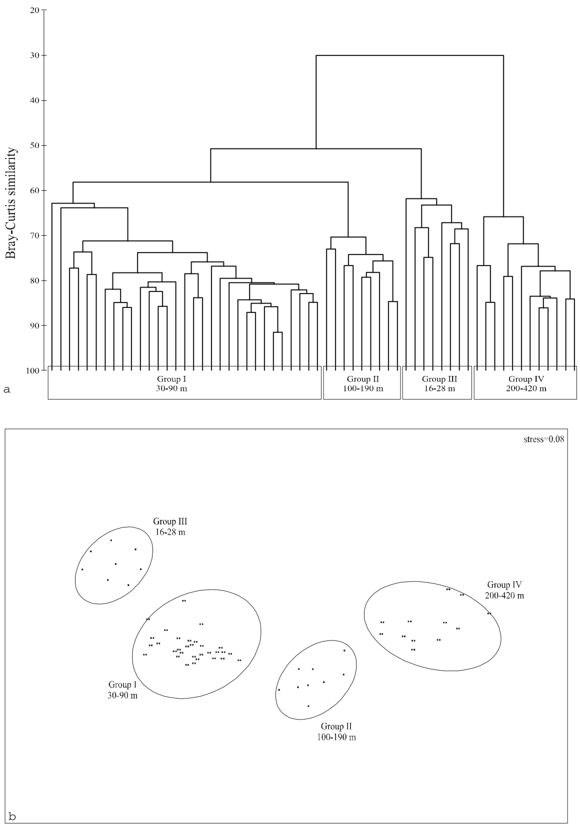

Fig. 1. – Classification (a) and ordination (b) of the sampling stations based on species abundance from the Thracian Sea and Thermaikos Gulf.

Differentiation between groups of station was evident in the *k*-dominance curves, in terms of both number and weight. Stations corresponded to groups I and II revealed more diversified and less dominated communities than those from the upper slope (group IV), with shallow stations (group III) having an intermediate position (Fig. 2). The curves got steeper and more elevated for group IV, suggesting that depths below 200 m were dominated by fewer species. Combined *k*-dominance curves for number and biomass (Fig. 3) showed that the dominant species occupied a larger proportion of the total when expressed as biomass rather than as numerical abundance in groups III and IV. At high species rank, both curves were steeper in gradient, indicating that fish assemblages in groups III and IV were dominated by few species. On the contrary, the *k*-dominance plots for group I exhibited an inverted pattern with the abundance curve more elevated than the biomass curve, indicating that several of the numerically most abundant species are small in size. A combination of large and small species, each with different rank in terms of abundance and biomass, produced *k*-dominance curves, which crossed for those hauls taken from depths between 100-190 m depth (group II). Estimations of the mean commercial/noncommercial ratio in terms of both number and weight of the species consisting each group revealed that commercially important species were dominant in the shallow zone (16-28 m). At intermediate depths (30-200 m) almost 50% of the total catches comprised of non-commercially important species, while non-commercially species predominated at depths below 200 m (Table 2).

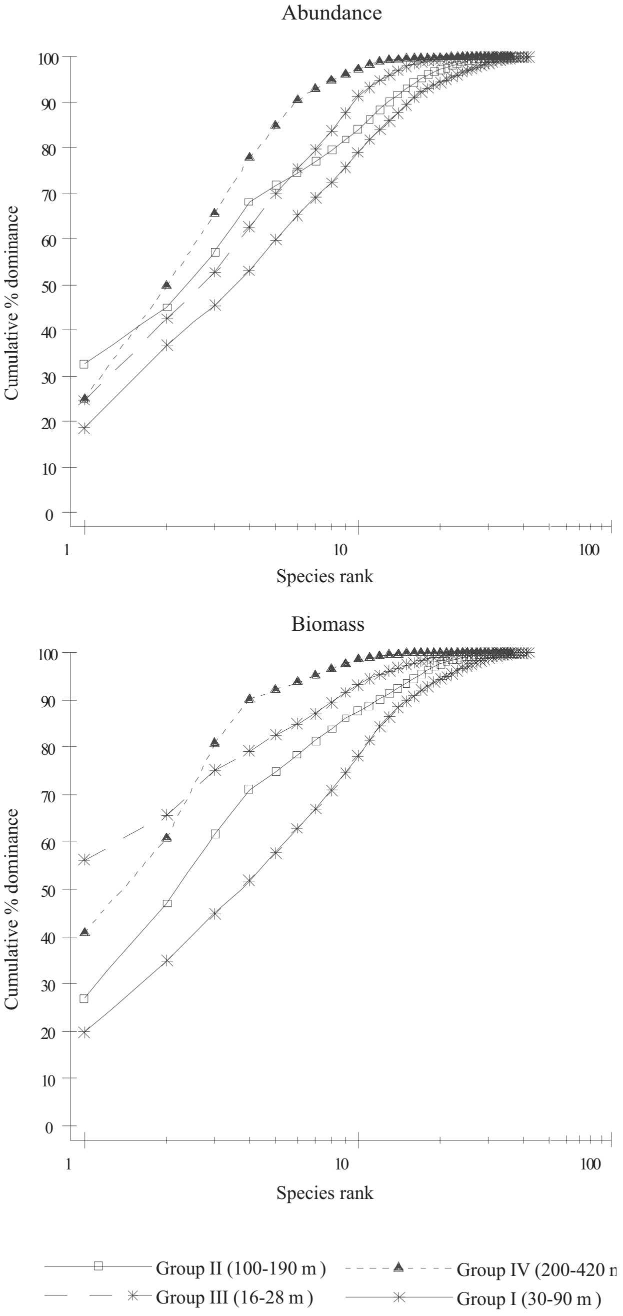

Fig. 2. – Cumulative species richness curves in the four groups identified by cluster analysis

Table 2. Estimates of commercial / non commercial ratio by number and weight for species in each group identified by cluster analysis

Commercial / non-commercial ratio	**Group III (16-28 m)**	**Group I (30-90 m)**	**Group II (100-190 m)**	**Group IV (200-420 m)**
Number	1.30	0.79	1.03	0.70
Weight	1.53	0.96	1.10	0.74

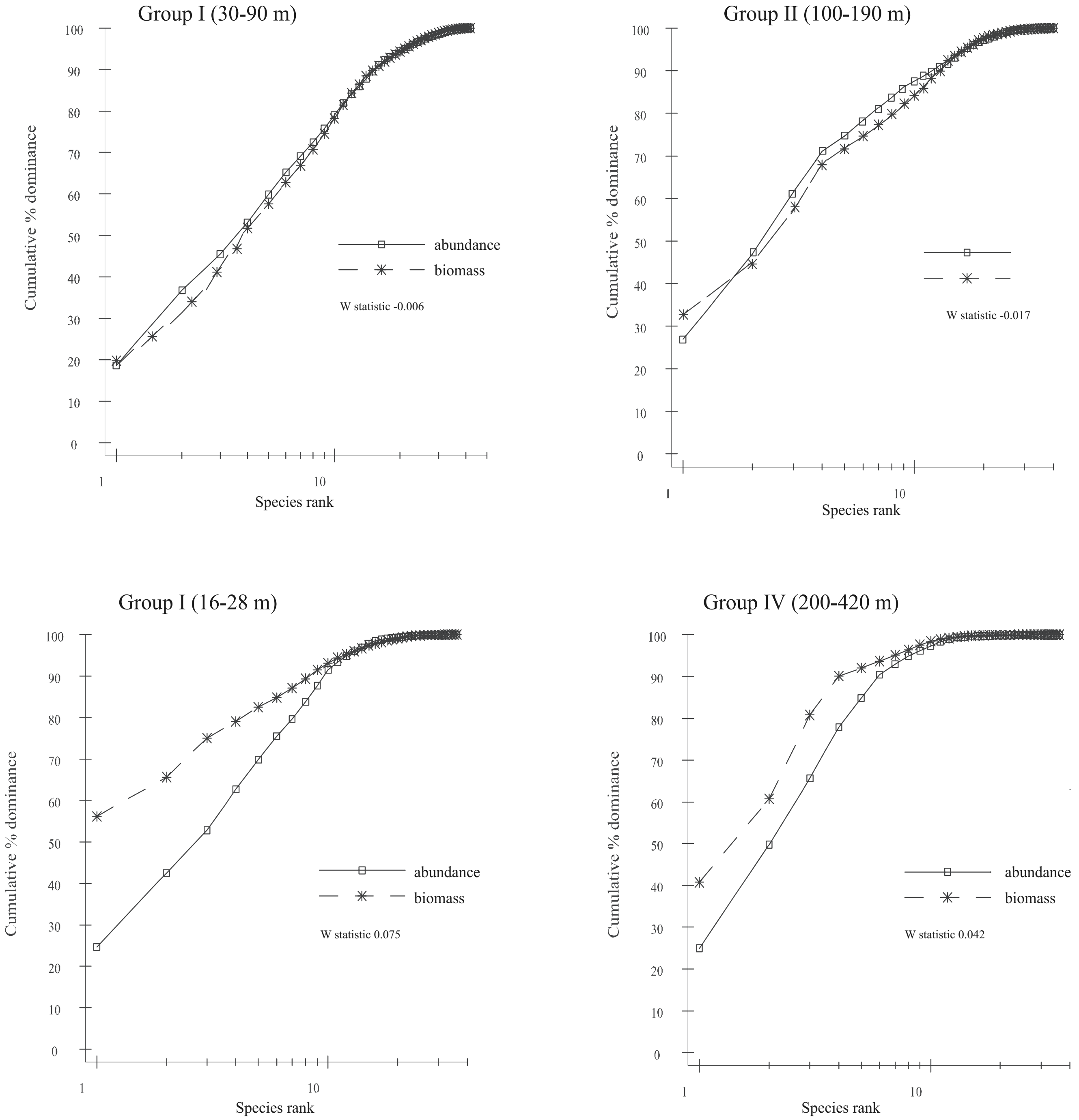

Fig. 3. – Comparison of *k*-dominance curves (abundance and biomass) for the demersal fish communities between the four station-groups from the Thracian Sea and Thermaikos Gulf

Significant differences in mean species abundance, biomass and diversity indices existed between the four station-groups (Fig. 4). The highest values of these parameters were found in samples from the continental shelf (Groups II and III, 30-190 m depth). A converse trend was noted from 200 m down to the maximum depth sampled (Group IV), as well as for the shallowest stations (<30 m, group I). However, ecological parameters appeared to be more or less uniform at depths between 30-190 m (P>0.05, Tukey HSD test). A steady decrease was observed for the stations of the upper slope together with the shallow-water coastal stations.

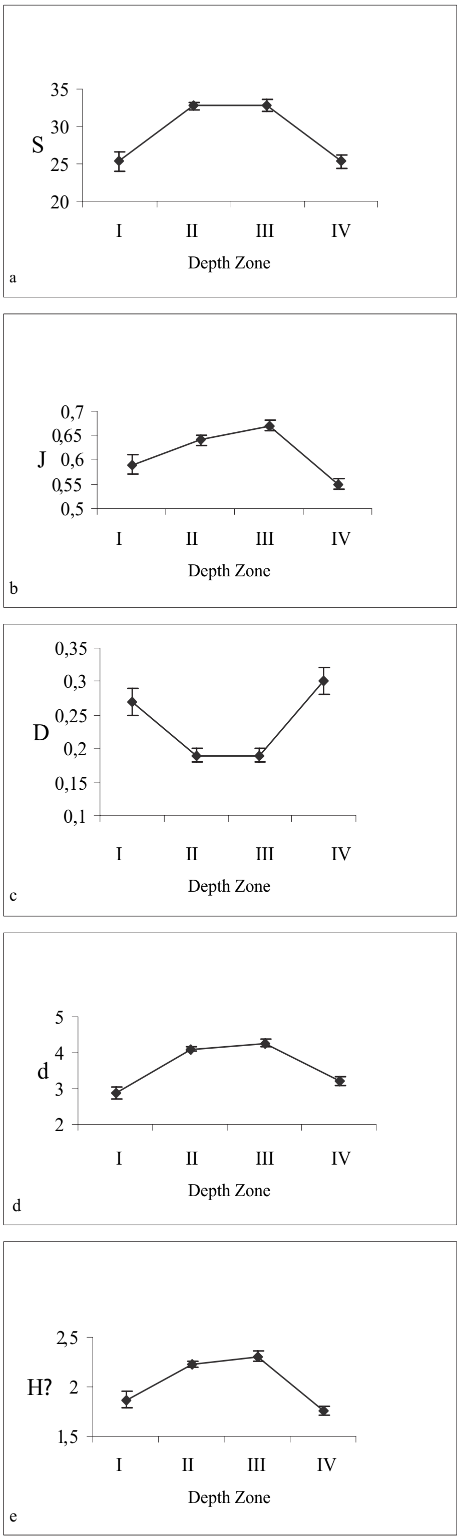

Fig. 4. – Ecological parameters (a : number of species, b : evenness, c : dominance, d : richness, e : Shannon-Wiener diversity) by depth zone (I : 16-28 m, II : 30-90 m, III : 100-190 m, IV : 200-420 m) for the demersal fish communities in the Thracian Sea and Thermaikos Gulf

DISCUSSION

Four distinct demersal fish assemblages were clearly associated with the topography of the study area. A shallow assemblage reached to about 30 m and represents coastal shallow bottom fauna of the continental shelf. Two assemblages corresponded to the middle (30-90 m) and deeper (100-190 m) parts of the continental shelf, and a deep assemblage extended beyond that depth which represents the upper slope. The continental shelf assemblages exhibited greater abundance and contained species of commercial interest such as : *Merluccius merluccius*, *Mullus barbatus*, *Mullus surmuletus, Pagellus erythrinus,* and *Trisopterus minutus capelanus*. The upper slope assemblage is characterized by the predominance of species like *Micromesistius poutassou*, *Gadiculus argenteus argenteus*, *Argentina sphyraena* and *Hymenocephalus italicus*, which are small and not commercially important. The main determining feature associated with the structure of the demersal fish assemblages is depth, as it reflects the changes from the continental shelf to the continental slope. However, other bottom and oceanographic characteristics must also play a role, at least for structuring assemblages on the continental shelf. These include the gradient in eutrophy, fresh/brackish water runoff, temperature and salinity differences along a NNW to SSE axis, and differences in the extent and the bottom type of the continental shelf (STERGIOU *et al.*, 1997). Nevertheless, the most important quantitative boundary for all areas was located around 200 m, a depth separating the species of the continental shelf from those of the upper slope extending down to 500 m.

High species richness and diversity characterized the continental shelf, but both variables decreased markedly at the deepest waters, while the reverse was true for species dominance. On the other hand, evenness also decreased with depth, but remained rather constant at depths between 30-190 m, indicating little variability in the numerical codominance of species over the continental shelf. The disparities in these general trends for the shallowest depths (group III) may be attributed to the more variable environmental characteristics (temperature and salinity) in shallow coastal waters. The *k*-dominance analysis suggested that the spatial trend in diversity and dominance was a strong feature of the species assemblages under study, with dominance being the highest in group IV. Consequently it appears that the highest values of species diversity at depths between 30-190 m, coincided with those depths where fishing pressure has been the greatest.

Increasing levels of disturbance have generally been considered to decrease diversity, species richness and evenness. These observations have also been made in many studies as response of demersal fish communities to intense fishing effort (GREENSTREET & HALL, 1996 ; RIJNSDORP *et al.*, 1996 ; HALL, 1999 ; JENNINGS *et al.*, 1999). However, recent theories on the influence of disturbance or stress on diversity suggest that at intermediate levels of disturbance, diversity could be the highest (MURAWSKI, 2000). Fishing might cause major species replacement but the actual changes in their reletive abundance are rather subtle. Other changes in assemblage's species composition generally involve relatively rare species and thus indices based on multispecies information do not always reflect major species replacement events (Murawski, 2000). Therefore, depending on the starting point of the community in relation to existing stress levels, increasing levels of stress may either result in an increase or decrease in diversity. Bianchi *et al.* (2000), who investigated whether changes in diversity and dominance of demersal fish communities could be related to fishing, concluded that the largest changes in diversity appeare to be due to changes in evenness or species richness, or both, often leading to an increase in diversity in response to heavy exploitation. Since diversity measures have a specific sensitivity to changes in weight or numbers, dominant or rare species occurrrences, evenness among species and other attributes (Maurawski, 2000), no consensus has developed yet on the utility of traditional diversity indices as a measure of ecosystem overfishing (Jennings & Reynols, 2000 ; Rice, 2000).

Some spatial effects of fishing in the study area were adequately well illustrated by abundance/biomass comparison (*ABC*) method. The logic behind using *ABC* curves to evaluate effects of perturbations is that in undisturbed communities the presence of large organisms results in the biomass curve lying entirely above the abundance curve, due to the dominance of few large species each represented by few individuals (Warwick & Clarke, 1994). Under environmental stress the communities become increasingly dominated by large numbers of small individuals and the abundance curve lies entirely above the biomass curve. In moderate disturbed communities these curves closely coincident and may cross over one or more times (Warwick, 1986). This method has successfully been used for assessing the degree to which macrobenthic communities respond to increasing levels of pollution-induced disturbance (Warwick, 1986 ; Warwick *et al.*, 1987 ; Warwick & Ruswahyuni, 1987 ; Meire & Dereu, 1990 ; Warwick & Clarke, 1994). Recently, Penczak & Kruk (1999) who employed the *ABC* comparison method for detecting human impacts on freshwater fish populations reported that it proves a useful tool for indicating disturbance in fish communities. Although *ABC* curves have not been widely used for evaluating fishery impacts on fish community structure, it appears, in the present study, that they can be a useful tool as an indicator of overfishing. The biomass and abundance curves are close together, crossing each other at depths between 30 and 190 m, where fishing pressure is the highest. Together with the negative values of *W* statistics obtained, these results indicate moderate disturbance of demersal fish communities. Also present in these communities are small, non-commercially important fish species, as confirmed by SIMPER analysis. These species are numerically dominant but do not represent a large proportion of the community biomass.

Studies in other areas, based on extended time series during which major increases in fishing effort took place, indicate that fishing leads to a decrease in catches and to increases in non-commercial species (Overholtz & Tyler, 1985 ; Rothschild, 1992). Furthermore, there is evidence that the size structure of demersal fish communities is affected by fishing (Pauly *et al.*, 1998). The overall trend is one of a reduction in large fish and a relative increase in small fish (Bianchi *et al.*, 2000 ; Zwanenburg, 2000). In the present study, the fish assemblages under consideration have suffered a long history of fishery exploitation. Therefore overfishing has affected the population structure and densities of the demersal fish communities, at least at depths up to 200 m, where most of the fishing activity is focused. It is possible that the organization of the demersal fish assemblages analysed is determined to a great extent by unidirectional trend induced by fishing, bottom topography and oceanographic features of the study area.

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Distribution and abundance of sepiolids (Mollusca : Cephalopoda) off the north-eastern Greek coasts

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ABSTRACT. Sepiolids are a lesser known group of cephalopods. This paper aims to increase knowledge of their distribution and abundance in the NE Mediterranean.

A total of 3404 sepiolids were collected off the north-eastern coasts of Greece, between 17 and 400 m of depth, during four seasonal trawl surveys carried out from November 1992 to August-September 1993. Nine species were identified *: Neorossia caroli, Rondeletiola minor, Rossia macrosoma, Sepietta neglecta, Sepietta oweniana, Sepiola affinis, Sepiola intermedia, Sepiola ligulata* and *Sepiola rondeleti*.

S. oweniana was the most abundant species among them, followed by *R. minor, R. macrosoma* and *S. rondeleti.* The results of multivariate analysis, based on Bray-Curtis similarity indices, showed the presence of three main groups : one related to the shallower hauls near the coast (<60m) where *S. rondeleti* and *S. intermedia* were more frequently caught, a second one consisting of hauls carried out at depths 55-105 m, in which *S. oweniana* was the dominant species, and a third one with deeper hauls characterised by the highest abundance of *S. oweniana, R.. minor* and *R. macrosoma.*

Length frequencies and maturity stages are presented by season and sex for the four most abundant species. Seasonal changes in the bathymetric distribution of these species are also discussed in relation to their life cycle.

KEY WORDS : cephalopoda, sepiolidae, Aegean, Mediterranean.

INTRODUCTION

Sepiolids are among the least known groups of cephalopods in the Mediterranean Sea at least with regard to their distribution and life history at sea. Although they present little interest for fisheries they seem to play an important role in the marine food webs since members of this family have been frequently found in the stomach contents of various marine organisms such as dolphins, sharks, demersal and pelagic fishes (BELLO, 1991, 1996, 1999; WÜRTZ et al., 1992; BLANCO et al., 1995; ORSI-RELINI et al., 1994, 1995).

Cephalopod species of the Sepiolidae family have been recorded in the Aegean Sea quite recently (KATAGAN & KOCATAS, 1990; D'ONGHIA et al., 1991,1996; SALMAN et al., 1997, 2002; LEFKADITOU & KASPIRIS, 1998; LEFKADITOU et al., 1999; KOUTSOUBAS et al., 2000). Within the last decade, biogeographic knowledge of sepiolids has greatly increased also in other areas of the western and central Mediterranean Sea (TURSI & D'ONGHIA, 1992; VILLANUEVA, 1992; BOLETZKY, 1995, JEREB et al., 1997; CASALI et al., 1998; QUETGLAS et al., 2000; SÁNCHEZ & DEMESTRE, 2001; GONZÁLEZ & SÁNCHEZ, 2002), as well as, in the Levantine basin (SALMAN et al, 1998; 2002) and the Marmara Sea (KATAGAN et al, 1993; ÜNSAL et al., 1999).

This work concerns the distribution and abundance of the sepiolid species found at the northernmost part of the Aegean Sea. In addition seasonal distribution of the most abundant species, *Sepietta oweniana, Rondeletiola minor, Rossia macrosoma* and *Sepiola rondeleti*, was examined in relation to their size and maturity.

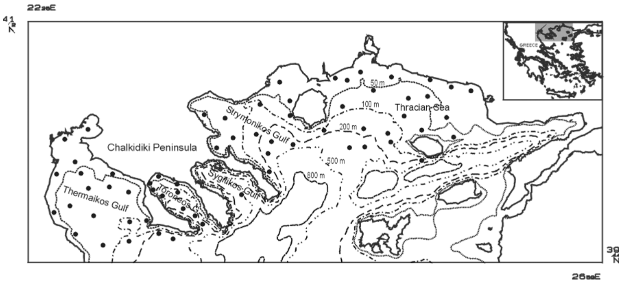

Fig. 1. – Illustration of the area investigated and the sampling stations of trawl surveys carried out from November 1992 to September 1993.

MATERIAL AND METHODS

Samples were collected from four bottom trawl surveys carried out seasonally from November-December 1992 to August-September 1993. The geographical area investigated extends off the coasts of north-eastern Greece, consisting of Thracian Sea, Strymonikos, Sygitikos, Toroneos and Thermaikos gulfs (Fig. 1). Four depth strata, 1-50, 51-100, 101-200 and 201-400 m, were considered and sampling was based on random-stratified design. A commercial trawler (115 tons gross tonnage, 250 Hp twin engines) and the typical nylon commercial bottom trawl net (16 mm cod-end mesh size from knot to knot) were used. Hauls were performed during daytime and ranged from 30 to 60 min in duration.

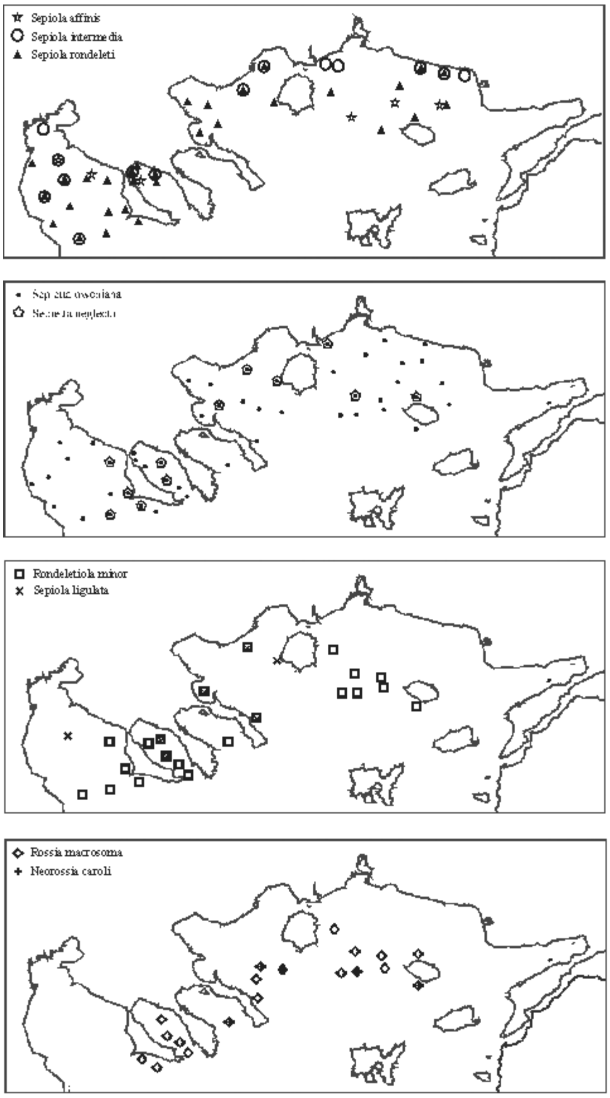

Fig. 2. – Distribution of sepiolid species in the studied area.

Sepiolids were present in 126 out of the 148 hauls performed in total. The specimens caught at each station were preserved in 5% formalin in sea water, and identified at the laboratory following the key for sepiolids in Guerra (1992). Dorsal mantle length (in mm), weight (in g), sex and maturity stage were reported for each specimen together with the haul data (date, location, duration, depth). A three stage scale : immature, maturing, mature, (Juanico, 1979) was used for sexual maturity.

To detect zonation patterns, the data of the survey carried out in August-September 1993 were considered because of the greater number of hauls performed during this survey. The data matrices comprising the numbers of individuals per hour of trawling of each species and station were log (x+1) transformed, and the haul-similarity percentage was calculated using the Bray-Curtis coefficient (Bray & Curtis, 1957) by the PRIMER-v5 software (Clarke & Gorley, 2001).

To investigate seasonal variation in the abundance and distribution of *Sepietta oweniana, Rondeletiola minor, Rossia macrosoma* and *Sepiola rondeleti*, the mean catch per unit of effort (CPUE) in number of individuals per fishing hour was calculated by species per depth stratum and survey, as well as the seasonal length-frequency distributions and percentages of maturity stages by species and sex.

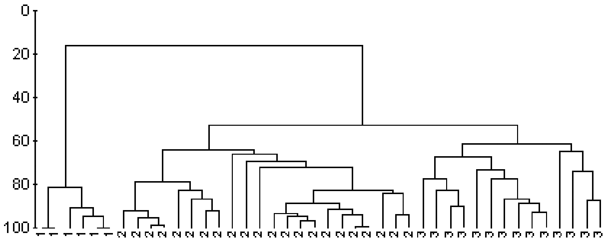

Fig. 3. – Dendrogram of the hauls carried out by bottom trawl in September 1993 off the north-eastern Greek coasts, using group-average linking of Bray-Curtis similarities calculated on log(x+1) transformed numbers of individuals of sepiolid species per fishing hour. 1 : cluster of shallower hauls (30-60m), 2 : hauls at intermediate depths (50-100m), 3 : deeper hauls cluster (over 100 m).

RESULTS

Taxonomic composition and species assemblages

A total of 3404 specimens comprising nine species belonging to two sepiolid subfamilies were collected between 17 and 400 m of depth (Table I). *S. oweniana* was the most abundant species followed by *R. minor, R. macrosoma* and *S. rondeleti.*

Dominant species were widely distributed over the whole study area, whereas the less frequently caught *S. affinis* was not found in Strymonikos gulf, *S. ligulata* was absent from catches in the Thracian Sea and the bathybenthic *N. caroli* did not appear in the deep hauls at Toroneos and Thermaikos gulfs (Fig. 2).

The results of the multivariate analysis, based on Bray-Curtis similarity indices, showed the presence of three main clusters (Fig. 3) : one consisting of hauls carried out at depths 30-60 m, another related with the depth stratum 50-100 m and a third one with deeper hauls (over 100 m). Although most of the species were present in several clusters, the species composition and catch rates distinguish them from each other. *S. rondeleti* and *S. intermedia* were the species more frequently caught in the shallower hauls (Table I), *S. oweniana* was the dominant species at depths between 50 and 100 m, whereas the deep-haul group (100-400 m) was characterised by the highest abundance of *S. oweniana, R. minor* and *R. macrosoma.*.

Seasonal distribution of the most abundant sepiolids.

S. oweniana

Over all, 2411 specimens were caught during the four surveys, at depths ranging between 40 and 400 m. Higher CPUE indices were estimated for waters deeper than 100 m (Fig. 4), where smaller individuals (ML<22 mm) generally constituted the greatest part of the catches (Fig. 5). Differences in the bathymetric distribution by size

TABLE 1

Number of individuals, depth range and catch rates in each bathymetric stratum (f%, percentage frequency of appearance in hauls, CPUE in number of individuals per fishing hour) for sepiolids caught by bottom trawl off the north-eastern Greek coasts from November 1992 to September 1993.

Species	**Number of individuals**	**Depth range (m)**	**Depth stratum**							
			<50		**50-100**		**100-200**		**200-400**	
			f%	**CPUE**	**f%**	**CPUE**	**f%**	**CPUE**	**f%**	**CPUE**
Sepiolinae										
Sepiola afinis	5	40-89	2.6	0.1	4.1	0.1				
Sepiola rondeleti	155	24-195	35.9	1.5	63.3	3.0	25.0	1.0		
Sepiola intermedia	34	17-113	17.9	1.2	2.0	0.1	3.6	0.3		
Sepietta oweniana	2411	40-400	7.7	0.3	87.8	16.6	100.0	29.0	90.3	43.9
Sepietta neglecta	64	24-262	2.6	0.4	8.2	0.6	17.9	0.9	6.5	0.6
Rondeletiola minor	360	66-338			8.2	0.2	64.3	5.4	38.7	8.9
Sepiola ligulata	14	80-328			4.1	0.1	14.3	0.3	9.7	0.2
Rossinae										
Rossia macrosoma	239	78-400			2.0	0.0	35.7	4.3	90.3	5.5
Neorossia caroli	124	237-400							32.1	4.0

TABLE 2

Maturity stages seasonal percentages and mantle length ranges of sepiolids collected off the north-eastern Greek coasts from November 1992 to September 1993

Species	**Sex**	**Maturity**	**Cruises**				**ML (mm)**	
			I	**II**	**III**	**IV**	**range**	**mean**
S. oweniana	females	immature	19	20	26	54	11-26	18
		maturing	26	21	25	15	14-29	21
		mature	55	59	49	31	18-35	25
	males	immature	1	0	3	7	12-20	16
		maturing	4	7	15	7	13-24	18
		mature	95	93	82	86	14-30	22
R. macrosoma	females	immature	62	61	30	35	15-50	31
		maturing	15	28	39	26	30-51	40
		mature	23	11	31	39	38-84	55
	males	immature	53	22	3	28	14-33	22
		maturing	12	6		3	17-28	24
		mature	35	72	97	70	26-51	39
R. minor	Females	immature		2			12	
		maturing	20	3	5	11	12-14	13
	Males	mature	80	95	95	89	13-21	16
		maturing	5			1	10-11	11
		mature	95	100	100	99	11-20	16
S. rondeleti	females	immature	20		8	8	14-22	18
		maturing	40		8	8	16-20	18
		mature	40	100	84	84	13-27	20
	males	mature	100	100	100	100	12-30	18
N. caroli	females	immature	75	90	20	60	15-34	26
		maturing	25	5	20		23-32	29
		mature		5	60	40	31-43	39
	males	immature	100	7		67	17-27	21
		maturing		23	12		22-29	24
		mature		70	88	33	22-40	31
S. neglecta	females	maturing		10			13	
		mature	100	90	100	100	12-23	17
	males	immature		20	50	25	15	
		maturing			50		19	
		mature	100	80		75	13-23	18
S.affinis	females	immature		100			16	
		mature	100				15	
	males	mature		100			16	
S. intermedia	females	mature	100		100	100	14-18	16
	males	mature	100	100	100		13-21	16
S.ligulata	females	mature	100	100		100	13-17	16
	males						22-40	31

were mainly observed in summer and autumn, when larger individuals (ML>22 mm) concentrated in shallow waters. Most males caught were mature, their percentage extending to 90% in November and March. Mature females represented 44.5% of the examined specimens, with a maximum percentage in March and a minimum in September (Table II). An analysis of the occurrence of mature individuals in relation to depth, showed higher percentages of mature females at depths less than 100 m all year round, whereas, no trend was identifiable in the distribution of mature males.

R. minor

This species is one of the smallest sepiolids (Table II). Mature individuals comprised over 95 % of the total of 360 individuals caught (Table II). The greatest part of the population was distributed deeper than 200 m from March to September. In November ‘92 the species was less abundant (Fig. 4) with a lower percentage of mature males and females (Table II), and only some smaller individuals (ML<16 mm) was fished at depths 200-400 (Fig. 5)

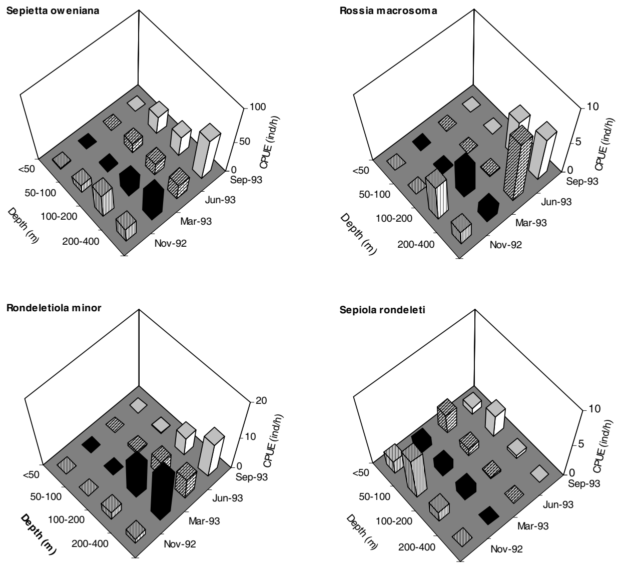

Fig. 4. – Seasonal abundance of *Sepietta oweniana, Rondeletiola minor, Rossia macrosoma* and *Sepiola rondeleti,* by bathymetric stratum in the study area, from November ‘92 to August-September ‘93.

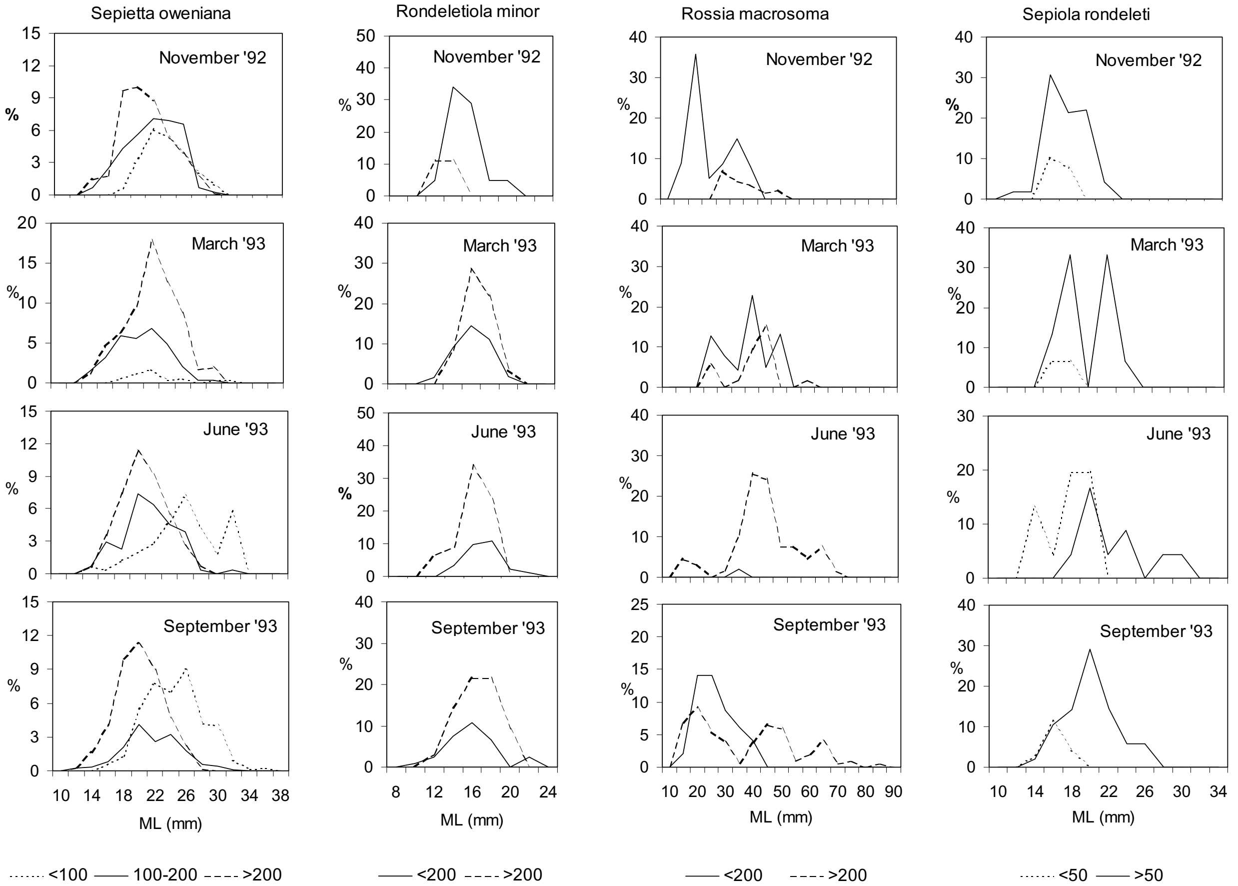

Fig. 5. – Length frequency distribution of *Sepietta oweniana*, *Rondeletiola minor*, *Rossia macrosoma* and *Sepiola rondeletti* by season and depth zone.

R. macrosoma

A total of 239 specimens were fished between 78 and 400 m. However findings at depths lower than 148 m were reported only in the Thracian Sea. As shown in Figs 4 and 5, in November and March the species was more abundant at depths 100-200 m, in June the population consisted mostly of larger individuals (ML>30 mm) distributed deeper than 200 m, whereas in September the strong recruitment in shallower waters resulted in almost equal abundance of the species in the two bathymetric strata, 100-200 and 200-400 m. Mature individuals of both sexes were mainly found deeper than 200 m all year, where as spawns of this species were always collected deeper than 250 m. The maximum percentage of mature females was observed in September and that of males in June.

S. rondeleti

This species was the most abundant of the genus *Sepiola* (Table I), with 153 individuals collected between depths 24 and 195 m. Large individuals (ML>20 mm) during all cruises were found deeper than 50 m (Fig. 5). Smaller ones were mostly recruited during early summer in shallow waters but during the rest of the year they were found deeper than 50 m. In March all males and females caught were mature.

DISCUSSION

The nine species found off north-eastern Greek coasts cover 2/3 of the 12 sepiolids recorded from the Aegean Sea (LEFKADITOU, unppublished data). Among the sepiolid species missing from our collection, *Sepiola robusta* and *Sepietta obscura* have been rarely caught in the southern and eastern part of the Aegean Sea (SALMAN et al., 1997, 2002), whereas the pelagic *Heteroteuthis dispar* was the most common cephalopod collected by frame mid-water trawl over the trench south of Chalkidiki peninsula (LEFKADITOU et al., 1999). In the Mediterranean Sea, up to now, there are records for 15 sepiolid species (BELLO, 1995), including three more species: the infralittoral *Sepiola aurantiaca,* and the bathyal *Sepiola steenstrupiana* and *Stoloteuthis leucoptera*, which generally have been very rarely caught.

The bathymetric distribution of the identified species and their numerical consistence in the catches is generally in accordance with what has been reported for other Mediterranean areas (ORSI-RELINI & BERTULETTI, 1989; BOLETZKY, 1995; JEREB et al., 1997, 1998; SÁNCHEZ & DEMESTRE, 2001).

S. oweniana was the most abundant and eurybathic sepiolid species, as has been observed in other areas of the Mediterranean Sea (BOLETZKY, 1995). Seasonal changes in the species abundance by depth are related to recruitment variation in deeper grounds, as well as to migration of larger individuals in shallower waters from early summer to autumn most probably for spawning since highest percentages of mature females were found in these depths. Similar migration has been reported by MANGOLD-WIRTZ (1963) in the northern Catalan Sea, whereas there was no evidence of such migration in areas with more abrupt waters such as the North Aegean Sea (D'ONGHIA et al., 1996) and the Strait of Sicily (JEREB et al., 1997).

R. minor and *R. macrosoma* seem to concentrate in deeper waters during summer and early autumn, whereas recruitment is mainly observed in November at depths shallower than 200 m. Similar concentration on the slope has been noted during summer in the Ligurian Sea for *R. minor* (ORSI-RELINI & BERTULETTI, 1989) and in the lower Tyrrhenian Sea during autumn for *R. macrosoma* (BOLETZKY, 1995). However, in the northern Catalan Sea, MANGOLD-WIRTZ (1963) observed a greater abundance of mature specimens on detritic bottoms shallower than 130 m during summer, supposing a population movement towards shallower waters for reproduction. The collection of *R. macrosoma* eggs, as well as the higher percentages of mature males and females on the slope of our study area, are not in agreement with the above consideration**.** The occurrence of mature individuals of these species all year-round indicates an extended spawning period, thus suggesting that the species' seasonal migrations should be rather attributed to other reasons than reproduction. Dense waters, rich in nutrients, formed over the shallow waters of the shelf areas of the North Aegean Sea during winter, slide towards the deep cavities (GEORGOPOULOS et al., 1988). This may result in higher biological productivity in deeper waters and could probably be related to the seasonal movement of these species.

R. minor was the second most abundant sepiolid species, caught mostly together with *S. oweniana* and *R. macrosoma.* These three species show an aggregation-forming behaviour as also reported for other areas (BOLETZKY, 1995), although the number of caught specimens per haul very rarely exceeded 100 in the area investigated. On the contrary, species of the genus *Sepiola* presented a low frequency of occurrence in the catches, never exceeding ten individuals per haul. Among them *S. rondeleti* was most frequently caught, extending its maximum depth distribution previously recorded (GUERRA, 1982). This species has been generally poorly represented in samples from the Mediterranean Sea, most probably due to its preference for shallow waters (JEREB et al., 1997).

Mature specimens of both sexes of the species caught during this study were generally present all over the year (Table II), indicating an extended reproductive period of sepiolids. For the species of the Rossinae subfamily, a seasonal peak of spawning activity, as well as earlier maturation of males could be detected, as has also been mentioned for other areas (D' ONGHIA et al., 1993, 1994; JEREB et al., 1998). For the species of Sepiolinae subfamily, as mentioned also by other authors (JEREB et al., 1997), mature specimens represent higher percentages with no substantial differences related to seasons. However it has to be noted that the low percentages of immature individuals of the species of the Sepiolinae subfamily and especially those of smaller sizes (Table II), may be due to the low efficiency of the commercial trawl net used in capturing smaller individuals.

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Analysis of the post-vitellogenic oocytes of three species of Danubian Acipenseridae

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ABSTRACT. Post-vitellogenic oocytes of beluga (*Huso huso* Linnaeus, 1758), Russian sturgeon (*Acipenser gueldenstaedtii* Brandt, 1883) and sterlet (*Acipenser ruthenus* Linnaeus, 1758), sampled downstream of the "Iron Gate II" dam on the Danube River, were characterised according to diameter, dry mass, water and protein contents. All oocytes examined were ovoid in shape with the major diameter being measured in the animal-vegetal axis. The beluga oocytes were the largest, with major and minor diameters of 4.18 ± 0.13 and 3.61 ± 0.14 mm, respectively. The oocytes of the Russian sturgeon were the next largest, with major and minor diameters of 3.69 ± 0.16 and 3.36 ± 0.15 mm, respectively, while those of the sterlet were the smallest, with major and minor diameters of 2.40 ± 0.10 and 2.14 ± 0.07 mm, respectively. Values for oocyte wet and dry mass (mg/ind) ranged from 25.9-32.1 for wet mass and 12.2-15.5 for dry mass of the beluga oocytes, 18.9 ± 1.4, and 9.01 ± 0.12 for wet and dry mass of the Russian sturgeon oocytes, to 6.5 ± 0.3 and 3.07 ± 0.14 of the sterlet oocytes. The water content of the oocytes of all three sturgeons was very similar (51-53% of wet mass). The protein content (% of dry mass) was highly conservative among the species at 53.0 ± 2.0, 55.9 ± 3.8 and 50.0 ± 1.2 for the oocytes of beluga, Russian sturgeon and sterlet, respectively.

KEY WORDS : Russian sturgeon, beluga, sterlet, oocytes, Acipenseridae, yolk proteins

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INTRODUCTION

The Acipenseriformes live almost exclusively in the Northern Hemisphere with half of the extant number of species occurring in Europe, mostly in the Ponto-Caspian region (Billard & Lecointre, 2001). Recently several associations have recommended that the status of beluga (*Huso huso*) be upgraded to Appendix I under current CITES listings since it has almost been extirpated from the Black Sea (Vecsei et al., 2002). Indeed many of the stocks of sturgeons have dramatically decreased, primarily as a result of over fishing and habitat deterioration. Habitat loss is predominantly caused by pollution and damming of rivers, which blocks migration and access to proper spawning grounds (STEVENSON & SECOR, 1999 ; Vecsei et al., 2002).

In Yugoslavia there was a significant drop in catch of all sturgeon species after 1970 and 1984, when the lower stretch of the Danube was dammed by, respectively, Djerdap I and II hydropower stations (JANKOVIC, 1993 ; VECSEI et al., 2002). Today, species of Acipenseridae, except sterlet, occur in Serbia and Montenegro only in a 17.8 km stretch of the Danube River, from the Djerdap II dam to the border with Bulgaria, close to the Timok River mouth.

Presently sturgeon farming, outside of Serbia and Montenegro, yields more than 2,000 tons of fish per year and about 15 tons of caviar. Such efforts could contribute to a reduction of fishing pressure on wild stocks (BILLARD & LECOINTRE, 2001).

The most significant research on the biology and cultivation of sturgeons was conducted in the former Soviet Union (DETTLAFF et al., 1993). Since the collapse of the Soviet Union, however, virtually all research effort has ceased through lack of funding.

The situation is very much the same in the countries bordering the lower region of the Danube (Serbia and Montenegro, Romania, Bulgaria and Ukraine). Despite the research effort of DETTLAFF et al. (1993), some problems regarding normal growth and success of fertilization of the oocytes and eggs still exist. According to AMIRKHANOV (1974) earlier studies suggested that protein concentration in oocytes can be a valid indicator of the staging, quality and successful fertilization and normal growth of the fertilized eggs (BRASHE, 1964 ; FEDOROVA & GRUDANOV, 1968). More recently, CHEBANOV (2001) conducted similar research on Russian sturgeon (*Acipenser gueldenstaedtii*) in which he followed protein and water contents in the oocytes over a ten year period. Together with other physiological parameters, these findings helped him to evaluate reproductive quality of the natural and artificially reared populations.

Consequently, the goal of this investigation was to make a preliminary comparative study of the biometry, gravimetry and protein contents of the oocytes of three species of Danube sturgeons : beluga, Russian sturgeon and sterlet (*Acipenser ruthenus*).

MATERIAL AND METHODS

All females were sampled during the spring and fall of 2001 in the Danube, downstream of "Iron Gate II" dam (863 km from the Danube delta). Oocytes were sampled from three beluga females (BeB, BeC, BeD) caught in April and May, total length (TL) = 282, 287, 304 cm and wet mass (W) = 161, 194.5, 159.6 kg respectively, one Russian sturgeon (GuA) caught in October, TL = 180 cm, W = 25 kg and two sterlets (RuA, RuB) caught in April, total length (TL) = 64, 68 cm and wet mass (W) = 1.3, 1.5 kg. The second sterlet (RuB) had undergone final oocyte maturation and provided ovulated eggs.

Major (D_1) and minor (D_2) diameters were measured in 0.9% NaCl. Wet masses were determined after removal of excess ovarian fluid, and the samples were frozen and stored at –20°C until lyophilisation, dry mass and protein content analyses.

Oocyte volume (V) was calculated using the formula :

$$v = \frac{4}{3} \bullet \pi \bullet \left[\frac{D_1}{2}\right] \bullet \left[\frac{D_2}{2}\right]^2$$

where D_1 and D_2 represent the major and minor diameters respectively.

Oocyte wet and dry masses were measured to the nearest 0.1 mg. Lyophilisation was performed for 48 hours.

Oocyte proteins were precipitated with 1 mL 6% trichloro-acetic acid TCA to remove free amino acids, then centrifuged (10,000 x *g*, 5 min, 4° C). The precipitate was washed once in 6% (TCA), then solubilised in 1M NaOH. Solubilisation was accomplished with sonification (3 x 15 sec at 400 Hz). Prior to analyses, 1 mL double-distilled water was added to give a final concentration of 0.5M NaOH. Following the addition of the Lowry reagents (Lowry et al., 1951), triplicate samples were read at 650 nm with a Pye Unicam spectrophotometer. Bovine serum albumin was used as standard.

RESULTS

The largest oocytes were obtained from beluga, and smallest from sterlet, while Russian sturgeon had intermediate sized oocytes (Fig. 1). The size classification was also evident for wet mass and dry mass, and reflected the size of the female caught. However, despite the differences in size, all oocytes had similar water content with values of 51-53% of wet mass. Similarly, the oocyte relative protein content (% of dry mass) was also conserved between the species and ranged from 50-56%.

Overall the data show that irrespective of size, the protein content and cell water are closely regulated components of the post-vitellogenic oocytes of the Danube sturgeons.

From one species only, the sterlet, we had the opportunity to sample oocytes (RuA) and ovulated eggs (RuB). From Fig. 1 it is possible to see that ovulated eggs of sterlet had bigger values for diameter, volume and protein content compared to the oocytes of the RuA female.

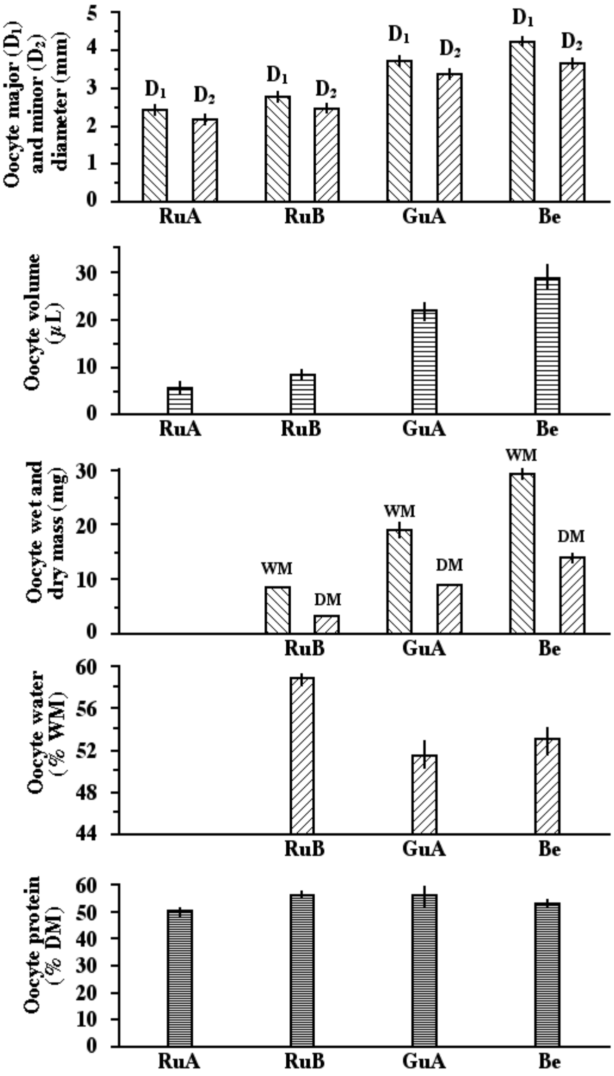

Fig. 1. – Major (D_1) and minor (D_2) diameter, volume, wet (WM) and dry (DM) mass, water and protein content of beluga (Be) oocytes, sterlet (RuA) oocytes, sterlet (RuB) eggs and Russian sturgeon (GuA) oocytes.

DISCUSSION

The data concerning oocyte biometry and gravimetry for three Danube sturgeon species were correlated with parental size. Beluga oocyte diameter, volume, wet and dry mass were the largest followed by Russian sturgeon, then sterlet.

Average diameters of three beluga oocytes were 4.18 mm for major and 3.61 mm for minor diameter. Data given by Holcik (1989) for this parameter were around 3.8 mm for major and 3.4 mm for minor diameter, which corresponded better to the data obtained for Russian sturgeon (3.7 and 3.4 mm). Between these two results are those (4.0 and 3.6 mm) obtained by Dettlaff & Ginsburg (1954). According to Berg (1949) 3.5 mm and 3.0 mm are average values for major and minor diameters respectively.

There are several data given for sterlet oocyte diameters by different authors. According to Holcik (1989) oocyte diameter is around 2.5 mm. Jankovic (1958) noted that oocyte diameters ranged from 2.0-2.9 mm for major axis and 1.8-2.8 mm for minor axis. Values obtained in the present study were 2.7 and 2.4 mm for the major and minor diameters of the ovulated eggs found in the abdomen of RuB, and 2.4 mm and 2.1 mm for the major and minor diameters of the post-vitellogenic oocytes of RuA.

Average wet mass of beluga oocytes was 29.3 mg, and 14.0 for its dry mass. Wet and dry mass for oocytes of Russian sturgeon were 18.9 mg and 9.0 mg, and 6.5 mg and 3.1 mg for sterlet oocytes. Chebanov (2001) found a difference in Russian sturgeon oocytes wet mass in the years 1991 - 2000. In that period, values ranged from 17.9 to 20.4 mg, which is very similar to results presented here.

Oocyte water and relative protein content of all three sturgeons were very similar. The water content results are at the lower range of 50-70 % reviewed by Kamler (1992) for freshwater fishes, and the protein content was similar to the lower range reviewed by Kamler (1992). Indeed the values found here for beluga are considerably lower than the recomputed 63% reported by Kamler (1992). Unlike the pelagic eggs of marine fishes (Finn et al., 2000 ; 2002a ; 2002b), sturgeon oocytes do not undergo proteolysis and hydration during final oocyte maturation (Finn et al., 2001 ; 2002c). Our findings suggest that, despite the difference in size of both female and oocyte, water content and protein levels are conservative aspects of the reproductive biology of sturgeons.

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Successional stages of experimental artificial reefs deployed in Vistonikos gulf (N. Aegean Sea, Greece) : Preliminary results

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ABSTRACT. In 1999 an artificial reef system, consisting of a protective zone (240 cubic modules) and a nucleus (9 Italian type and 9 French type artificial reefs), was constructed and deployed at cape Fanari (Vistonikos Gulf, North Aegean Sea) occupying an area of 6 Km2 (25m depth). Samples, (8 cement plates, 35cmx35cm) were collected seasonally with SCUBA-diving from March 2000 till May 2001. Overall 46986 individuals were counted belonging to 13 classes, while 88 species were recorded. Common biocoenotic parameters (numerical abundance, frequency, mean dominance) were calculated. Shannon-Weaver index ranged from 2.509 to 3.741 and evenness from 0.388 to 0.579, both exhibiting a maximum in summertime. The analysis revealed a clear dominance of Serpulids during the first three periods and of Peracarida for the last two. Filter-feeder organisms including *Pomatoceros triqueter*, *Spirobranchus polytrema* and *Corophium sextonae* dominated the samples. Two-way ANOVA indicated significant differences in numerical abundance of each taxon with time. However, no differences were recorded among taxon from the top and the base of the pyramids except for Gastropods,which showed a significant increase in numerical abundance at the top blocks. Cluster analysis provided a dendrogram with 6 groups at a 73% similarity level, 5 of which group together the replicates of each period, except one replicate, from the last period, that forms the 6th cluster. Filter-feeders appeared to be the prevailing organisms in artificial reefs communities.

KEY WORDS : artificial reefs, benthic communities, filter- feeder organisms, Aegean Sea.

INTRODUCTION

The establishment of artificial reefs is a measure of global importance for the management of coastal marine ecosystems (FITZHARDINGE & BAILEY-BROCK, 1989 ; RELINI et al., 1990). During the last ten years, artificial reefs have proved to be a very effective means for fishery enhancement (PICKERING et al., 1998). However, they can play an important role for the coastal zone marine biocoenoses, including protection from the mechanical impact of trawling, habitat restoration, increase of the spatial heterogeneity and variety of substrata on soft seabeds, aquaculture and, recently, tourism (BOMBACE et al., 1994 ; PICKERING et al., 1998). Consequently, the majority of the studies concern the potential and capability of these structures to act as fish attracting and aggregating devices. However, an aspect of artificial reef studies that is often overlooked is their colonization by sessile and other invertebrate organisms, which provide food and shelter for fish and crustaceans (CARTER et al., 1985).

Although artificial reefs have been deployed in Europe since 1960s, their use has increased in the last two decades (SANTOS & MONTEIRO, 1998). In Greece, the first experimental reefs were deployed in July 1998 (SINIS et al., 2000) and the first extensive protective zone with artificial reefs was established in October 1999, primarily in order to increase fish production and protect the existing *Posidonia oceanica* meadows. The aim of this study was to provide preliminary information on the successional stages of benthic invertebrates during the first year of the reef's deployment at cape Fanari (Vistonikos gulf).

MATERIAL AND METHODS

Description of the deployment area

The deployment area, located between Vistonikos Gulf and cape Corosmilou (N Aegean Sea) (Fig.1), included the nucleus of the artificial reefs (3.500 m^2) and the protective zone (6 km^2). The bottom of the study area slopes slightly offshore, forming a flat field at a depth of 20 m, which is covered by a dense, well-developed *Posidonia oceanica* meadow. However, during the last years, repeated mechanical damaging caused mainly by otter- and beam-trawling, resulted to serious regression of these meadows and their associated biota. Thus, the main part of the seabed consists of a completely degraded meadow, which is often replaced by muddy sheets containing organic detritus and characterized by the presence of *Turitella communis* (BELLAN-SANTINI et al., 1994). Only 25% of the area is covered by a well-developed and continuous *Posidonia oceanica* meadow. Seawater samples, at the broader coastal region, were carried out at approximately bimonthly intervals from October 1997 to April 1998, using NISKIN (5L) sampler. Nutrients (phosphate, nitrate, nitrite, silica, and ammonia), organic carbon, chlorophyll-a and phaeopigments concentrations for the critical periods (October and February) are shown in Table 1. The coastal area of Rodopi could be characterized as typically eutrophic, with relatively high primary productivity that, often, favours phytoplankton blooms (DOUNAS, unpubl. data). Moreover, prevailing currents are easterly and their velocity ranges from 1cm/sec to 24.4 cm/sec, with a mean value of 6.8 cm/sec (DOUNAS, 1998).

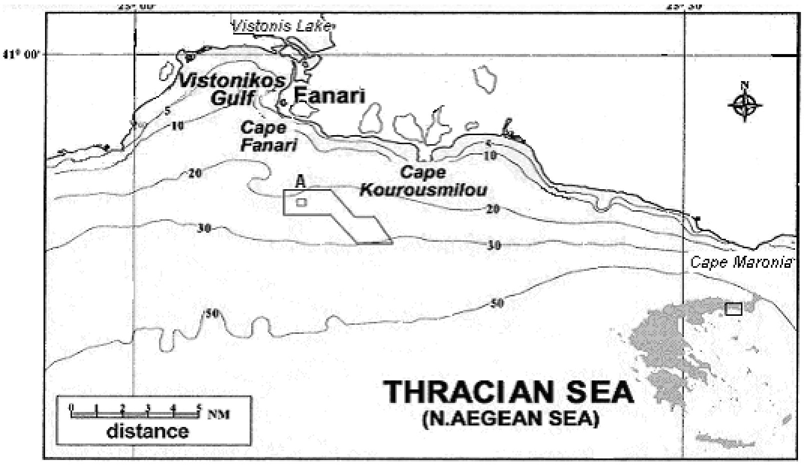


Fig. 1. – Location of the deployment area. Site A represents the protective zone and the nucleus.

TABLE 1

Nutrients, organic carbon (POC), chlorophyll-a and phaeopigments concentrations in Vistonikos Gulf during October 1997 and February 1998 (Mean value, Standard deviation and range).

Parameter	October 1997		February 1998	
	Mean value (SD)	Range	Mean value (SD)	Range
Chlorophyll (μ/L)	0.292 (0.387)	0.096-1.897	0.663 (0.29)	0.213-1.381
Phaeopigments (μ/L)	0.236 (0.386)	0.044-1.828	0.601 (0.252)	0.046-1.113
POC (μ/L)	499.8 (197.69)	308-1053	661 (208.4)	276-1029
Nitrate NO_3 (μM)	2.8 (0.989)	1.41-4.40	1.12 (0.53)	0.38-2.52
Nitrite NO_2 (μM)	0.46 (0.306)	0.14-1.38	0.42 (0.211)	0.11-0.97
Phosphorus PO_4 (μM)	0.056 (0.026)	0.035-0.160	0.115 (0.041)	0.065-0.2
Silica SiO_2 (μM)	2.68 (0.995)	1.12-4.78	3.04 (1.867)	1.26-9.65
Ammonium NH_4 (μM)	0.496 (0.149)	0.256-0.768	0.454 (0.304)	0.16-1.17

Description of the reef

Two groups of artificial reefs, located 25 m apart from each other, formed the nucleus zone of the deployment area. The first group was formed of 9 pyramids (Italian type), which are placed in a three-series arrangement. Each pyramid was made of 5 cubic concrete blocks (2x2x2 m), four at the base and one at the top, placed at about 15 m from each other. At the sides of the blocks holes of different diameter were created, increasing shelter availability (BOMBACE et al., 1994 ; ARDIZZONE & BOMBACE, 1983 ; BOMBACE, 1977 ; BOMBACE, ; RELINI & RELINI, 1989). The second group was consisted of nine more units, each one made of bulky cement-bricks on a cement base.

At the broader protective zone, 240 smaller units of artificial reefs (1,2x1,2x1, 2m), were placed on the seabed at distances ranging from 80 to 250 m. The aim of these units was, mainly, the prevention of the illegal trawling at the nucleus zone, in order to protect fish stocks and the meadow. Moreover, they provided additional hard substrata for benthic fauna thus increasing environmental carrying capacity of the reef.

Data collection

The survey of the colonization process was restricted to the Italian type units. For this purpose, square concrete plates (35x 35 cm) were placed at the 2 upper corners at each side of each block. A total of 5 samplings were carried out from March 2000 till May 2001. The initial sampling took place 5 months after immersion of the reef. At each sampling, 8 plates (3 from the top and 5 from the base block) were collected by divers, while visual monitoring of the reef was carried out using an underwater camera. The plates were transferred to the laboratory where the surface of each plate was scraped, washed through sieve with 0.5 mm mesh size and preserved in a 10% formalin solution. After sorting, all faunal elements were counted and identified to species level.

Data analysis

Common biocoenotic parameters, including numerical abundance (number of individuals/m^2), mean dominance (number of ind. of each species/ total number of ind.), frequency and total species richness were calculated for each period. Species diversity was estimated by using Shannon-Wiener (H') and Pielou's Evenness (J') indices based on $\log_2$ (BAKUS, 1990 ; HONG, 1983). Two-way analysis of variance was applied in order to check for significant differences in each taxon's mean numerical abundance with time and, also, to compare between replicates of each sample from different sites. Fisher's Least Significant Difference (LSD) test was used to compare across all pairs of group means when corresponding ANOVA tests were significant ($p<0.05$). Prior to performing these statistical tests, data were transformed ($\log_{10}$), when necessary, to meet the assumptions of ANOVA. Numerical abundance data were analyzed using multivariate techniques (i.e., cluster analysis and multidimensional scaling), based on the Bray-Curtis similarity, as adopted in the PRIMER package (CLARKE & WARWICK, 1994 ; CLARKE & GREEN, 1988). All data were transformed ($\log (x+1)$) in order to weight the contribution of common and rare species (KLUIJVER, 1997 ; CLARKE & WARWICK, 1994). The significance of the multivariate results was assessed by ANOSIM test.

RESULTS AND DISCUSSION

Overall 46,986 individuals were counted belonging to 13 classes, while 88 species were recorded (Table 2). During the first three sampling periods (March/2000, May/2000, July/2000) the dominant taxon was Polychaetes, mainly Serpulids, followed by Bivalves. During March/2000 and May/2000 the species are dominated by *Spirobranchus polytrema* (27.1% and 54.6% for the first and second period respectively), while in July/2000 this species was replaced by *Pomatoceros triqueter* (18.4%). Concerning Bivalves*,* *Anomia ephippium* showed the highest mean dominance during March/2000, May/2000 and July/2000, followed by *Hiatella arctica*. During December/2000 Polychaetes and Peracarida exhibited equal values of mean dominance (34.0% and 32.0% respectively) with *Pomatoceros triqueter* constituting on its own 28.7% of the mean dominance followed by *Corophium sextonae* (26.4%). Bivalves were the third dominant taxon (16.0%) represented mainly by *Hiatella arctica* (6.8%). During May 2001, settlement was characterized by the clear dominance of Peracarida (56.0%) with *Corophium sextonae (56.1%)* being the most important species.

TABLE 2

Species found at each sampling period (from March 2000 until May 2001) on the cement blocks immersed in Vistonikos Gulf (F: Frequency, mD: mean Dominance).

Species	Sampling period									
	March 2000		May 2000		July 2000		December 2000		May 2001	
	F	mD	F	mD	F	mD	F	mD	F	mD
Foraminifera	0	0	100	8,01	100	9,84	100	3,70	25	0,02
Calcarea										
Sycon sp.	0	0	0	0	0	0	0	0	87,5	0,22
Polychaeta										
Harmothoe spinifera (Ehlers, 1864)	37,5	0,23	25	0,05	37,5	0,04	87,5	0,24	100	0,25
Chrysopetalum debile (Grube, 1855)	0	0	0	0	0	0	0	0	12,5	0,004
Phyllodoce madeirensis(Langerhans,1880)	12,5	0,03	0	0	0	0	12,5	0,01	87,5	0,10
Kefersteinia cirrata (Keferstein, 1862)	0	0	0	0	0	0	0	0	12,5	0,004
Odontosyllis ctenostoma (Claperede, 1868)	12,5	0,03	0	0	0	0	0	0	0	0
Syllis hyaline (Grube, 1863)	0	0	0	0	0	0	12,5	0,01	100	0,37
Trypanosyllis zebra (Grube, 1860)	0	0	0	0	0	0	0	0	12,5	0,004
Autolytus edwardsii (Saint-Joseph, 1887)	12,5	0,09	0	0	0	0	0	0	0	0
Nereis rava (Ehlers, 1868)	0	0	12,5	0,01	12,5	0,01	62,5	0,35	100	1,13
Platynereis dumerilii (Fauvel, 1916)	12,5	0,03	25	0,03	37,5	0,10	75	0,24	37,5	0,03
Glycera tesselata (Ehlers, 1868)	0	0	0	0	0	0	0	0	25	0,01
Eunice vittata (delle Chiaje, 1929)	0	0	12,5	0,01	0	0	50	0,05	87,5	0,11
Lysidice ninetta (Audiuin & Edwards, 1834)	0	0	0	0	0	0	25	0,02	12,5	0,004
Marphysa fallax (Marion & Bobretzky, 1857)	0	0	0	0	0	0	0	0	12,5	0,01
Scoletoma funchalensis (Kinberg, 1865)	0	0	0	0	0	0	0	0	75	0,06
Terebella lapidaria (Linnaeus, 1767)	0	0	0	0	0	0	0	0	37,5	0,01
Polyophthalmus pictus (Claparede, 1864)	0	0	0	0	0	0	0	0	100	0,29
Nematonereis unicornis (Grube, 1840)	0	0	0	0	0	0	0	0	100	0,50
Branchiomma bombyx (Dalyell, 1853)	0	0	0	0	0	0	0	0	37,5	0,03
Hydroides pseudouncinata (Zibrowius, 1971)	100	2,90	100	1,62	100	1,40	100	0,82	100	0,80
Pomatoceros triquete (Linnaeus, 1865)	100	12,49	100	18,09	100	18,39	100	28,73	100	14,93
Placostegus tridentatus (Fabricius, 1779)	100	0,82	0	0	0	0	0	0	0	0
Serpula vermicularis (Linnaeus, 1767)	100	3,29	100	2,59	100	1,97	100	2,89	100	4,72
Spirobranchus polytrema (Philippi, 1844)	100	54,58	100	27,10	100	14,66	100	1,87	100	1,06
Vermilliopsis infundibulum (Gmelin, 1788)	12,5	0,03	0	0	0	0	0	0	87,5	0,16
Protula sp. (Risso, 1826)	0	0	0	0	0	0	0	0	25	0,01
Bivalvia										
Chlamys varia (Linnaeus, 1758)	0	0	50	0,15	100	0,32	62,5	0,14	50	0,05
Acanthocardia tubercolata (Linnaeus, 1758)	0	0	100	0,56	37,5	0,07	100	0,35	37,5	0,01
Mytilus galloprovincialis (Lamarck, 1819)	12,5	0,06	37,5	0,31	75	0,38	62,5	0,26	87,5	0,13
Musculus subpictus (Cantraine, 1835)	100	2,43	100	1,25	100	3,79	100	1,41	0	0
Modiolus adriaticus (Lamarck, 1819)	100	1,84	100	0,68	100	1,19	100	2,28	87,5	0,85

TABLE 2 (CONT.)

Species found at each sampling period (from March 2000 until May 2001) on the cement blocks immersed in Vistonikos Gulf (F: Frequency, mD: mean Dominance).

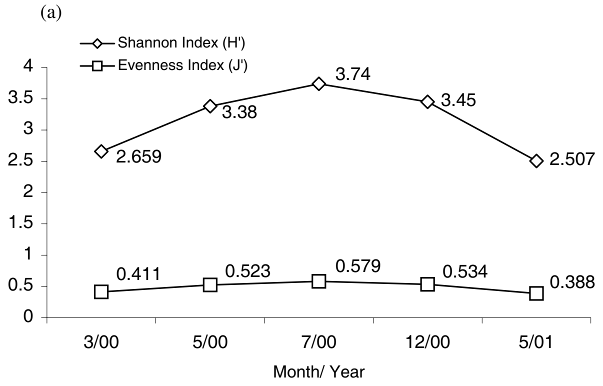
Species	**Sampling period**									
	March 2000		**May 2000**		**July 2000**		**December 2000**		**May 2001**	
	F	**mD**	**F**	**mD**	**F**	**mD**	**F**	**mD**	**F**	**mD**
Hiatella arctica (Linnaeus, 1767)	100	2,10	100	6,11	100	6,79	100	6,80	87,5	6,19
Anomia ephippium (Linnaeus, 1758)	100	6,32	100	15,50	100	16,16	100	4,31	87,5	4,64
Ostrea edulis (Linnaeus, 1758)	0	0	12,5	0,05	0	0	0	0	62,5	0,03
Chamelea gallina (Linnaeus, 1758)	0	0	0	0	0	0	0	0	12,5	0,01
Arca tetragona (Poli, 1795)	0	0	0	0	0	0	0	0	37,5	0,01
Polyplacophora										
Acanthochitona fascicularis (Risso, 1826)	0	0	0	0	0	0	0	0	12,5	0,004
Gastropoda										
Jujubinus exasperatus (Pennant, 1777)	0	0	0	0	100	0,17	75	0,19	62,5	0,02
Bittium latreillei (Payraudeau, 1826)	0	0	0	0	100	1,44	100	7,14	87,5	2,32
Pusillina radiate (Philippi, 1836)	37,5	0,23	87,5	0,81	100	2,24	100	1,38	87,5	0,05
Odostomia conoidea (Brocchi, 1814)	12,5	0,03	12,5	0,05	0	0	0	0	50	0,05
Raphitoma echinata (Brocchi, 1814)	12,5	0,03	0	0	37,5	0,04	0	0	0	0
Anatoma crispate (Fleming, 1828)	0	0	0	0	0	0	0	0	87,5	0,27
Cerithium vulgatum (Bruguiere, 1792)	0	0	0	0	0	0	0	0	37,5	0,03
Acmaea virginea (Mueller O.F., 1776)	0	0	0	0	0	0	0	0	25	0,01
Nassarius incrassatus (Stroem, 1768)	0	0	0	0	0	0	100	0,33	100	0,13
Turritella communis (Risso, 1826)	0	0	0	0	0	0	0	0	12,5	0,004
Copepoda	100	0,92	100	3,53	100	1,31	75	0,24	12,5	0,01
Cirripedia										
Balanus trigonus (Darwin, 1854)	100	1,51	100	1,82	87,5	0,85	75	0,44	100	0,32
Balanus perforatus (Bruguiere, 1789)	50	1,61	75	1,41	50	0,52	62,5	1,33	37,5	0,87
Verruca stroemia (Mueller O.F., 1776)	0	0	0	0	0	0	0	0	37,5	0,01
Malacostraca										
Microdeutopus anomalus (Rathke, 1843)	100	3,85	100	3,94	100	5,48	100	0,31	75	0,03
Caprella acanthifera (Mayer, 1890)	37,5	0,36	50	0,22	100	0,68	100	0,51	62,5	0,03
Corophium sextonae (Crawford, 1937)	100	2,01	100	2,26	100	6,80	100	26,41	100	56,13
Dexamine spinosa (Montagu, 1813)	25	0,06	75	0,15	100	1,45	37,5	0,05	62,5	0,06
Stenothoe antennulariae (Della Valle, 1893)	75	0,56	25	0,05	50	0,36	0	0	0	0
Stenothoe bosphorana (Sowinsky, 1898)	0	0	87,5	1,07	25	0,12	0	0	75	0,07
Stenothoe monoculoides (Montagu, 1815)	37,5	0,16	87,5	1,98	75	1,79	87,5	0,21	100	0,30
Stenothoen gallensis (Walker, 1904)	0	0	0	0	12,5	0,05	0	0	0	0
Metaphoxus sp. (Bonier, 1890)	0	0	0	0	25	0,02	0	0	0	0
Metaphoxus simplex (Bate, 1857)	0	0	25	0,07	12,5	0,01	12,5	0,01	0	0
Lysianassa caesarea (Ruffo, 1987)	37,5	0,09	37,5	0,07	75	0,14	100	0,91	100	0,11
Phtisica marina (Slabber, 1796)	12,5	0,06	0	0	25	0,02	0	0	0	0
Leucothoe spinicarpa (Abildgaard, 1789)	0	0	0	0	0	0	75	0,32	25	0,01
Liljeborgia dellavallei (Stebbing, 1906)	0	0	0	0	0	0	87,5	0,53	37,5	0,02
Synchelidium longidigitatum (Ruffo, 1947)	0	0	0	0	0	0	25	0,02	0	0
Iphimedia minuta (G.O. Sars, 1882)	0	0	12,5	0,01	0	0	62,5	0,11	25	0,01
Elasmopus rapax (A. Costa, 1853)	12,5	0,13	0	0	0	0	0	0	12,5	0,01
Gnathia vorax (Lucas, 1849)	0	0	12,5	0,01	12,5	0,01	50	0,09	62,5	0,03
Gnathia sp praniza (Leach, 1814)	0	0	37,5	0,05	25	0,03	37,5	0,04	37,5	0,03
Idotea baltica (Audouin, 1827)	0	0	0	0	0	0	0	0	37,5	0,01
Leptochelia savignyi (Kroyer, 1842)	50	0,16	12,5	0,01	100	0,35	87,5	2,21	87,5	0,08
Thorulus cranchii (Leach, 1817)	37,5	0,39	37,5	0,07	75	0,21	100	0,90	87,5	0,15
Athanas nitescens (Leach, 1814)	50	0,26	12,5	0,01	75	0,11	100	0,21	87,5	0,08
Alpheus dentipes (Guérin, 1832)	0	0	0	0	0	0	75	0,17	50	0,03
Galathea intermedia (Lilljeborg, 1851)	0	0	0	0	0	0	0	0	25	0,05
Pisidia longicornis (Linnaeus, 1767)	0	0	0	0	25	0,10	100	0,42	75	0,05
Pilumnus spinifer (Edwards, 1834)	0	0	0	0	50	0,05	100	0,39	100	0,17
Pilumnus hirtellus (Linnaeus, 1761)	0	0	0	0	25	0,02	0	0	0	0
Pycnogonida										
Achelia longipes (Hodge, 1864)	0	0	0	0	0	0	0	0	37,5	0,02
Echinoidea (juveniles)	0	0	0	0	75	0,26	50	0,08204	25	0,01
Ophiuroidea (juveniles)	0	0	0	0	0	0	12,5	0,01	12,5	0,004
Ascidiacae										
Didemnum sp.	0	0	0	0	0	0	12,5	0,01	50	0,01
Styela partita (Stimpson, 1852)	0	0	0	0	12,5	0,02	62,5	0,12	87,5	0,19
Styela plicata (Lesueur, 1823)	12,5	0,06	37,5	0,07	12,5	0,03	75	0,09	0	0
Phallusia mammillata (Cuvier, 1815)	12,5	0,09	12,5	0,01	25	0,02	62,5	0,08	87,5	0,07
Number of individuals		3034		5655		9461		8532		20304
Number of species		36		39		46		50		74
Shannon index (H')		2,6594		3,3801		3,741		3,45028		2,5076
Evenness index (J')		0,4117		0,5233		0,5792		0,53415		0,3882

The performance of two-way ANOVA indicated significant differences among samples for every taxa : Peracarida (F=36.05, $p<0.05$), Polychaetes (F=30.14, $p<0.05$), Eucarida (F =12.74, $p<0.05$), Bivalves (F=63.06, $p<0.05$) and Gastropods (F=16.82, $p<0.05$). The results of Fisher's Least Significant Difference (LSD) test are shown in Table 3. As regards Peracarida, higher differences were recorded between samples from March/2000 and May/2001, May/2000 and May/2001, March/2000 and December/2000. Polychaetes showed higher significant differences between samples from March/2000 and May/2001, May/2000 and May/2001, December/2000 and May/2001.

TABLE 3

Results of two-way ANOVA (Fisher's LSD) among samples for each taxon. (* denotes a statistically significant difference).

	Polychaeta	**Peracarida**	**Eucarida**	**Bivalves**	**Gastropods**
March/00-May/00	-67,5	*-0,444	0,446	*-0,567	*-0,901
March/00-July/00	*150,0	*-0,928	-0,039	*-0,851	*-1,03
March/00-December/00	*93,5	*-1,15	*-0,709	*-0,553	*-0,665
March/00-May/01	*344,0	*-1,695	*-0,493	*-0,902	-0,296
May/00-July/00	*82,5	*-0,484	*-0,485	*-0,283	-0,131
May/00-December/00	-26	*-0,706	*-1,154	0,014	0,235
May/00-May/01	*276,5	*-1,251	*-0,939	*-0,334	*0,605
July/00-December/00	56,5	-0,222	*-0,669	*0,297	*0,366
July/00-May/01	*194,0	*-0,767	*-0,454	-0,051	*0,736
December/00-May/01	*250,5	*-0,544	0,215	*-0,349	*0,369



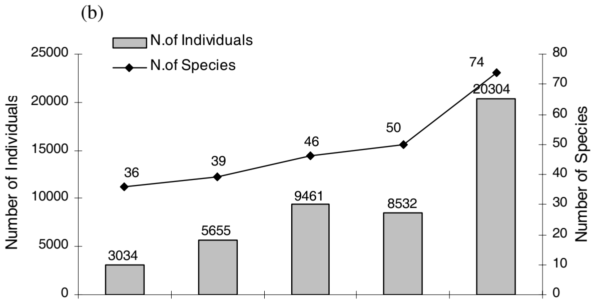


Fig. 2. – (a) Shannon (H') and evenness (J') indices, based on $\log_2$ transformation, and (b) number of individuals and number of species for each sampling period (from March 2000 until May 2001) in Vistonikos Gulf.

Finally, comparing replicates from the top and the base of the pyramids, there were no significant differences for the four taxa except for Gastropods, which showed a significant increase in numerical abundance at the top blocks (F=37.33, $p<0.05$). At the top blocks algae exhibited faster growth due to better light conditions which favoured higher productivity. For instance, in July/2000, algal mean wet biomass at the top blocks was 169.8 g m^{-2} and at the base ones was 9.79 g m^{-2}. Consequently, Gastropods, which are mainly grazers, showed higher numbers at the top of the pyramids.

Serpulids, which was the main taxon in the present study, have been reported among the first fouling organisms that settle after the development of the bacterial film (BOUGIS, 1976). Moreover, in our case the dense colonization of Serpulids may be attributed to the eutrophic character of the deployment area of the reefs. Consequently a high occurrence of filter-feeder organisms is expected. Amphipods with the prevailing species *Corophium sextonae* which is also a filter-feeder organism and builds its tubes among Serpulids, using them as a shelter from predators (BARNARD, 1958). The clear dominance of the latter species in May/2001 could be attributed to its rapid maturation and long reproductive periods, lasting, sometimes, for the whole year. Additionally, turbid waters bear organic and mineral particles, which are useful to fouling organisms for tube construction and food (BARNARD, 1958). BOMBACE et al. (1994), studying settlement on artificial substrata of sessile organisms, report that the dominant organisms are always filter-feeders, including serpulids (*Pomatoceros triqueter* and *Serpula vermicularis)* ascidians and some bivalve species *(Hiatella arctica* and *Anomia ephippium)*, that they were present in this study too.

Shannon-Wiener index (H') values ranged from 2.509 to 3.741 and Evenness (J') from 0.388 to 0.579, both showing a maximum in summertime (July 2000) (figure 2 (a)). For both indices, the lowest value was recorded during May/2001 due to the clear dominance of *Corophium sextonae.*The low evenness values revealed that the community has not reached the final climax stage yet (FITZHARDINGE, & BAILEY-BROCK, 1989 ; RELINI et al., 1990 ; RELINI, ; ODUM, 1993). The pattern of total species richness and number of individuals (figure 2(b)) differed from that of species diversity (H') with the highest values recorded during the last period (May/2001), when it rose from 50 to 74 species. Such an increase was mainly attributed to Errantia (Polychaeta) and Gastropods, which were represented more frequently at this period.

The results of cluster analysis and MDS are shown in figure 3. Cluster analysis indicated two main groups at the 49.5% similarity level. The first one consisted of all replicates of the last sampling period (May/2001), due to high total species richness, while the other one comprised the remaining ones. The second group included four main subgroups of clusters at about 60% similarity level, each corresponding to all replicates of the four periods. The results of ANOSIM (R=0.948, p<0.01) indicate discrimination between the groups of samples, so the cluster is confirmed. The results of MDS agreed with those of cluster analysis. The stress value for the two dimensional MDS configuration was 0.09 indicating very good group separation (Clarke & Warwick, 1994).

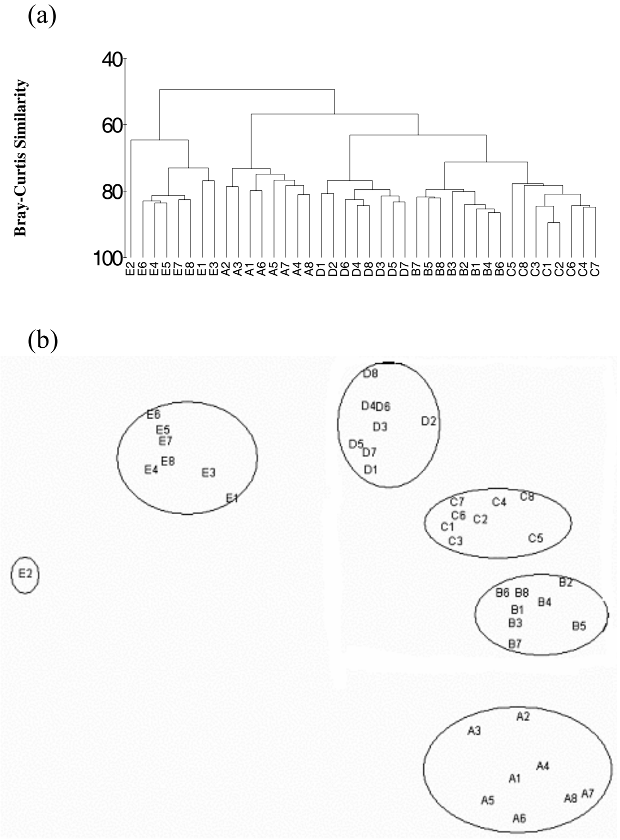


Fig. 3. – Results of (a) cluster and (b) multidimensional scaling (stress value=0.09) based on Bray-Curtis similarity index, of the cement blocks immersed in autumn 1999 (A1-A8 : March 2000, B1-B8 : May 2000, C1-C8 : July 2000, D1-D8 : December 2000, E1-E8 : May 2001).

As mentioned in the introduction, the studies that refer to the colonization of artificial reefs are very few in number. However, Fager (1971) noted that algae and invertebrates usually colonize new reef materials rapidly, although attaining an equilibrium community structure can take several years. A review of the relevant bibliography revealed that filter-feeders appeared to be the prevailing organisms in artificial reefs communities (Bombace et al., 1994 ; Relini et al., 1990). However, initial colonization, successional patterns and the final composition and abundance of benthic organisms can depend on the composition of the substrate, the season the material was deposit and on environmental variables including water temperature, chemistry and current patterns (Bohnsack & Sutherland, 1985). This study reveals that sufficient amount of nutrients is very important for the development of the colonization, as they favour the faster completion of the colonization process. The high abundance of the individuals recorded in this study (about 20.000 ind. / m2 in the last period), are not consistent with the results reported by Antoniadou et al. (2001, and, also, from unpublished data), in a similar study that was conducted in the oligotrophic system of Chalkidiki (N. Aegean Sea). While the dominant taxon in Chalkidiki was Mollusca (herbivore grazers), it is the filter-feeders that prevail in Cape Fanari (Peracarida, Serpulidae). These facts imply that the feeding types of the colonizing fauna depend mainly on the available food supply in the area where the reefs are deployed. Apparently, as Carter et al. (1985) noted, the best areas for reef deployment, in order to achieve the optimum growth of the fishing stock, are those that favour a fast qualitative and quantitative colonization growth.

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Movements, activity patterns and home range of a female brown bear (*Ursus arctos, L.*) in the Rodopi Mountain Range, Greece

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ABSTRACT. Movements and activity patterns of an adult radio-tagged female brown bear accompanied by her cubs were documented for the first time in Rodopi area (NE Greece) from August 2000 to July 2002. Average daily movements were 2.45 ±2.26 SD km, (range 0.15-8.5 km). The longest daily range could be related to human disturbance (hunting activity).The longest seasonal distance (211 km), during summer 2001 coincided with the dissolution of the family. With cubs, the female was more active during daytime (73% of all radio-readings) than when solitary (28%). The female switched to a more crepuscular behaviour, after separation from the yearling (July 2001). According to pooled data from 924 activity - recording sessions, during the whole monitoring period, the female was almost twice as active during day time while rearing cubs (51% active) than when solitary (23%). The autumn and early winter home range size of the family was larger (280 km^2) than after the separation from the cubs (59 km^2). During the family group phase, home range size varied from 258 km^2 in autumn to 40 km^2 in winter (average denning period lasted 107 days : December 2000-March 2001). The bear hibernated in the Bulgarian part of the Rodopi Range during winters of 2001 and 2002.

KEY WORDS : *Ursus arctos*, brown bear, movements, activity patterns, home range, Rodopi, Greece.

INTRODUCTION

The brown bear (*Ursus arctos, L.*) distributional range in Greece comprises two distinct nuclei located in the Pindos Mountain Range (NW Greece) and the Rodopi Mountain Complex (NE Greece). The total area of continuous bear range comprises 8,600 sq.km, while re-colonization of former range appears in southern Pindos Mountains (Fig. 1). The minimum population has been estimated at 130-160 individuals (MERTZANIS, 1999). The minimum brown bear sub-population in Rodopi area is estimated up to 25-30 individuals (MERTZANIS, 1999), which is 19% of the total bear population in Greece. This sub-population is connected only with the southern Bulgarian bear sub-population (Bulgarian Rodopi).

The brown bear is a fully protected species in Greece under national and EU legislation. Since 1994 and until 2003 systematic monitoring programs for brown bear conservation purposes in Greece are conducted on a continuous basis by the NGO "Arcturos" in cooperation with the national competent authorities. Telemetry techniques to study bear behaviour and ecology were implemented for the first time in 1997. Until then monitoring data came from observation and compilation of bear activity signs. In Rodopi area, the first successful capture and radio-tagging of an adult female bear with her cubs occurred in summer (August) 2000.

This study was carried out from August 2000 to July 2002 within the framework of a "LIFE-Nature" project for the Conservation of the brown bear in Greece. The fragile status of brown bears in Europe and especially in the southern parts of the continent, as well as the lack of data on the ecology and behaviour of the animals in Greece, incited us to undertake this study. The present paper aims to document for the first time movements and activity patterns of a radio-tagged adult female brown bear accompanied by her cubs in the Rodopi area. This and similar results will contribute to the adjustment and orientation of conservation measures for the species.

MATERIAL AND METHODS

Study Area

The study area is located in NE Greece and comprises the medium and higher altitudes of the western and central Rodopi Mountain Complex (Fig. 1). The Mountain Complex is located between 41° 12' and 41° 36' N and 24° and 25° 06' E. The total surface is about 1,731 sq km. It is a vast granitic complex covered with large forests and located in the drainage of the Nestos River valley.

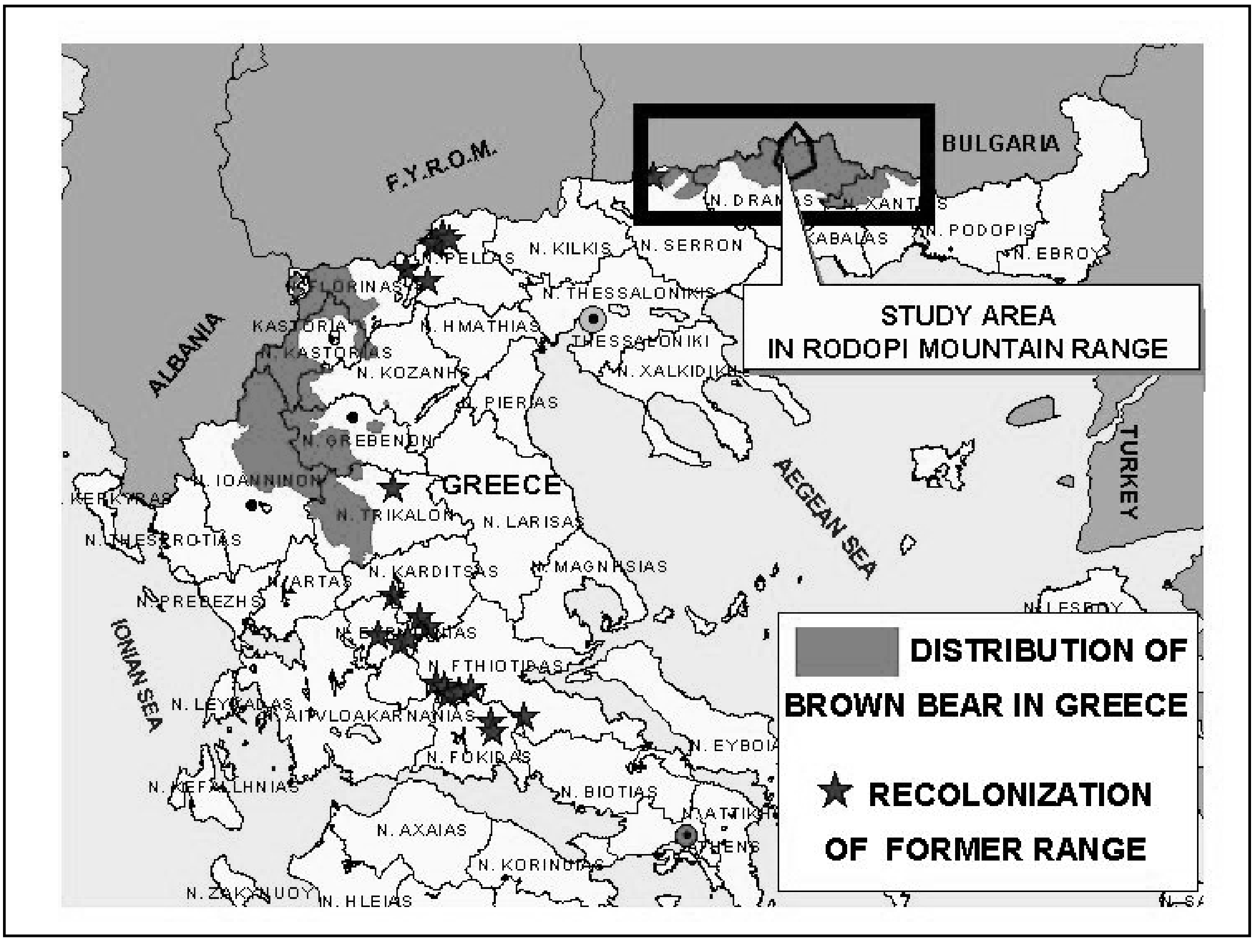


Fig. 1. – Location of the study area and brown bear range in Greece.

Continuous forest covers about 68% of the study area. Main forest types and percentage of coverage are : oak (*Quercus* sp.) (60%) at lower altitudes, beech (*Fagus* sp.) (20%), Spruce (*Picea excelsa*) (15%), Scots pine (*Pinus sylvestris*) (17.5%) and black pine (*Pinus nigra*) (3%). The terrain is generally rugged and is characterized by perennial, cold water streams and rivers. Elevations range from 500-2,232 m above sea level. Mean annual temperatures range from 27.1° C in summer to -4.7° C in winter. Mean annual precipitation is 980 mm. Nearly all native European mammal species are present in the area, including the wolf (*Canis lupus*), roe deer (*Capreolus capreolus*), chamois (*Rupicapra rupicapra*), wild cat (*Felis sylvestris*) and otter (*Lutra lutra*). The study area is remote, characterized by low human density and scattered human settlements. Abandoned villages have increased the diversity of bear food because of abundant orchards. A high density of forest road network related to timber activities reaches almost 15m/ha, and gives access to a relatively high level of hunting pressure. Hunting is allowed from August to January. Game reserves cover 6.16% of the core part of the study area.

Study Animals and Methods

An adult female brown bear, aged 8-10 years [age estimated *in situ* from dentition characteristics (Jonkel, 1993)], weighing approx. 120 kg and accompanied by two cubs of the year was captured with an 'Aldrich Foot Snare' trap on 4 August 2000 (at 20:30) after 64 trapping nights. The bait used was an active beehive. The bear was sedated with KHCl/xylazine (Rompun) (initial volume 750mg/3ml injected with blowpipe) and a booster volume of 750mg/3ml (with intra-muscular injection). Time to anaesthesia was less than 5 minutes. Total immobilization time was approx. 30min. The bear was fitted with a radio-collar ('Telonics MOD-500 NH') with bi-modal "activity-inactivity" signal. The antagonist used was "Yohimbine" (25 mg /ml). Radiolocations were taken on a daily basis using a TR-4 "Telonics" receiver, with a minimum of three bearings using the "raised antenna - null signal" (RA – NS) technique.

Data Processing and plotting was achieved using 'LOCATE' and GIS (ArcInfo, ArcView) software. Daily movements were calculated from consecutive day to day radiolocations, using ArcView program extension "Animal Movement Analysis" (Kenward, 2001). Geographic coordinates of the bearing points were obtained by GPS and were processed through LOCATE software for triangulation. Subsequently, the exported co-ordinates were used in several functions (as well as by the standard ArcView functions). The line coverage that was used was optimised with the "point to polyline" tool in the program.

Two approaches were used to evaluate activity levels. The first approach consisted of recording the activity status at each daily bearing and radio-location. In this case activity levels were examined over the whole dataset, which was separated into two different groups : the daylight hours, that is from 07:00-19:00, and the night hours, 19:00-07:00. The second approach was achieved through 24h monitoring sessions operated once every month. The bear's activity was recorded every half hour for 3-5 min of continuous listening. Activity status was deduced by measuring the time of the active and inactive signal modes. Mann-Whitney U Tests were used for statistical comparisons of results. Home Range estimation was based on the 'Minimum Convex Polygon' (MCP) method (MOHR 1947, HAYNE 1949).

RESULTS

Between August 2000 and December 2001, daily movements of the bear family were defined with 924 bearings, which yielded 365 radiolocations that were plotted, averaging one location /1.3 days. Average straight-line distance between successive daily radiolocations of the bear averaged 2.45 km (± 2.26 SD). Of all daily movements 65% were less than 2.45 km. The shortest distance was 0.15 km whereas the longest daily distance was 8.5 km and occurred in early autumn (September) 2000. In both autumn 2000 and 2001 (mid September to end of November) daily distances travelled in weekends were significantly higher than those travelled during weekdays (Mann-Whitney U-Test : autumn 2000 : p<0.05 ; autumn 2001 : p<0.05,).

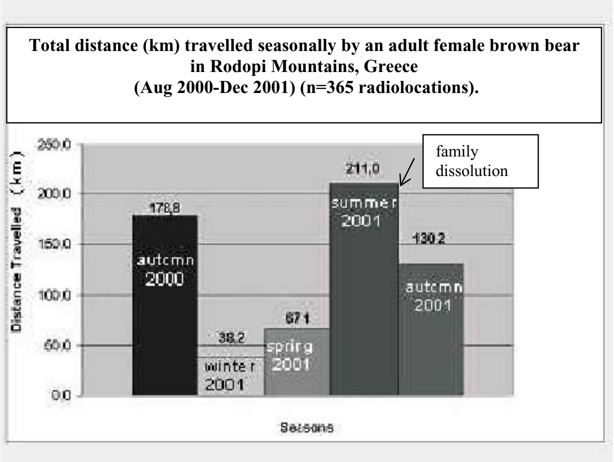


Fig. 2. – Seasonal mouvements of the brown bear family inthe Rodopi Mountains, from August 2000 to December 2001.

For the same monitoring period and at a seasonal scale, total seasonal movements of the bear family and the lone female showed also characteristic variations (Fig. 2). The highest values were obtained in three periods : mid June to mid September 2001, time of the family dissolution, autumn 2000, bear with cubs, and mid September to end of November 2001, when the bear was solitary without yearling with 211, 178.8 and 130.2 km travelled respectively.

Another shift in the female bear's activity pattern occurred after separation from her cub(s). The female bear was significantly more active during the daylight hours when the family group was still together (Mann-Whitney U-Test, p<0.05,). This pattern was confirmed by comparing the overall activity frequencies (924 bearings) between day (from 07:00 to 19:00) and night (from 19:00 to 07:00) hours (Fig. 3). The activity of the female during daylight fell from 52.1% while with her cubs, to 23.1% after having separated from her cubs in July 2001. On 12 July 2001 a short visual contact with the bear family confirmed the presence of one cub.

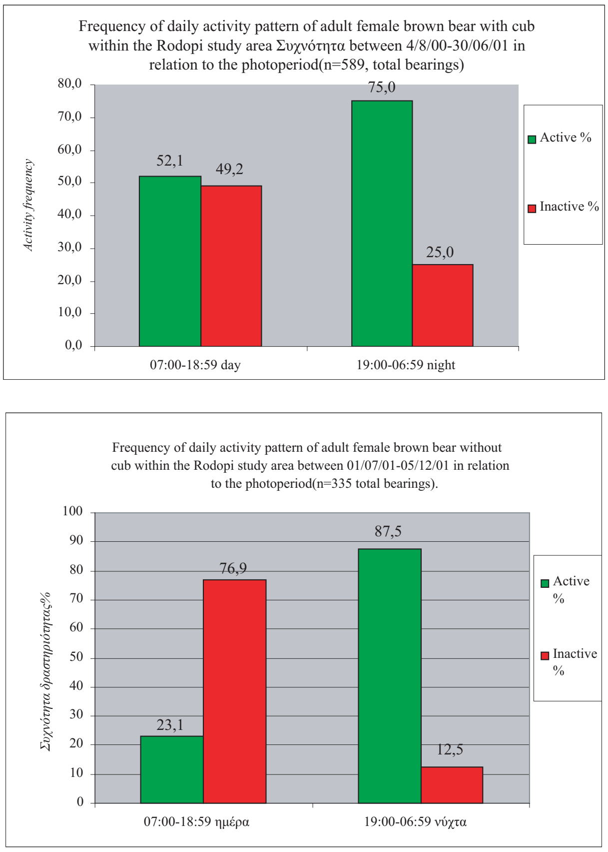
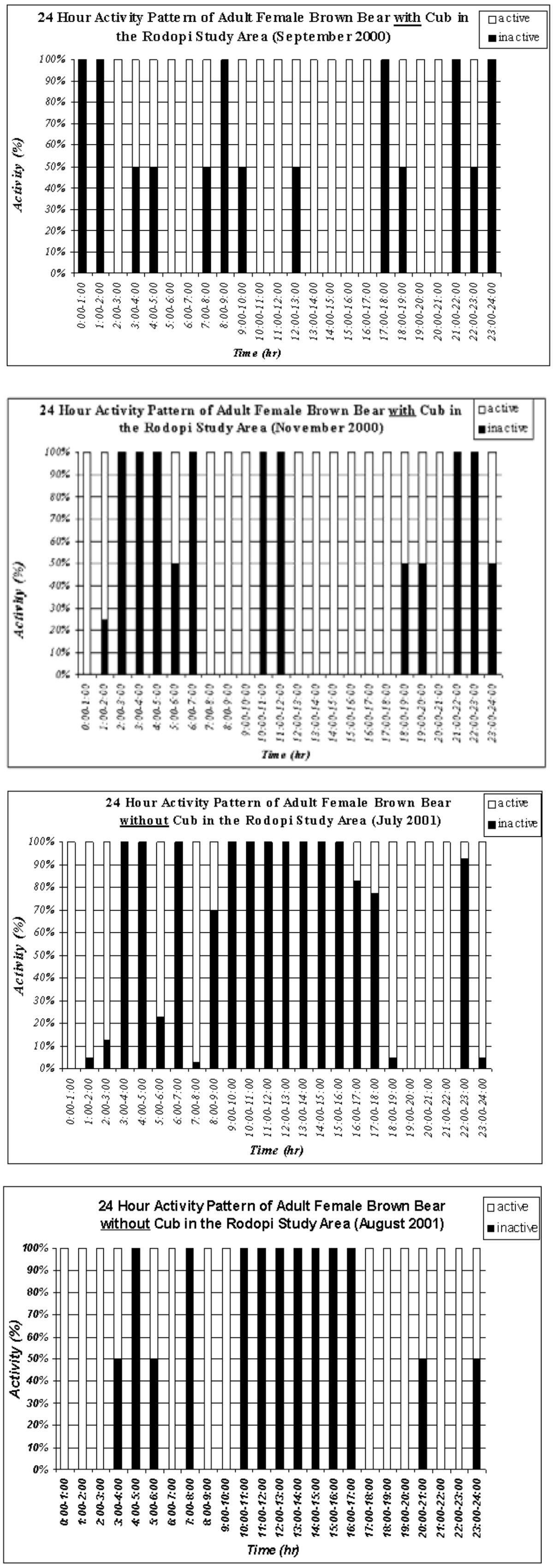


Fig. 3. – Female brown bear activity patterns with and without cubs in the Rodopi Mountains, Greece, as shown by daily locations (n=924).

Diel activity of the female during the two periods with and without cub(s), was also recorded. While with her cub(s) the female showed more continuous periods of activity throughout the day, and especially during daytime. In this case the 24h cycle was interrupted by relatively short intervals of inactivity (Fig. 4). After separation from her cub(s) the 24h activity pattern became much longer with clearly continuous intervals of inactivity during the day, from 10:00 to 17:00, and clear bouts of activity during the night, between 19:00 and 03:00 (Fig. 4).

Winter inactivity of the female bear during two denning periods averaged 107 days and concerned the same denning site that was used repeatedly for two consecutive winters (2000 and 2001). The site was located on Bulgarian territory in the Rodopi Mountain Range, in a small and steep canyon covered by spruce (*Picea excelsa*) forest. This small valley had a northern exposure and was characterized by harsh winter conditions. The den was dug under a rock, and the entrance was camouflaged with spruce branches.


24 Hour Activity Pattern of Adult Female Brown Bear with Cub in the Rodopi Study Area (September 2000)

24 Hour Activity Pattern of Adult Female Brown Bear with Cub in the Rodopi Study Area (November 2000)

24 Hour Activity Pattern of Adult Female Brown Bear without Cub in the Rodopi Study Area (July 2001)

24 Hour Activity Pattern of Adult Female Brown Bear without Cub in the Rodopi Study Area (August 2001)

Fig. 4. – Female brown bear diel activity patterns with and without cubs as shown by 24h monitoring sessions in autumn 2000 and summer 2001.

Data on home range area also showed notable variation most likely related to the separation of the female from her cub(s). The most marked difference occurred from mid September to end of November declining from 349 sq. km in 2000 (female with cubs) to 107.5 sq. km in 2001 (solitary female). This can be associated with the overall decrease of the home range area, which was 280 sq km in mid September to mid December 2000 when the family was intact, to 59 sq km at the same period in 2001 when the female was solitary (Fig. 5). In addition the smallest home range area was recorded during the winter, from mid December to early March and measured 40 sq km, at the pre-denning period. In contrast, the largest home range area was recorded during the period from mid September to end of November, and measured 280 sq km, when the family group was together. In general, seasonal variations of home range area appeared to follow and correspond to the seasonal variations of movements.

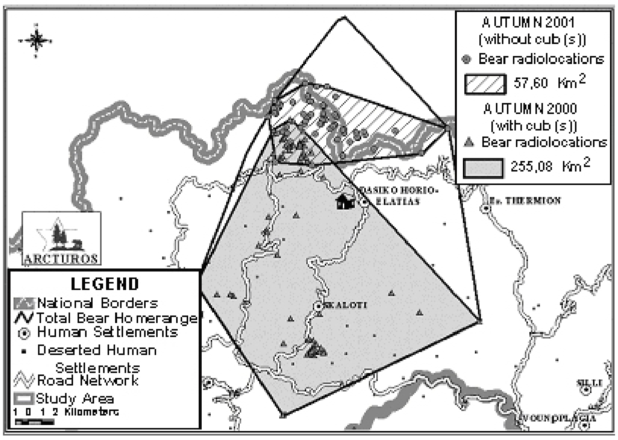


Fig. 5. – Female brown bear home range areas in autumn 2000 (with cubs) and autumn 2001 (without cubs).

DISCUSSION

In terms of daily movements, the female bear covered distances more or less similar to bears in other European countries, such as those for male and female bears in Croatia (Huber & Roth, 1986 ; 1993) and for a male bear in Spain (Clevenger et al., 1990). On the other hand, the significant differences of the bear family's daily movements in autumn 2000 and notably during weekends could be related to the high hunting pressure occurring in the study area in weekends. Many hunters were present during the weekends, they were organized into groups, used base camps within the forest as headquarters and conducted drive-hunts as the main hunting practice for wild boars (*Sus scrofa*). This was a major factor of disturbance probably causing the bear family to move continuously to avoid humans. Drive-hunts have been also identified as a serious human caused mortality factor for bears in the study area (Mertzanis, 1994).

Field observations, corroborating telemetry data, confirmed that displacement of the bear family from undisturbed sectors (with continuous presence and activity during the week), coincided with hunting activity occurring in the same sectors during the weekends. Similar avoidance movements in response to human activities, such as recreation, have also been recorded for a bear family in the Cantabrian Mountains in Spain (NAVES et al., 2001).

On the other hand, the long distances travelled by the family (176.8 km) as well as the high home range values (255.08 sq km) in autumn 2000 might further be related to educational processes of the female towards the cub(s). This process includes learning of locations with available and suitable food resources, safe shelter as well as avoidance of human disturbance. In contrast, the relatively long distances (130.2 km) travelled by the solitary female in autumn 2001, within a comparatively smaller home range (57.6 sq km), could be related to avoidance behaviour of the mother towards her yearling(s). This happened after the dissolution of the family, which is assumed to have occurred in late July 2001.

As far as dial activity is concerned, the patterns found in Rodopi are very similar to the ones observed for five males and one female adult bear in Pindos Mountain Range, Greece (MERTZANIS et al., 2003), as well as for solitary bears in Italy (ROTH, 1983), Croatia (ROTH & HUBER, 1986) and Spain (CLEVENGER et al., 1990). On the other hand, the differences in diel patterns observed between the solitary and family phases of the same female bear and more particularly, the increased level of activity during daylight hours for the bear accompanied by the yearling(s) could be associated with an increased nutritional need due to lactation, the education of the yearling and its familiarisation with the surrounding habitat, as well as with the avoidance of infanticidal males that kill cubs (SWENSON et al., 2001).

Lastly, results concerning the home range areas of solitary females are very similar to those recorded for solitary animals in Croatia (HUBER & ROTH, 1993). Larger home ranges for the family could be related to greater nutritional needs not only of the female but also for the cubs in search for suitable and patchy food sources.

The combination of the results of the present study with previous systematic surveys enhances considerably the proposed delineation of important bear habitat units in the study area. These results have been incorporated in the final zoning proposals for the creation of a National Park in the Rodopi area, as processed by “Arcturos” NGO and in cooperation with national competent authorities, under the National Environment Law 1650/86. In addition, the above results confirmed the ecological importance of the “NATURA” 2000 (pSCI) site "Elatia" (GR1140003) located in the study area. Moreover, we hope that similar results will also contribute in the reorganisation of warden patrols during the hunting season in order to minimize disturbance related to hunting pressure, and a co-ordination of management actions engaged on a trans-border scale.

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Dry Weights of the Zooplankton of Lake Mikri Prespa (Macedonia, Greece)

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ABSTRACT. Length-weight regressions and dry weight estimates of the main crustaceans of Lake Mikri Prespa are presented. The calanoid copepod and most of the cladocerans were heavier during summer than in other seasons, while the rest of the crustaceans were heavier during spring. The mean calculated dry weights were : (a) 0.005 µg (*Keratella cochlearis*), 2.268 µg (*Asplanchna priodonta*), 0.033 µg (*Trichocerca capucina*), 0.024 µg (*Filinia longiseta*) for the predominant rotifer species ; and (b) 0.420 µg for the planktonic larvae of the molluscan *Dreissena polymorpha*.

KEY WORDS : *Dry weights, length-weight regressions, zooplankton, Greece*

INTRODUCTION

Dry weight data exist for several areas mainly in Europe and America (e.g. Nauwerk 1963 ; Dumont et al., 1975; Schindler & Noven 1971, Lawrence et al., 1987; Malley et al., 1989), while the length-weight relationships of freshwater zooplankton species from the same areas are reviewed by Bottrell et al. (1976) and McCauley (1984). Nevertheless, no data are available for the Balkan lakes, including for the calanoid copepod *Arctodiaptomus steindachneri,* an endemic species of the Western Balkan. On the other hand, many factors have been found to control the individual weight underlining the necessity to develop length-weight relationships specific to an area (Rahkola et al., 1998). Thus, the data presented herein will allow the estimation of the zooplanktonic biomass and production of the lakes in the surrounding area.

MATERIAL AND METHODS

Samples were collected monthly from June 1990 to October 1992 from Lake Mikri Prespa. A detailed description of the lake, the phytoplankton and zooplankton communities as well as the sampling procedure has been presented by Tryphon et al. (1994) and Michaloudi et al. (1997).

Crustacean samples were preserved immediately in 4% formalin. Individuals were sorted from the samples and grouped according to species, sex, developmental stage (copepodites, nauplii), and size class (see Table 1) in the laboratory. Each group comprised 30-100 individuals. The individual length was measured (to the nearest 0.01 mm) and the animals were rinsed with distilled water, placed on pre-weighed and pre-dried (60° C for 48 h) aluminium boats, dried at 60° C for 48 h, cooled in a desiccator and weighed on a microbalance (10 µg precision). Ovigerous females were not selected. The developmental stages of copepods were not separated by species except for the copepodites of the calanoid *Arctodiaptomus steindachneri*. The above procedure was done for each season separately except for the groups of very low density (e.g. *Daphnia cucullata* of IV size class), for which individuals were sorted out from all the samples throughout the year. Length-weight regressions were performed using the linear form ln(W)=lna+bln(L), where L is body length in mm and W is body weight in µg dry weight.

For rotifers, the wet weight was calculated using the geometric formulae of Ruttner-Kolisko (1977), applied on live individuals. Wet weight was consequently transformed to dry weight assuming that dry weight is 10% of wet weight except for *Asplanchna* for which it was assumed to be 4% (Dumont et al., 1975). The same method was applied for the dry weight calculation of the planktonic larvae of *Dreissena polymorpha* using the 10% factor to convert wet to dry weight (M. Vranovsky, pers. comm.). The biovolume estimates for *Dreissena* were based on the formula of the ellipsoid of revolution (Ruttner-Kolisko, 1977).

RESULTS

Weight data for the crustacean populations of Lake Mikri Prespa are shown in Table 1. The main filter feeders *Daphnia cucullata*, *Diaphanosoma* cf. *mongolianum*, *Ceriodaphnia pulchella* and *Arctodiaptomus steindachneri* were heavier during summer than in other seasons. *Bosmina longirostris*, *Mesocyclops leuckarti* and the calanoid copepodites were heavier during spring, while nauplii were heavier in the winter.

The length-weight regressions are shown in Table 2. The slopes of the length-weight regressions were all significantly ($p<0.01$) different from zero and ranged from 1.9 to 3.5.

For rotifers and the molluscan larvae of *Dreissena polymorpha* the dimensions (mean values) and calculated dry weights for each species are shown in Table 3.

TABLE 1

Dry weights (in µg) of the crustacean species of Lake Mikri Prespa. W=winter, Sp=spring, SU=summer, A=autumn. *Data refer to groups for which the number of individuals was not enough for seasonal weight determination, and which were sorted out from all samples throughout the year.

Species size class (µm)	**W**	**SP**	**SU**	**A**	**all***
Daphnia cucullata Sars, 1862					
300-500	0.47	0.4	0.4	0.408	
501-700	0.606	0.909	2.75	1.886	
701-900	2.5	2.258	3.125	2.058	
901-1100					4.8
Diaphanosoma cf. *mongolianum* Ueno, 1938					
300-500			0.5	0.425	
501-700			0.82	0.43	
701-900			2	1.38	
901-1100				2.727	
males				0.57	
Bosmina longirostris (O.F. Müller, 1758)					
200-300	0.29	0.48		0.224	
301-400	0.78	1		0.886	
401-500	1.14	1.54			
Ceriodaphnia pulchella Sars, 1862					
200-300			0.309	0.156	
301-400			0.64	0.454	
401-500			0.816	0.816	
Leptodora kindtii (Focke, 1844)					13.33
Arctodiaptomus steindachneri (Richard, 1897)					
females	5	6	6.845	3.47	
males	3	4	3.66	2.325	
copepodites					
300-500	0.45	0.92	0.8	0.416	
501-700	1.304	1	1.13	0.8	
701-900	1.67	3.45	2	1	
901-1100	3.6	5.2	2.67	1.79	
Mesocyclops leuckarti (Claus, 1857)					
females		4.117	1.38	2	
males		1.034	1.33	1	
Cyclops vicinus Ulianine, 1875					
females	21.67	25.315			
males	10	9			
Macrocyclops albidus (Jurine, 1820)					
females	20				
males	5				
Eucyclops serrulatus (Fischer, 1851)					
females		7.5			
males		6.25			
cyclopoid copepodites					
300-500		0.4	0.2	0.196	
501-700	1.76	0.87	0.46	0.884	
701-900	1.272	2.33		2.72	
901-1100					4.29
nauplii					
200-300	0.303	0.202	0.235	0.119	
301-400	0.58	0.5	0.303	0.303	
401-500					1.35

DISCUSSION

The filter feeders *Daphnia cucullata*, *Diaphanosoma* cf. *mongolianum*, *Ceriodaphnia pulchella* and *Arctodiaptomus steindachneri* are the main components of the spring and summer crustacean community (Michaloudi et al., 1997). They increase in numbers after the nanoplankton peak and dominate throughout summer (Michaloudi et al., 1997) when their main food source is probably bacteria (Gliwicz, 1969 ; Sommer et al., 1986). At the same period they were also heavier (Table 1). This could be the result of the increased food availability as well as the increase of temperature that has a positive effect on their filtering rate (Burns, 1969 ; Mourelatos & Lacroix, 1990). Such a coincidence of maximum weight and abundance is also reported by Vuille & Maurer (1991). On the other hand, *Bosmina longirostris* was heavier during spring although it reaches maximum abundance during autumn (Michaloudi et al., 1997). At this time the phytoplankton community is dominated by Cyanobacteria while during spring nanoplankton biomass is at its peak (Tryphon et al., 1994). Moreover, it has been found that although temperature has no considerable effect on its filtration rates (Bogdan & Gilbert, 1982 ; Mourelatos & Lacroix, 1990), high concentration of inedible particles has a distinct negative effect (Bogdan & Gilbert, 1982).

TABLE 2

Length-dry weight relationships of the planktonic crustaceans (all size classes included) in Lake Mikri Prespa ln(W)=lna+bln(L), R^2=coefficient of determination, p=probability of b being different from zero, S.E.=standard error of b. L in mm and W in µg.

Species	**N**		**R^2**	**p**	**S.E.**
D. cucullata	13	Ln(W)=1.586+2.963Ln(L)	0.797	0.0001	0.451
B. longirostris	8	Ln(W)=3.203+3.466Ln(L)	0.909	0.0002	0.448
C. pulchella	6	Ln(W)=1.807+2.517Ln(L)	0.836	0.0107	0.557
D. cf. *mongolianum*	7	Ln(W)=1.046+2.501Ln(L)	0.857	0.0028	0.458
A. steindachneri (1)	24	Ln(W)=1.111+2.121Ln(L)	0.796	0.0001	0.229
copepodites cyclopoida	11	Ln(W)=1.535+3.532Ln(L)	0.908	0.0001	0.376
Cyclopoida (1)	25	Ln(W)=1.205+2.685Ln(L)	0.902	0.0001	0.185
nauplii	9	Ln(W)=1.777+1.914Ln(L)	0.715	0.0041	0.457

1.Pooled data for adults and copepodites

The weights of *Bosmina longirostris*, *Mesocyclops leuckarti*, *Cyclops vicinus* and *Diaphanosoma* cf. *mongolianum* (Table 1) are in good agreement with those reported by Burgis (1974) ; Dumont et al. (1975) ; Gophen (1976) ; Lawrence et al. (1987) and Vuille & Maurer (1991) for individuals of the same length. On the other hand *Ceriodaphnia pulchella* is much lighter than *C. quandrangula* (Dumont et al., 1975) probably because the first one is a pelagic and the second one a littoral species (Vuille & Maurer, 1991). As for the non pelagic *Eucyclops serrulatus* and *Macrocyclops albidus,* they were found to be lighter though bigger than the individuals reported by Dumont et al. (1975). Considering the altitude of Mikri Prespa (850 m asl) it is evident that the assumption of Dumont et al. (1975), that non-pelagic species tend to be lighter at high altitudes, is true for the above species.

From the above it can be concluded that crustacean weight is controlled by geographical distribution, differ-

TABLE 3

Mean dimensions (in µm) and calculated dry weight (in µg) of the rotifers and *D. polymorpha* in Lake Mikri Prespa, n=number of individuals, S.E.=standard error.

		a=lenght		**b=height**		**c=width**		**w=weight**	
Species	**n**	**Mean**	**S.E.**	**Mean**	**S.E.**	**Mean**	**S.E.**	**Mean**	**S.E.**
Asplanchna priodonta Gosse, 1850	145	653.55	16.06	397.50	13.12			2.268	0.1000
Brachionus angularis Gosse, 1850 (1)	30	102.08	0.81	92.29	1.11	52.29	1.18	0.026	0.0010
B. diversicornis (Daday, 1883)	99	262.50	6.18	157.19	5.39	85.13	5.01	0.188	0.0210
B. forficula Wierzejski, 1891	30	87.50	1.09	78.00	1.71	49.50	1.06	0.018	0.0010
Conochilus hippocrepis (Schrank, 1830)	30	301.50	9.08	72.50	1.74			0.043	0.0030
Filinia longiseta (Ehrenberg, 1834)	46	39.75	25.25	54.58	6.83			0.024	0.0100
Keratella cochlearis (Gosse, 1851)	359	118.46	3.53	55.02	1.07			0.005	0.0003
Polyarthra sp.	60	142.75	0.25	95.00	5.00	65.63	1.13	0.090	0.0300
Synchaeta pectinata Ehrenberg, 1832	60	294.75	6.25	205.50	1.50			0.343	0.0200
Trichocerca capucina Wierzejski & Zacharias, 1893	4	202.50	4.33	56.25	2.17			0.033	0.0020
T. cylindrica (Imhof, 1891)	33	284.88	5.13	64.38	4.38			0.012	0.0020
T. similis (Wierzejski, 1893)	142	148.39	3.71	46.55	1.74			0.017	0.0020
Dreissena polymorpha (Pallas, 1771)	240	185.88	6.47	206.88	8.28			0.420	0.0400

1. Measures on preserved specimens

ent habitat types, temperature and food availability and composition. Moreover, the trophic status of a lake may have an impact on the seasonal variations of the weights. This could be seen when comparing the results of the present study, where most crustaceans were heavier during summer, with the results from HAWKINS & EVANS (1979) at the oligotrophic Lake Michigan, where most crustaceans were heavier during winter and spring.

The slopes of the length-weight regressions were all significantly ($p<0.01$) different from zero and ranged from 1.9 to 3.5 (Table 2). The smallest b value was found for nauplii, which could be attributed to the fact that they tend to elongate faster than they grow in the other two dimensions (MALLEY et al., 1989). The values of lna and b found for the crustacean species in Lake Mikri Prespa (Table 2) generally fall within the range of values for other species of the world (DUMONT et al., 1975 ; MCCAULEY, 1984 ; LAWRENCE et al., 1987 ; MALLEY et al., 1989 ; VUILLE & MAURER, 1991).

As for rotifers, comparing the results from the present study with those from other lakes worldwide (Table 4) it is evident that rotifer volumes cover quite a wide range of values. Thus, it seems that rotifer biomass estimates must be calculated for each lake separately.

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TABLE 4

Volumes (µm^3 10^{-6}) of rotifer species from Lake Mikri Prespa and other lakes.

Species	Volume	Site	Country	Trophic Status	Source
Asplanchna priodonta	57.16	Lake Mikri Prespa	Greece	eutrophic	present study
	33.6	Lake Volvi	Greece	eutrophic	Zarfdjian 1989
	30-300	Lake Erken	Sweden	eutrophic	Nauwerk 1963
	200	Lake Windermere	England	eutrophic	Ruttner-Kolisko 1977
	44	Lake Suwa	Japan	eutrophic	Bottrell et al. 1976
	37.5	Lake Kinneret	Israel	eutrophic	Gophen 1973
	22.5	Lake Lucerne	Switzerland	mesotrophic	Burgi et al. 1985
	20	Danube river+ sidearms	Slovakia	mesotrophic	Vranovsky (pers.comm.)
	16	Lake Lunz	Austria	mesotrophic	Ruttner-Kolisko 1977
	13.12	ELA lakes	Canada	oligotrophic	Malley et al. 1989
Brachionus angularis	0.26	Lake Mikri Prespa	Greece	eutrophic	present study
	0.4	Lake Volvi	Greece	eutrophic	Zarfdjian 1989
	0.5	Lake Suwa	Japan	eutrophic	Bottrell et al. 1976
	0.1	Lake Kinneret	Israel	eutrophic	Gophen 1973
	0.28	Funada-ike pond	Japan	eutrophic	Urabe 1992
	0.45-0.63	Lake Lough Neagh	Ireland	eutrophic	Andrew & Fitzisimons 1992
	0.4	Danube river+ sidearms	Slovakia	mesotrophic	Vranovsky (pers.comm.)
Brachionus diversicornis	1.88	Lake Mikri Prespa	Greece	eutrophic	present study
	2.9	Lake Volvi	Greece	eutrophic	Zarfdjian 1989
	1.5	Lake Suwa	Japan	eutrophic	Bottrell et al. 1976
	3	Danube river+ sidearms	Slovakia	mesotrophic	Vranovsky (pers.comm.)
Brachionus forficula	0.18	Lake Mikri Prespa	Greece	eutrophic	present study
	0.22	Funada-ike pond	Japan	eutrophic	Urabe 1992
Conochilus hippocrepis	0.43	Lake Mikri Prespa	Greece	eutrophic	present study
	0.6	Lake Erken	Sweden	eutrophic	Nauwerk 1963
	0.15	Lake Suwa	Japan	eutrophic	Bottrell et al. 1976
Filinia longiseta	0.24	Lake Mikri Prepsa	Greece	eutrophic	present study
	1.5	Lake Suwa	Japan	eutrophic	Bottrell et al. 1976
	0.41	Funada-ike pond	Japan	eutrophic	Urabe 1992
	0.17-0.24	Lake Lough Neagh	Ireland	eutrophic	Andrew & Fitzisimons 1992
	0.32	Lake Lucerne	Switzerland	mesotrophic	Burgi et al. 1985
	0.3	Danube river+ sidearms	Slovakia	mesotrophic	Vranovsky (pers.comm.)
	0.52	ELA lakes	Canada	oligotrophic	Malley et al. 1989

TABLE 4 (CONT.)

Volumes ($\mu m^3\ 10^{-6}$) of rotifer species from Lake Mikri Prespa and other lakes.

Species	Volume	Site	Country	Trophic Status	Source
Keratella cochlearis	0.05	Lake Mikri Prespa	Greece	eutrophic	present study
	0.05	Lake Volvi	Greece	eutrophic	Zarfdjian 1989
	0.05	Lake Erken	Sweden	eutrophic	Nauwerk 1963
	0.15	Lake Windermere	England	eutrophic	Ruttner-Kolisko 1977
	0.1	Lake Kinneret	Israel	eutrophic	Gophen 1973
	0.09	Funada-ike pond	Japan	eutrophic	Urabe 1992
	0.046	Lake Lough Neagh	Ireland	eutrophic	Andrew & Fitzisimons 1992
	0.07	Lake Lanao	Philippine	eutrophic	Lewis 1979
	0.11	Lake Lunz	Austria	mesotrophic	Ruttner-Kolisko 1977
	0.04	Lake Lucerne	Switzerland	mesotrophic	Burgi et al. 1985
	0.25	Danube river+ sidearms	Slovakia	mesotrophic	Vranovsky (pers.comm.)
	0.15	Lake Balaton	Hungary		Ruttner-Kolisko 1977
	0.15	ELA lakes	Canada	oligotrophic	Malley et al. 1989
	0.7	ELA lakes	Canada	oligotrophic	Schindler & Noven 1971
Polyarthra spp.	0.9	Lake Mikri Prespa	Greece	eutrophic	present study
	1.1	Lake Volvi	Greece	eutrophic	Zarfdjian 1989
	0.55	Lake Erken	Sweden	eutrophic	Nauwerk 1963
	0.65	Lake Winderermere	England	eutrophic	Ruttner-Kolisko 1977
	2	Lake Suwa	Japan	eutrophic	Bottrell et al. 1976
	0.3	Lake Kinneret	Israel	eutrophic	Gophen 1973
	0.23	Funada-ike pond	Japan	eutrophic	Urabe 1992
	0.3-0.54	Lake Lough Neagh	Ireland	eutrophic	Andrew & Fitzisimons 1992
	0.29	Lake Lanao	Philippine	eutrophic	Lewis 1979
	0.3	Lake Valencia	Venezuela	eutrophic	Saunders & Lewis 1988
	0.4	Lake Lunz	Austria	mesotrophic	Ruttner-Kolisko 1977
	0.14	Lake Lucerne	Switzerland	mesotrophic	Burgi et al. 1985
	0.1-1	Danube river+ sidearms	Slovakia	mesotrophic	Vranovsky (pers.comm.)
	0.38	Lake Balaton	Hungary		Ruttner-Kolisko 1977
	0.5	ELA lakes	Canada	oligotrophic	Malley et al. 1989
	1.4	ELA lakes	Canada	oligotrophic	Schindler & Noven 1971
Synchaeta pectinata	3.43	Lake Mikri Prespa	Greece	eutrophic	present study
	1.5	Lake Volvi	Greece	eutrophic	Zarfdjian 1989
	2	Lake Erken	Sweden	eutrophic	Nauwerk 1963
	4.5	Lake Kinneret	Israel	eutrophic	Gophen 1973
	0.65	Lake Lucerne	Switzerland	mesotrophic	Burgi et al. 1985
	1	Danube river+ sidearms	Slovakia	mesotrophic	Vranovsky (pers.comm.)
Trichocerca capucina	0.33	Lake Mikri Prespa	Greece	eutrophic	present study
	0.7	Lake Volvi	Greece	eutrophic	Zarfdjian 1989
	0.15	Lake Erken	Sweden	eutrophic	Nauwerk 1963
	1	Lake Kinneret	Israel	eutrophic	Gophen 1973
	0.11	Lake Lucerne	Switzerland	mesotrophic	Burgi et al. 1985
	0.2	Danube river+ sidearms	Slovakia	mesotrophic	Vranovsky (pers.comm.)
Trichocerca cylindrica	0.12	Lake Mikri Prespa	Greece	eutrophic	present study
	0.2	Danube river+ sidearms	Slovakia	mesotrophic	Vranovsky (pers.comm.)
	1	ELA lakes	Canada	oligotrophic	Malley et al. 1989
	0.1	ELA lakes	Canada	oligotrophic	Schindler & Noven 1971
Trichocerca similis	0.17	Lake Mikri Prespa	Greece	eutrophic	present study
	0.3	Lake Volvi	Greece	eutrophic	Zarfdjian 1989
	0.15	Lake Erken	Sweden	eutrophic	Nauwerk 1963
	1	Lake Kinneret	Israel	eutrophic	Gophen 1973
	0.08	Lake Lucerne	Switzerland	mesotrophic	Burgi et al. 1985
	0.2	Danube river+ sidearms	Slovakia	mesotrophic	Vranovsky (pers.comm.)

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Deep-water fish fauna in the Eastern Ionian Sea

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ABSTRACT. Existing information on the ichthyofauna of the Eastern Ionian Sea (Greece) was enriched by a recent research project carried out in its northern part at depths ranging from 300 to 1200 m. The frequency of occurrence of the identified fish species and their abundance were examined. In total, 101 fish species were identified. Their number and abundance decreased significantly with depth. *Argentina sphyraena* presented the highest frequency of occurrence and *Chlorophthalmus agassizi* the highest abundance at depths ranging between 300 and 500 m. In the depth zone 500-700 m, *Chlorophthalmus agassizi* predominated in abundance and *Phycis blennoides* in frequency of occurrence. In the zone 700-900 m, *Galeus melastomus* and *Nezumia sclerorhynchus* showed both the highest abundance and frequency of occurrence. These two species were also the most abundant at depths 900-1200 m, whereas *Lampanyctus crocodilus* was the most frequently encountered. Four species (*Benthocometes robustus*, *Microichthys coccoi, Nemichthys scolopaceus* and *Epigonus constanciae*) are reported for the first time in Greek waters, and twenty species are reported for the first time in the Greek Ionian Sea. Moreover, one specimen of *Caelorinchus mediterraneus* Iwamoto & Ungaro, 2002, a species that has only recently been described for the Mediterranean Sea, was also identified.

KEY WORDS : deep sea, fish fauna, Eastern Ionian Sea, Greece

INTRODUCTION

The ichthyofauna of the Eastern Ionian Sea (Greece) consists of Atlantic-Mediterranean and cosmopolitan species. Few studies exist, most of which concern the fish fauna of the continental shelf and the upper slope (Kaspiris, 1973; Papaconstantinou, 1986; Papaconstantinou et al., 1987). The previously available data on the fish fauna of the deep waters of the Eastern Ionian Sea were derived from the research expeditions “Dana” and “Thor” (Tåning, 1918; 1923; Ege, 1930; 1934; 1948; 1953). No recent published data appear in the literature, although unpublished data for depths down to 800 m of the central and southern part of the Greek Ionian Sea exist from research projects carried out in recent years.

The present work provides information on the qualitative and quantitative fish species composition of the Eastern Ionian Sea for depths ranging between 300 and 1200 m.

MATERIALS AND METHODS

Sampling was carried out in the deep waters of the northern part of the Eastern Ionian Sea (Fig. 1) during four experimental surveys (September 1999, April 2000, July 2000 and September 2000). Two hired commercial trawlers equipped with trawls of 40 mm (stretched) mesh size in the cod-end were used for sampling. The study area included between the 300 and 900 m isobaths, and was divided into three depth strata (300-500, 500-700, 700-900 m). A random stratified design was applied for the sampling, taking into account the depth and the surface of each stratum (Cochran, 1977). However, for experimental purposes, sampling was also extended to depths 900-1200 m with some additional stations. In total, 148 hauls were carried out during the four surveys (Fig. 1), three hauls of which were not considered valid. The duration of the hauls was 30 min for depths <500 m and one hour for depths >500 m. Catches were identified to species level and the abundance of each species was recorded on board.

The number of species and their total abundance per fishing hour in each haul were examined and the relation of their logarithms to depth was tested using linear regression. Moreover, the frequency of occurrence (F) and the mean abundance (A) in terms of number per fishing hour per species for each depth stratum were estimated as follows :

$F = \sum hn * 100 / \sum h$,

where $\sum hn$ = sum of the number of the n hauls where a species was present in a depth stratum, and $\sum h$ = sum of the number of all the hauls carried out in that depth stratum, and

$A = \sum Nn / \sum tn$,

where $\sum Nn$ = sum of the numbers of a species in the n hauls carried out in a depth stratum and $\sum tn$ = sum of the fishing time of the n hauls in that depth stratum.

RESULTS

In total, 101 fish species were caught in the study area, of which 81 were osteichthyes and 20 were chondrichthyes (Table 1). The relationships of the number of species and their total abundance with depth were statistically significant with decreasing trend ($b = -0.001$, $r = 0.65$, $DF = 144$, $P<0.05$ and $b = -0.006$, $r = 0.79$, $DF = 144$, $P<0.05$, respectively) (Figs. 2, 3). Similar results were obtained from the analysis of the number of osteichthyes ($b = -0.009$, $r = 0.57$, $DF = 144$, $P<0.05$) and their total abundance ($b = -0.0069$, $DF = 144$, $P<0.05$) with depth as well as for the number of chondrichthyes ($b = -0.002$, $DF = 141$, $r = 0.61$, $P<0.05$) and their total abundance with depth ($b = -0.002$, $DF = 141$, $r = 0.40$, $P<0.05$).

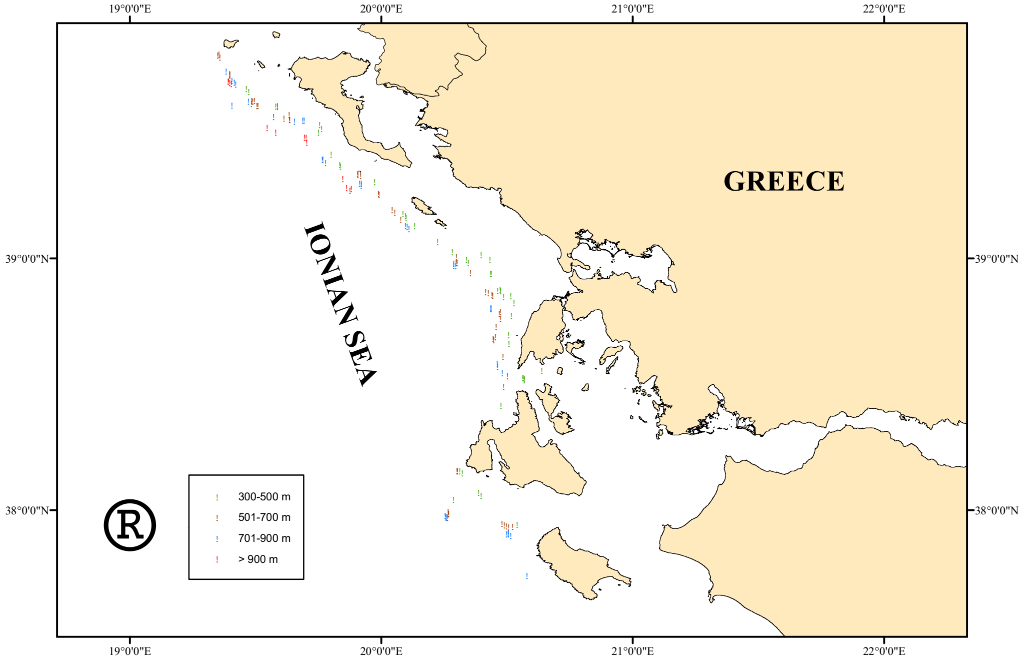

Fig. 1. – Map of the study area showing sampling stations.

TABLE 1

List of fish species collected in the E. Ionian Sea with species depth range, frequency of occurrence (%) and abundance (N/h) per depth stratum. Species names are given according to FishBase. (* species for the first time in the Greek ionian Sea)

	Depth range (m)	**Depth strata (m)**							
		300-500		**500-700**		**700-900**		**900-1200**	
	No. of hauls	**44**		**52**		**36**		**13**	
Species		**%**	**N/h**	**%**	**N/h**	**%**	**N/h**	**%**	**N/h**
CHONDRICHTHYES									
Centrophorus granulosus (Bloch & Schneider, 1801)	512-823			7.7	0.2	10.5	0.1		
Chimaera monstrosa Linnaeus, 1758 *	514-1171			7.7	0.1	7.9	0.1	15.4	0.2
Dalatias licha (Bonnaterre, 1788)	655-764			3.8	0.1	15.8	0.2		
Dipturus batis (Linnaeus, 1758) *	700					2.6	0.1		
Galeus melastomus Rafinesque, 1810	305-1171	55.6	60.8	98.1	54.6	94.7	36.1	92.3	18.4
Heptranchias perlo (Bonnaterre, 1788) *	388-501	4.4	0.2	1.9	0.1				
Hexanchus griseus (Bonnaterre, 1788) *	700					2.6	0.1		
Leucoraja circularis (Couch, 1838)	463-676	2.2	0.1	7.7	0.1				
Mustelus mustelus (Linnaeus, 1758) *	624			1.9	0.1				
Oxynotus centrina (Linnaeus, 1758) *	549-777			3.8	0.1	7.9	0.1		
Raja asterias Delaroche,1809	333-343	6.7	0.3						
Raja clavata Linnaeus, 1758	300-577	44.4	3.1	3.8	0.1				
Raja miraletus Linnaeus, 1758	462	2.2	0.1						
Raja montagui Fowler 1910 *	318-345	11.1	0.3						
Raja oxyrinchus Linnaeus, 1758	288-640	77.8	3.9	15.4	0.2				
Raja polystigma Regan,1923	328	2.2	0.1						
Raja sp.	462-473	4.4	0.3						
Scyliorhinus canicula (Linnaeus, 1758)	288-780	88.9	25.1	7.7	0.1	2.6	0.1		
Squalus blainville (Risso, 1827)	300-780	77.8	20.1	17.3	0.5	15.8	0.2		
Torpedo marmorata Risso, 1810	317-368	6.7	0.2						
Torpedo nobiliana Bonaparte, 1835 *	300-388	4.4	0.1						
OSTEICHTHYES									
Acantholabrus palloni (Risso,1810)	351	2.2	0.1						
Argentina sphyraena Linnaeus, 1758	288-700	95.6	760.6	28.8	2.9				
Argyropelecus hemigymnus Cocco,1829	460-1082	4.4	0.2	32.7	0.7	15.8	0.2	23.1	0.3
Arnoglossus rueppelli (Cocco, 1844) *	288-897	73.3	26.0	5.8	0.1	5.3	0.1		
Bathypterois dubius Vaillant, 1888 *	700-1171					34.2	1.1	84.6	4.6
Bellottia apoda Giglioli, 1883	460-569	2.2	0.1	3.8	0.1				
Benthocometes robustus (Goode & Bean, 1886)	503			1.9	0.1				
Benthosema glaciale (Reinhardt, 1837)	541-1085			9.6	0.4	2.6	0.1	7.7	0.1

TABLE 1

List of fish species collected in the E. Ionian Sea with species depth range, frequency of occurrence (%) and abundance (N/h) per depth stratum. Species names are given according to FishBase. (* species for the first time in the Greek ionian Sea)

	Depth range (m)	**Depth strata (m)**							
		300-500		**500-700**		**700-900**		**900-1200**	
	No. of hauls	**44**		**52**		**36**		**13**	
Species		**%**	**N/h**	**%**	**N/h**	**%**	**N/h**	**%**	**N/h**
Caelorinchus caelorinchus (Risso, 1810)	305-710	51.1	175.7	65.4	22.5	7.9	0.2		
Caelorinchus mediterraneus Iwamoto & Ungaro, 2002	1032							7.7	0.1
Capros aper (Linnaeus, 1758)	288-700	68.9	283.1	3.8	0.1				
Centracanthus cirrus Rafinesque, 1810	327-464	13.3	1.6						
Centrolophus niger (Gmelin 1789) *	624-770			1.9	0.1	2.6	0.1		
Ceratoscopelus maderensis (Lowe, 1839)	460-1082	2.2	0.1	1.9	0.1	2.6	0.1	7.7	0.2
Chauliodus sloani Bloch & Schneider, 1801	473-1192	2.2	0.3	32.7	0.9	39.5	0.6	30.8	0.9
Chelidonichthys cuculus (Linnaeus, 1758)	288-356	22.2	3.8						
Chelidonichthys gurnardus (Linnaeus, 1758)	340	2.2	0.1						
Chelidonichthys lucerna (Linnaeus, 1758)	318	2.2	0.1						
Chlorophthalmus agassizi Bonaparte, 1840	300-897	88.9	3958.2	78.8	165.7	5.3	1.0		
Conger conger (Linnaeus, 1758)	305-1171	24.4	1.1	23.1	0.9	26.3	0.5	23.1	0.4
Deltentosteus quadrimaculatus (Valenciennes, 1837)	333	2.2	0.8						
Diaphus holti Tåning, 1918	300-777	4.4	0.1	3.8	0.1	5.3	0.1		
Diaphus metopoclampus (Cocco, 1829)	518-1085			5.8	0.2	7.9	0.1	7.7	0.1
Diaphus rafinesquii (Cocco, 1838)	616-660			3.8	0.1				
Electrona risso (Cocco, 1829)	614			1.9	0.1				
Epigonus constanciae (Giglioli, 1880)	351-742	2.2	1.1	15.4	0.3	2.6	0.1		
Epigonus denticulatus Dieuzeidei, 1950 *	351-660	2.2	0.1	5.8	0.1				
Epigonus spp	620			1.9	0.1				
Epigonus telescopus (Risso, 1810)	351-780	4.4	0.1	1.9	0.1	5.3	0.1		
Etmopterus spinax (Linnaeus, 1758)	327-1171	4.4	0.1	40.4	3.2	65.8	2.0	69.2	1.4
Gadella maraldi (Risso, 1810)	368-748	2.2	0.1	7.7	0.1	2.6	0.1		
Gadiculus argenteus argenteus Guichenot, 1850	300-518	66.7	647.0	1.9	0.4				
Gaidropsarus biscayensis (Collette, 1890) *	549			1.9	0.1				
Gnathophis mystax (Delaroche, 1809)	700					2.6	0.1		
Gonostoma denudatum Rafinesque, 1810	531			1.9	0.1				
Helicolenus dactylopterus (Delaroche, 1809)	288-852	91.1	35.0	94.2	53.6	78.9	8.8		
Hoplostethus mediterraneus Cuvier, 1829	388-897	6.7	1.1	94.2	47.6	73.7	10.5		
Hymenocephalus italicus Giglioli, 1884	305-897	53.3	321.5	96.2	70.1	47.4	2.1		
Ichthyococcus ovatus (Cocco, 1838)	614			1.9	0.1				
Lampanyctus crocodilus (Risso, 1810)	318-1192	4.4	0.1	71.2	11.2	92.1	14.4	100.1	6.4
Lepidopus caudatus (Euphrasen, 1788)	333-620	8.9	0.2	9.6	0.1				
Lepidorhombus boscii (Risso, 1810) *	300-700	51.1	18.0	80.8	10.1	2.6	0.1		
Lepidorhombus whiffiagonis (Walbaum, 1792) *	288-700	55.6	3.7	40.4	1.2	2.6	0.1		
Lepidotrigla dieuzeidei Blanc & Hureau, 1973	288-596	55.6	73.0	1.9	0.1				
Lestidiops sphyrenoides (Risso, 1820)	518			1.9	0.1				
Lesueurigobius suerii (Risso, 1810) *	322-337	6.7	0.3						
Lobianchia dofleini (Zugmayer, 1911)	318	2.2	0.2						
Lophius budegassa Spinola, 1807	300-1013	42.2	2.8	32.7	0.5	10.5	0.1	7.7	0.1
Lophius piscatorius Linnaeus, 1758	370-770	2.2	0.1	5.8	0.1	7.9	0.1		
Macroramphosus scolopax (Linnaeus, 1758)	322-342	4.4	0.2						
Maurolicus muelleri (Gmelin,1789) *	318-351	6.7	4.8						
Merluccius merluccius (Linnaeus, 1758)	288-764	86.7	35.3	50.1	2.8	13.2	0.1		
Microichthys coccoi Rüppell, 1852	549			1.9	0.1				
Micromesistius poutassou (Risso, 1827)	305-676	26.7	14.1	44.2	1.1				
Molva macrophthalma (Rafinesque, 1810)	388-754	4.4	0.3	26.9	0.4	7.9	0.1		
Mora moro (Risso, 1810)	512-1171			28.8	3.5	92.1	9.3	92.3	13.3
Mullus barbatus Linnaeus, 1758	328	2.2	0.2						
Mullus surmuletus Linnaeus, 1758	305-409	22.2	2.8						
Myctophidae	754-1082					5.3	0.1	7.7	0.2
Myctophum punctatum Rafinesque, 1810 *	549			1.9	0.2				
Nemichthys scolopaceus Richardson, 1848	390-1079	2.2	0.1	1.9	0.1			7.7	0.1
Nettastoma melanurum Rafinesque, 1810	305-1171	11.1	0.3	84.6	3.5	89.5	9.1	76.9	4.8
Nezumia sclerorhynchus (Valenciennes, 1838)	388-1171	2.2	0.2	98.1	46.5	94.7	35.1	92.3	18.5
Notacanthus bonaparte Risso, 1840	487-1034			1.9	0.1	13.2	0.2	15.4	0.2
Pagellus acarne (Risso, 1827)	302-318	6.7	3.0						
Pagellus bogaraveo (Brünnich, 1768)	305-700	37.8	8.6	50.1	2.1				
Paralepis coregonoides Risso, 1820	1032							7.7	0.1
Paralepis speciosa Bellotti, 1878	660			1.9	0.1				
*Peristedion cataphractum (*Linnaeus, 1758)	288-848	91.1	141.9	42.3	2.1	2.6	0.1		
Phycis blennoides (Brünnich, 1768)	300-1047	75.6	10.6	100.1	29.0	92.1	7.3	61.5	0.8
Polyprion americanus (Bloch & Schneider, 1801)	503-577			3.8	0.1				
Scorpaena elongata Cadenat, 1943	300-710	31.1	0.9	1.9	0.1	2.6	0.1		
Spicara smaris (Linnaeus, 1758)	328	2.2	0.1						
Stomias boa (Risso, 1810)	473-1032	2.2	0.2	28.8	1.5	26.3	0.8	7.7	0.1
Symphurus ligulatus (Cocco, 1844) *	531-761			15.4	0.4	7.9	0.1		
Symphurus nigrescens Rafinesque, 1810	533-601			7.7	0.2				
Synchiropus phaeton (Günther, 1861)	302-848	31.1	3.3	17.3	0.5	2.6	0.1		
Trachurus picturatus (Bowdich, 1825)	305-368	8.9	0.3						
Trachurus trachurus (Linnaeus, 1758)	300-318	6.7	0.3						
Trachyrincus scabrus (Rafinesque, 1810) *	480-1171	2.2	0.1			15.8	0.9	46.2	0.7
Trigla lyra Linnaeus, 1758	288-620	57.8	5.4	9.6	0.1				
Trisopterus minutus (Linnaeus, 1758)	333	2.2	0.4						
Zeus faber Linnaeus, 1758	328	2.2	0.1						

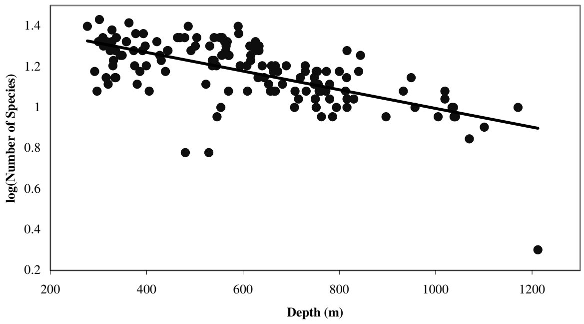

Fig. 2. – Relationship of the number of species with depth.

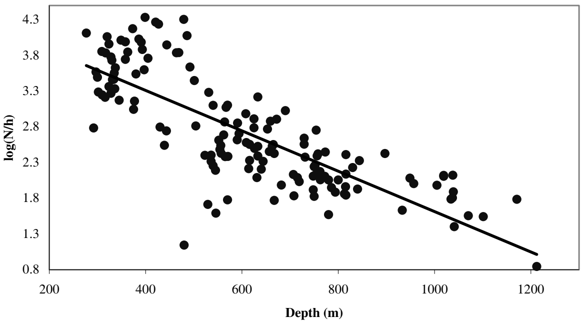

Fig. 3. – Relationship of the total abundance (N/h) with depth.

In the depth zone 300-500 m, 72 species were found (59 osteichthyes and 13 chondrichthyes). *Argentina sphyraena*, *Peristedion cataphractum*, *Helicolenus dactylopterus, Chlorophthalmus agassizi, Scyliorhinus canicula* and *Merluccius merluccius* presented high frequency of occurrence (Table 1). *Chlorophthalmus agassizi* was dominant in terms of abundance (Table 1). Most of the chondrichthyes caught in this zone belonged to species of the genus *Raja*.

In the zone 500-700 m, 70 fish species were identified (58 osteichthyes and 12 chondrichthyes) (Table 1). *Chlorophthalmus agassizi* still predominated in terms of abundance (Table 1). *Phycis blennoides* was present at all stations (100% frequency of occurrence). *Galeus melastomus*, *Nezumia sclerorhynchus*, *Hymenocephalus italicus*, *Helicolenus dactylopterus* and *Hoplostethus mediterraneus* were also found in high frequency of occurrence (Table 1).

From the 47 species (38 osteichthyes and 9 chondrichthyes) caught in the depth zone 700-900 m and from the 22 species (20 osteichthyes and 2 chondrichthyes) caught in the zone 900-1200 m, *Galeus melastomus* and *Nezumia sclerorhynchus* were the most abundant in both zones (Table 1). *Galeus melastomus*, *Nezumia sclerorhynchus*, *Lampanyctus crocodilus* and *Mora moro* were the most frequent in the zone 700-900 m (Table 1). Their order of importance in terms of frequency of occurrence changed in the deeper zone as follows : *Lampanyctus crocodilus, Galeus melastomus*, *Nezumia sclerorhynchus* and *Mora moro*. Furthermore, *Phycis blennoides* was also frequently present in the depth zone 700-900 m, but less so in deeper waters (Table 1).

DISCUSSION

From the 101 species identified in the present work, one fish was identified as the new Mediterranean macrurid species, *Caelorinchus mediterraneus* IWAMOTO & UNGARO, 2002 (Table 1). It was caught at a depth of 1032 m, which is within the depth range reported in the literature for the species (IWAMOTO & UNGARO, 2002). This species has been recently described from specimens collected in the Catalan, Ligurian and Adriatic Seas (IWAMOTO & UNGARO, 2002) but it has not been reported so far from the Ionian Sea.

Four species are recorded for the first time in Greek waters : *Benthocometes robustus, Microichthys coccoi*, *Nemichthys scolopaceus* and *Epigonus constanciae*. The first two were found only in one station at depths 500-700 m. The third one was encountered in three depth zones (300-500, 500-700 and 900-1200 m) in very low frequencies and abundances (Table 1). Finally, *Epigonus constanciae* was caught at depths between 351 and 742 m, with higher occurrence at depths 500-700 m (Table 1). According to the literature, *Benthocometes robustus* has been rarely found in the Mediterranean Sea and *Microichthys coccoi* is reported only from the Strait of Messina (Italy) (WHITEHEAD et al., 1989). *Nemichthys scolopaceus* is recorded for the first time for all the Ionian Sea, although it is known in the western Mediterranean and the Atlantic (WHITEHEAD et al., 1989). *Epigonus constanciae* has also been found in the western Mediterranean and eastern Atlantic off West Africa with a maximum of occurrence between 200 and 400 m (WHITEHEAD et al., 1989).

Twenty species (indicated in Table 1 by asterisk) are reported for the first time for the fish fauna of the Greek Ionian Sea. Most of them are species encountered mainly at depths >500 m, which have only recently been investigated.

The results of this study showed a general decrease in the number of fish species and of their abundance with depth. More specifically, the number of fish species decreased considerably in waters deeper than 700 m, whereas the species abundance declined sharply in waters deeper than 500 m. The decline in both number of species and abundance is also true for other Mediterranean areas as well as for other taxonomic groups (ABELLO et al., 1988; BIAGI et al., 1989; CARTES et al., 1994; STEFANESCU et al., 1994; ABELLA & SERENA, 1995; D'ONGHIA et al., 1998; 2002 KALLIANIOTIS et al., 2000).

The ichthyofauna in the Eastern Ionian Sea (Greece) is quite similar to that of the North-western Ionian Sea (Italy) (D'ONGHIA et al., 1998), a fact also mentioned by D'ONGHIA et al., (2002). However, important differences were detected concerning the abundance of various species. *Gadiculus argenteus argenteus* and *Hymenocephalus italicus* are the most abundant fish in the upper slope of the Italian Ionian (D'ONGHIA et al., 2002), whereas *Chloropthalmus agassizi* was found to be the dominant species in the Greek Ionian with considerably higher abundance values. Moreover, abundance values were generally much higher in Greek than Italian Ionian Sea. Another remarkable discrepancy between the two neighbouring areas is the higher number of species and abundance of chondrichthyes in the upper slope of the Greek

Ionian than the Italian one. The higher abundance for many species, the dominance of few species and the greater number of species and specimens of chondrichthyes, characteristics found for the Eastern Ionian (Greece), could be explained by the environmental and fisheries conditions prevailing in each area. It must be underlined that fishing pressure is low at the Greek Ionian upper-slope bottoms, and fisheries activities are scarcely exercised at depths greater than 500 m in Greek waters, whereas the Italian waters are fished intensively down to 700 m by commercial trawlers. Fisheries exploitation affects species abundance and especially long-lived, large-sized species, and species generally positioned high in the food web (Pauly et al., 1998) such as chondrichthyes (Stevens et al., 2000). However, some Chondrichthyes species such as *S. blanville* and *R. clavata* not found in the north-western Ionian (Italy) (Matarrese et al., 1996; D'Onghia et al., 2002) are frequently found in the neighbouring Sicilian channel (Relini et al., 2000). This indicates that the environmental conditions should also be considered in order to explain the differences in the fish fauna between the Greek and Italian Ionian Sea.

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Deep-water decapod crustacean fauna of the Eastern Ionian Sea

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ABSTRACT. Knowledge on the decapod crustacean fauna of the E. Ionian Sea was enriched by a recent research program, carried out in deep waters (300-1200 m) of its northern part. The data were collected from a total of 148 hauls towed during four experimental trawl surveys from September 1999 to September 2000.

Thirty nine decapod species were identified, of which eight were Dendrobranchiata and 31 Pleocyemata (17 Caridea, 9 Brachyura, 3 Anomura, 1 Astacideum and 1 Palinurum). Concerning their depth distribution, 30 species were found in the depth zone 300-500 m, with *Parapenaeus longirostris* being the most abundant species. *Plesionika heterocarpus* and *P. antigai* followed in terms of abundance. Of the 27 species caught in the zone 500-700 m, *Aristaeomorpha foliacea* and *Plesionika martia* were the most abundant. In the zone 700-900 m, 19 species were found and *Aristaeomorpha foliacea* with *Aristeus antennatus* were the most numerous. Finally, the 18 decapod species encountered in the zone 900-1200 m showed low abundance, and *Sergia robusta* with *Polycheles typhlops* predominated in numbers.

From the identified decapods, *Acanthephyra eximia*, *Philoceras echinulatus* and *Pontophilus norvegicus* were mentioned for the first time in the E. Ionian Sea. Some other species, such as *Acanthephyra pelagica*, *Geryon longipes, Munida tenuimana, Paromola cuvieri, Parthenope macrochelos, Pasiphaea multidentata, Plesionika narval, Polycheles typhlops, Sergestes arachnipodus* and *Sergestes arcticus* have been reported for the area only in the gray literature. Additionally, new depth distribution records for the Mediterranean were obtained for some species.

KEY WORDS : Decapoda, deep-water, Ionian See, Mediterranean.

INTRODUCTION

The literature on the decapod crustacean fauna of the Eastern Ionian Sea (Greece) is limited comparing to that referring to other Greek seas and more specifically to the Aegean Sea (e.g. THESSALOU-LEGAKIS & ZENETOS, 1985 ; THESSALOU-LEGAKIS, 1986 ; D'UDEKEM D'ACOZ, 1995). The systematic investigation of the decapod fauna of the Greek waters in the Ionian Sea has started quite recently in the framework of larger projects (MEDITS projects 1994-2001) or in restricted areas of the Ionian Sea, always at depths not exceeding 800 m ("Deep Water Fisheries" and RESHIO projects). Some information, obtained during the MEDITS project, is given by POLITOU et al. (1998, 2000).

The aim of the present work is to enrich the knowledge on the decapod crustacean fauna of the Eastern Ionian Sea with information obtained in the framework of the project INTERREG Italy-Greece, which was carried out in deep waters (300-1200 m) of its northern part. This information concerns the decapod faunistic composition, the species depth distribution, their frequency of occurrence and abundance.

MATERIALS AND METHODS

Sampling took place in depths from 300 to 1200 m of the Greek Ionian Sea during four experimental trawl surveys carried out from September 1999 to September 2000 (Fig. 1) using two chartered commercial trawlers. The gear used was a commercial bottom trawl with a cod end mesh size of 20 mm (side). The vertical and horizontal opening of the trawl were estimated, using a remote acoustic sensing system attached to the gear, as 1.5 m and 17 m respectively at a towing speed of 2.4 knots. The random stratified sampling design was applied using depth for the stratification of the study area. Three depth zones were defined, 300-500 m, 500-700 m and 700-900 m. Some additional experimental hauls were carried out in the depth zone 900-1200 m. A total of 148 hauls were carried out. The tow duration was 30 minutes for depths <500 m and one hour for depths >500 m. After each haul, catches were identified to species level. Species abundance was recorded on board. The mean abundance in number of individuals per fishing hour (CPUE) was estimated for each depth zone as :

$$CPUE=\Sigma Nn/\Sigma tn$$

where ΣNn=sum of individuals of a species in the n hauls carried out in the depth zone and Σtn=sum of fishing time of the n hauls in the depth zone.

RESULTS

Thirty nine decapod species were identified in total in the study area. Of them eight were Dendrobranchiata and 31 Pleocyemata (17 Caridea, 9 Brachyura, 3 Anomura, 1 Astacideum and 1 Palinurum) (Table 1).

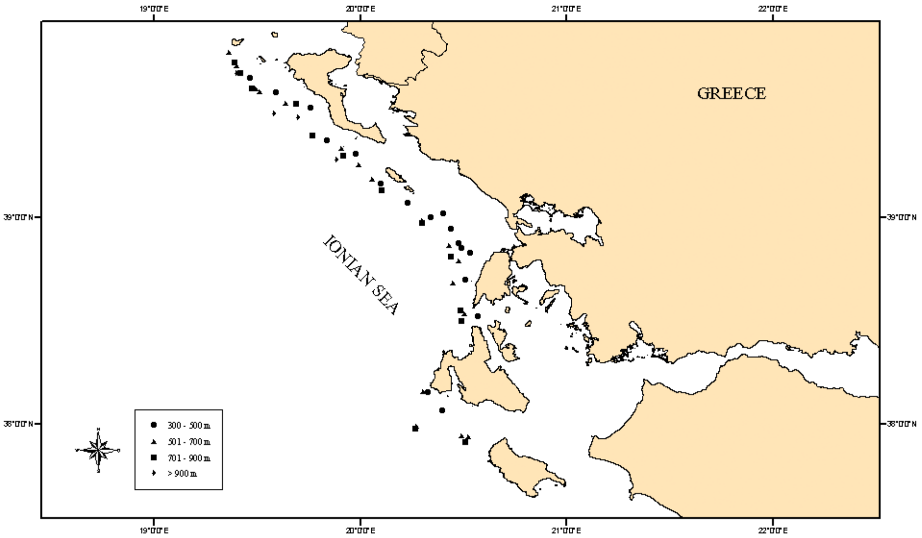

Fig. 1. – Map of the study area showing the sampling stations.

Thirty species were found in the depth zone 300-500 m (6 Dendrobranchiata and 24 Pleocyemata : 14 Caridea, 6 Brachyura, 2 Anomura, 1 Astacideum and 1 Palinurum). *Parapenaeus longirostris* was the most important species, since it presented a remarkably high frequency of occurrence and abundance (Fig. 2). Although different species, such as *Plesionika antigai, P. gigliolii, P. heterocarpus, Nephrops norvegicus, Munida rutllanti, P. edwardsii* and *Chlorotocus crassicornis,* were also found frequently, only *P. heterocarpus, P. antigai* and *P. edwardsii* were worth a mention in terms of their abundance.

Of the 27 species caught in the zone 500-700 m, six were Dendrobranchiata and 21 Pleocyemata : 9 Caridea, 7 Brachyura, 3 Anomura, 1 Astacideum and 1 Palinurum. *P. martia* was present in all stations, whereas other highly occurring species were, in order of importance, *Polycheles typhlops, Aristaeomorpha foliacea, P. acanthonotus, P. gigliolii, P. longirostris, N. norvegicus* and *P. antigai. Aristaeomorpha foliacea* and *Plesionika martia* were dominant in terms of abundance.

In the zone 700-900 m, 19 species were found (7 Dendrobranchiata and 12 Pleocyemata : 7 Caridea, 3 Brachyura, 1 Astacideum and 1 Palinurum). Many species, such as *A. foliacea, Polycheles typhlops, Aristeus antennatus, P. martia, Sergia robusta* and *P. acanthonotus,* showed high frequency of occurrence. However, their abundance was generally low with *A. foliacea* followed by *Aristeus antennatus* being the most numerous.

Finally, of the 18 decapod species encountered in the zone 900-1200 m, six were Dendrobranchiata and 12 Pleocyemata : 7 Caridea, 4 Brachyura and 1 Palinurum. *S. robusta* was the most frequently occurring species followed by *A. antennatus, P. typhlops, Acanthephyra pelagica, Pasiphaea multidentata, Sergestes arachnipodus, Acanthephyra eximia* and *P. acanthonotus.* Although, *Sergia robusta* and *Polycheles typhlops* predominated in numbers, their abundance was remarkably low.

DISCUSSION

Including results from the present study, the number of known decapods from the Ionian Sea has now reached 82 species. Of the identified decapods, *Acanthephyra eximia*, *Philoceras echinulatus* and *Pontophilus norvegicus* are reported for the first time in the E. Ionian Sea. *Acanthephyra eximia* was found in waters deeper than 800 m, which were not investigated earlier. Only one specimen of *Philoceras echinulatus* was caught in a single station. Finally, only one specimen of *Pontophilus norvegicus* was found in a deep station (965 m). Some other species, such as *Acanthephyra pelagica*, *Geryon longipes, Munida tenuimana, Paromola cuvieri, Parthenope macrochelos, Pasiphaea multidentata, Plesionika narval, Polycheles typhlops, Sergestes arachnipodus* and *Sergestes arcticus,* have been reported for the area only in the gray literature (Deep Water Fisheries technical report, unpublished data ; D'ONGHIA et al., 2001 ; POLITOU et al., 2001). Most of them are also uncommon species or mainly found in the two deepest strata. The two commercial deep-water shrimps *Aristaeomorpha foliacea* and *Aristeus antennatus* that were absent from the list of POLITOU *et al.* (1998) were found during the surveys of the Deep Water Fisheries project and later in the framework of the MEDITS project (KAPIRIS *et al.,* 1999 ; KAPIRIS & THESSALOU-LEGAKI, 2001 ; PAPAKONSTANTINOU & KAPIRIS, 2001 ; CAU *et al.*, 2002). Most of the decapod species found in the present study, with the exception of *Acanthephyra eximia*, *Aegaeon lacazei, Munida rutllanti, Paromola cuvieri, Philoceras echinulatus, Plesionika edwardsii, Plesionika narval* and *Pontophilus norvegicus,* were also found in the SE Adriatic Sea, which is adjacent to the E. Ionian (VASO & GJIKNURI, 1993 ; UNGARO et al., 1999 ; MARSAN *et al.*, 2000). Comparing data from the rest of the Greek waters (Aegean and Cretan Sea) reveals that all the species found in the present study, with the exception of *Pontophilus norvegicus* and *Sergestes arachnipodus,* have been reported in the existing literature for these areas (KOUKOURAS et al., 1992, 1997, 1998, 2000 ; KALLIANIOTIS et al., 2000).

TABLE 1

List of decapod species collected in the E. Ionian Sea with species depth range and frequency of occurrence (%) per depth stratum.

		Depth strata (m)			
	Depth range (m)	**300-500**	**500-700**	**700-900**	**900-1200**
No. of hauls		**45**	**52**	**38**	**13**
Dendrobranchiata					
Aristaeomorpha foliacea (Risso, 1827)	388-1047	2.2	88.5	94.7	15.4
Aristeus antennatus (Risso, 1816)	480-1171	2.2	53.8	89.5	76.9
Gennadas elegans (Smith,1882)	1082-1192				15.4
Parapenaeus longirostris (Lucas, 1846)	288-840	93.3	57.7	10.5	
Sergestes arcticus Kröyer, 1855	700-1192			2.6	23.1
Sergestes arachnipodus (Cocco, 1832)	318-1171	2.2	5.8	10.5	46.2
Sergia robusta (S.I. Smith, 1882)	480-1192	2.2	23.1	63.2	84.6
Solenocera membranacea (Risso, 1816)	322-823	6.7	1.9	2.6	
Pleocyemata					
Anomura					
Munida intermedia A. Milne Edwards & Bouvier, 1899	328-503	11.1	1.9		
Munida rutllanti Zariquiey Alvarez, 1952	300-533	37.8	3.8		
Munida tenuimana G.O. Sars, 1872	518-518		1.9		
Astacidea					
Nephrops norvegicus (Linnaeus, 1758)	317-700	42.2	57.7	2.6	
Brachyura					
Bathynectes longipes (Risso, 1816)	620		1.9		
Bathynectes maravigna (Prestandrea, 1839)	322-1003	6.7	23.1	13.2	15.4
Calappa granulata (Linnaeus, 1758)	302-553	8.9	1.9		
Geryon longipes A. Milne Edwards, 1881	644-965		1.9	7.9	7.7
Macropipus tuberculatus (Roux, 1830)	343-462	11.1			
Macropodia longipes A. Milne Edwards & Bouvier, 1899	340-1003	2.2			7.7
Monodaeus couchii (Couch, 1851)	460-965	2.2	1.9		7.7
Paromola cuvieri (Risso, 1816)	597-742		7.7	2.6	
Parthenope macrochelos (Herbst, 1790)	302-582	11.1	1.9		
Caridea					
Acanthephyra eximia S.I. Smith, 1886	897-1047			2.6	38.5
Acanthephyra pelagica (Risso, 1816)	480-1192	2.2		15.8	61.5
Aegaeon lacazei (Gourret, 1887)	340-464	17.8			
Alpheus glaber (Olivi, 1792)	373	2.2			
Chlorotocus crassicornis (Costa, 1871)	300-614	35.6	3.8		
Pasiphaea multidentata Esmark, 1866	518-1171		9.6	28.9	53.8
Pasiphaea sivado (Risso, 1816)	377-1082	6.7	23.1	10.5	7.7
Philoceras echinulatus (M. Sars, 1861)	407	2.2			
Plesionika acanthonotus (Smith, 1882)	317-1047	13.3	86.5	44.7	30.8
Plesionika antigai Zariquiey Alvarez, 1955	288-700	77.8	34.6		
Plesionika edwardsii (Brandt, 1851)	305-700	35.6	23.1	2.6	
Plesionika gigliolii (Senna, 1903)	300-700	75.6	61.5		
Plesionika heterocarpus (Costa, 1871)	300-676	64.4	23.1		
Plesionika martia (A. Milne Edwards, 1883)	317-1085	15.6	100	65.8	15.4
Plesionika narval (Fabricius, 1787)	356	2.2			
Pontophilus norvegicus (M. Sars, 1861)	965				7.7
Pontophilus spinosus (Leach, 1815)	322-460	8.9			
Palinura					
Polycheles typhlops Heller, 1862	328-1171	17.8	98.1	92.1	76.9

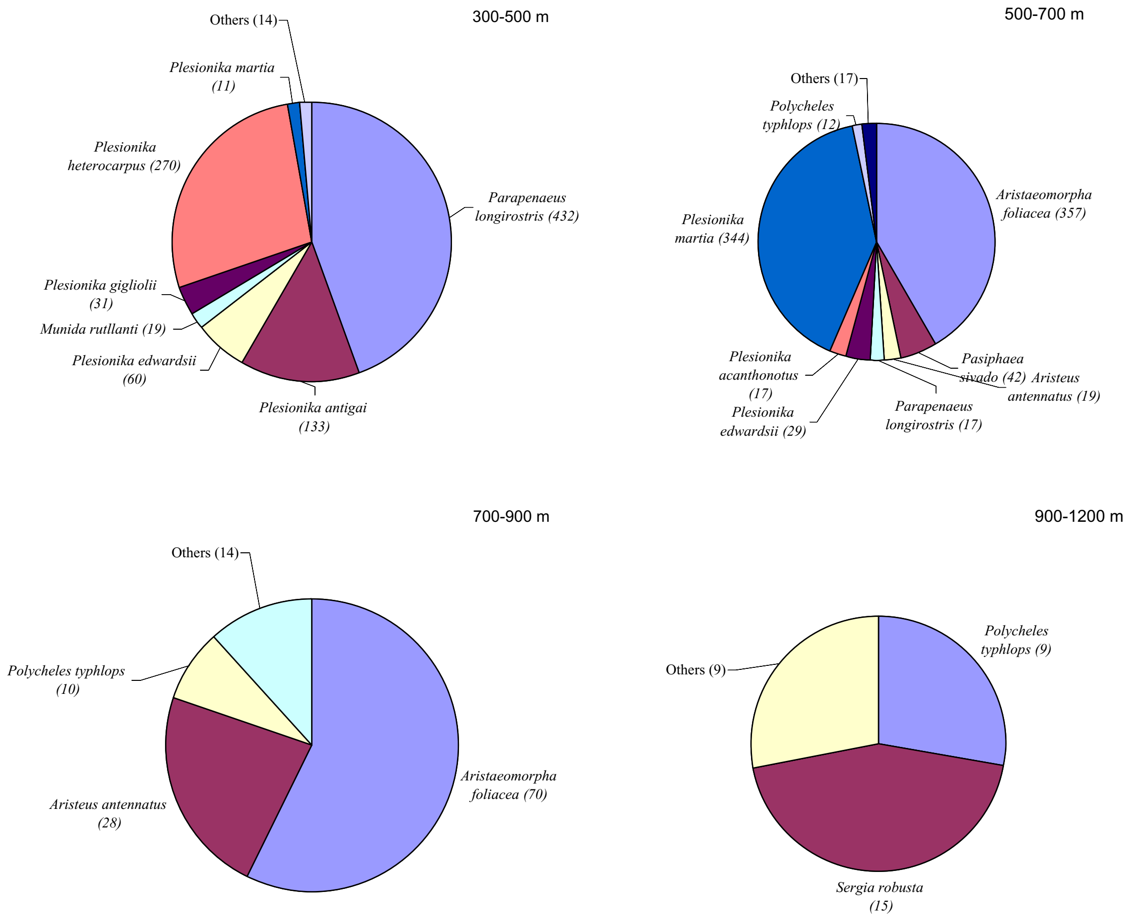

Fig. 2. – Relative abundance of decapod species per depth stratum in the E. Ionian Sea. In parenthesis the mean number of specimens caught per hour (CPUE) is given.

Although comparison of abundance with other studies is difficult, because of the different types of gear and methods used, the general fauna distribution is quite similar to that found in other Mediterranean areas (Abello et al., 1988 ; Cartes & Sarda, 1992, 1993 ; Cartes et al., 1994 ; Ungaro et al., 1999 ; Abello et al., 2002). A dominance of shrimps in all depth strata observed in the present study was mentioned also by Politou *et al.* (1998) for the slope of the region. In relation to the western Mediterranean, our results are more comparable with those of Abello et al. (1988), whose samples were collected with a commercial trawl. A high presence of small species, such as *Calocaris macandreae* Bell, 1864 and *Processa nouveli* Al-Adhub & Williamson, 1975, was mentioned by some authors (Cartes & Sarda, 1992 ; Cartes et al., 1994) for these depths in the Catalan Sea. These species were not found in the present study. This discrepancy can be explained by the smaller cod-end mesh size of the experimental trawl used in the former studies. Furthermore, although the species depth distribution observed in the present study was generally within the ranges given in the literature for the Mediterranean, in some cases new depth records were obtained (Table 2). More specifically, the distribution of the species *Aristaeomorpha foliacea, Bathynectes maravigna, Monodaeus couchii, Parapenaeus longirostris, Pasiphaea sivado, Plesionika antigai, Plesionika edwardsii* and *Plesionika martia* was extended into waters deeper than those reported for the Mediteranean. Concerning *Bathynectes longipes,* it is considered a scarce species (Abello et al., 2001) and no depth distribution ranges are given for it.

A remarkable difference between the Greek Ionian Sea and the westernmost areas of the Mediterranean is the high abundance of *A. foliacea* in the former area and its absence or scarcity in the latter ones. This difference may be explained by the vulnerability of this species to overfishing (Orsi Relini & Relini, 1985 ; Matarrese et al., 1997) in combination with the fishing pressure exercised in the deep waters of the westernmost areas. Such pressure is negligible in the Greek Seas. Furthermore, different hydrological conditions (i.e. salinity and temperature) between areas are reported as factors affecting the distribution of the species along the Mediterranean (Relini & Orsi Relini, 1987 ; Murenu et al., 1994). *A. foliacea* is considered to prefer waters of relatively high salinity and temperature such as those of the E. Ionian Sea in comparison to the westernmost Mediterranean areas (Theocharis et al., 1993 ; Hopkins, 1985).

A decline in the number of decapod species and of their abundance with depth was evident in the Ionian Sea. This pattern was observed also in the western Mediterranean (Cartes & Sarda, 1992, 1993 ; Cartes, 1993). The upper part of the slope (300-700 m) was characterized by a relatively high number of species found in abundance. *Parapenaeus longirostris, Aristaeomorpha foliacea, Ple-*

sionika martia, P. heterocarpus, P. antigai and *P. edwardsii* were the species that displayed the highest abundance values, and most of them are of important commercial value. Below 700 m of depth, the number of species and mainly their abundance decreased sharply, although red shrimps (mainly *A. foliacea* and secondarily *A. antennatus*) were found in non negligible quantities in the zone 700-900 m. Given the relatively constant environmental conditions in these depths and the high oligotrophy of the area (Stergiou et al., 1997), the main factor determining this reduction with depth seems to be the low trophic resource availability.

TABLE 2

Depth range of occurrence for decapod species in the Mediterranean updated with the results of the present study.

Species	**Depth range (m)**	
	Min	**Max**
Acanthephyra eximia	421 (Abello et al., 2002)	2261 (Cartes, 1993)
Acanthephyra pelagica	176 (Abello et al., 1988)	2261 (Cartes, 1993)
Aegaeon lacazei	13 (Abello et al., 1988)	1041 (Cartes, 1993)
Alpheus glaber	3 (Abello et al., 1988)	871 (Abello et al., 1988)
Aristaeomorpha foliacea	150 (Matarrese et al., 1995)	1047 (present study)
Aristeus antennatus	150 (Matarrese et al., 1995)	2200 (Sardà et al., 1994)
Bathynectes longipes	620 (present study)	
Bathynectes maravigna	245 (Abello et al., 2001)	1003 (present study)
Calappa granulata	25 (Abello et al., 2002)	712 (Abello et al., 2002)
Chlorotocus crassicornis	55 (Abello et al., 1988)	742 (Pipitone & Tumbiolo, 1993)
Gennadas elegans	250 (Koukouras et al., 1997)	2261 (Cartes, 1993)
Geryon longipes	439 (Abello et al., 1988)	1895 (Cartes, 1993)
Macropipus tuberculatus	48 (Abello et al., 1988)	748 (Abello et al., 1988)
Macropodia longipes	18 (Abello et al., 1988)	748 (Abello et al., 1988)
Monodaeus couchii	44 (Abello et al., 2002)	965 (present study)
Munida intermedia	35 (Abello et al., 1988)	871 (Abello et al., 1988)
Munida rutllanti	40 (Abello et al., 2002)	587 (Abello et al., 2002)
Munida tenuimana	286 (Abello et al., 2002)	1899 (Cartes, 1993)
Nephrops norvegicus	58 (Abello et al., 2002)	871 (Abello et al., 1988)
Parapenaeus longirostris	26 (Pipitone & Tumbiolo, 1993)	840 (present study)
Paromola cuvieri	267 (Pipitone & Tumbiolo, 1993)	795 (Pipitone & Tumbiolo, 1993)
Parthenope macrochelos	20 (Abello et al., 1988)	655 (Pipitone & Tumbiolo, 1993)
Pasiphaea multidentata	128 (Abello et al., 1988)	2261 (Cartes, 1993)
Pasiphaea sivado	33 (Abello et al., 1988)	1082 (present study)
Philoceras echinulatus	55 (Abello et al., 1988)	871 (Abello et al., 1988)
Plesionika acanthonotus	141 (Pipitone & Tumbiolo, 1993)	1680 (Cartes, 1993)
Plesionika antigai	98 (Abello et al., 2002)	700 (present study)
Plesionika edwardsii	250 (Garcia-Rodriguez *et al*, 2000)	700 (present study)
Plesionika gigliolii	101 (Abello et al., 1988)	748 (Abello et al., 1988)
Plesionika heterocarpus	45 (Abello et al., 2002)	699 (Abello et al., 1988)
Plesionika martia	165 (Abello et al., 1998)	1085 (present study)
Plesionika narval	5 (Thessalou-Legaki et al., 1989)	510 (Politou et al., 2000)
Polycheles typhlops	241 (Abello et al., 2002)	1927 (Cartes, 1993)
Pontophilus norvegicus	366 (Abello et al., 1998)	2261 (Cartes, 1993)
Pontophilus spinosus	69 (Abello et al., 2002)	871 (Abello et al., 1998)
Sergestes arachnipodus	279 (Abello et al., 2002)	1224 (Cartes, 1993)
Sergestes arcticus	160 (Abello et al., 2002)	2188 (Cartes, 1993)
Sergia robusta	220 (Abello et al., 1998)	2261 (Cartes, 1993)
Solenocera membranacea	3 (Abello et al., 1998)	871 (Abello et al., 1998)

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Nesting and hatching success of the sea turtle *Caretta caretta* on Marathonissi island (Zakynthos, Ionian Sea, Greece)

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ABSTRACT. Nesting behaviour and hatching success of the sea turtle *Caretta caretta* (loggerhead) were studied on Marathonissi island in Zakynthos (Ionian Sea, Greece) during the summer of 1995. On this island there exist two discrete nesting areas : the North sector and the West sector. Nesting activity was greatest in both sectors during July. The number of nests was significantly higher in the North sector, whereas remarkably more attempts were observed in the West sector. Hatching success was also greater in the North sector where there were significantly more empty eggshells, mark of successful hatching, than in the West sector. Moreover, the number of dead embryos was significant in the West sector. The current study demonstrates a correlation between the choice of nesting area and hatching success.

KEY WORDS : *Caretta caretta*, loggerhead, hatching success, nesting behaviour, sea turtle.

INTRODUCTION

Caretta caretta (loggerhead or caouanne in French) is one of the two common sea turtle species in the East Mediterranean Sea. The other one is the green turtle, *Chelonia mydas*. The reproductive behaviour of loggerhead is not so clear while most of the existing data concern its nesting behaviour. *C. caretta* displays a wide geographical distribution, encompassing Mexico, Australia and the Mediterranean Sea. A typical characteristic of the loggerhead's nesting behaviour is migration (MEYLAN et al., 1983; HUGHES, 1989; LIMPUS et al., 1992). Scientific data obtained via tagging of the females during nidification (MARGARITOULIS, 1988a) as well as by examination of the mitochondrial DNA (BOWEN et al., 1994; LAURENT et al., 1993) enhance the hypothesis of the existence of different populations of *C. caretta*. The age of reproductive maturity is 22-26 years for the West Atlantic population (KLINGER & MUSIK, 1995) and more than 30 years for the Australian loggerhead population (BOWEN et al., 1994; LAURENT et al., 1993). Regarding the present study, the population nesting on the Greek beaches passes the winter months in Tunisia (LAURENT & LESCURE 1994). Only the adult females leave the sea so as to nest and their corresponding behavioural patterns have been described (HAILMAN & ELOWSON, 1992). During the same reproductive period the females nest more than once (HUGHES et al., 1967; WORTH & SMITH, 1976). Several studies have examined the factors implicated in juvenile mortality (PRITCHARD 1980; YNTEMA & MROSOVSKY, 1980; BLANCK & SAWYER, 1981; YNTEMA & MROSOVSKY, 1982; WYNKEN et al., 1988; HAYS & SPEAKMAN, 1993). The aim of the current study is to investigate whether a correlation exists between the females' choice of nesting site and the hatching success.

MATERIAL AND METHODS

Laganas bay in Zakynthos is one of the most important nesting places of the loggerhead *C. caretta*. The sites of the present study are located on the beaches of Marathonissi island. Seven discrete nesting beaches occur in Laganas bay : Laganas, Kalamaki, Theiafi, Sekania, Daphni, Gerakas and Marathonissi. Marathonissi is a small, uninhabited island in Laganas Bay, allowing all field observations to be carried without interference from anthropogenic activities (i.e. tourism). The nesting area of Marathonissi is dense and for the needs of this study was subdivided into two sectors : West sector and North sector (Fig. 1).

One nesting area, that of the North sector, was 200 m long and closer to the sea, comprising rocks and stones. Halophytic vegetation began at a distance of 150 m from the beach. The slope of the infralittoral zone was steep. A dense meadow of the phanerogam *Posidonia oceanica* was located close to the beach. The other area, that of the West sector, was 150 m long and narrower than that of the North sector. A dense meadow of the phanerogam *Cymodocea nodosa* at 0-2 m, as well as a deeper meadow of *P. oceanica* characterized the infralittoral zone. All field observations and consequent data collections were conducted between 28 May and 25 September 1995.

The first part of the study involved observation of the adult females, coming out to the beach so as to nest. The term "nest" was utilized to characterize the successful oviposition along with all the distinctive behavioural patterns. Occasionally, exit of the females from the sea was followed by unsuccessful oviposition, attributed to various reasons. In this case, the term “attempt” was used to characterize such a behaviour. Observations were direct during the night watch, when animals were tagged, and indirect every morning via examination of tracks on the beach.

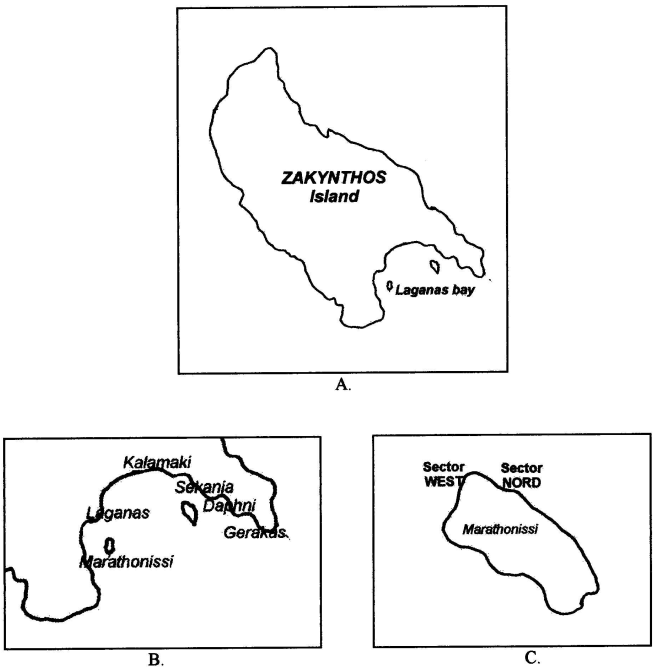

Fig. 1. – Map of the nesting areas on Marathonissi island in Zakynthos (A), Laganas bay with the potential nesting beaches (B) and Marathonissi nesting beaches (C).

Similar methods were applied during the second part of the study to estimate the hatching success, including indirect observations of the tracks of hatchlings and direct observations after excavation of the nests. Each nest excavation was carried out five days after the last tracks. Empty eggshells were characterized as successful hatching.

RESULTS

Nests and attempts were observed in both sectors. One of the factors influencing the hatching success was the distance of the nest from the sea. This distance was significantly greater in the North sector (24.6±7.6 m; n : 131) than in the West sector (20.9±7.5m; n : 97) (t-impaired : t=3.582, d.f. =226, $p<0.001$). As shown in Fig. 2, more nests were present in both sectors during July. However, the number of nests was significantly higher in the North sector than in the West sector during July (t-impaired : t=1.935, d.f. =73, $p<0.05$). Based on Fig. 3, the number of attempts was also greater in both sectors during July. In contrast to nests, significantly more attempts were observed in the West sector than in the North sector during July (t-impaired: t=3.426, d.f. =, $p<0.05$). As a general remark the percentage of nests was higher in the North sector (39% nests/61% attempts) than in the West sector (27% nests/73% attempts) during the nesting phase.

The second phase of the current study focused on hatching. The data demonstrated in Table 1 were collected via excavation of the nests five days after the last hatchlings’ tracks. The time of the incubation period was practically the same in both sectors (t-impaired : t=1.1, d.f.=16, $p>0.05$). The mean incubation period was 72.0±8.4 days (n: 8) in the North sector and 66.0±13.4 days (n: 10) in the West sector. Another parameter not significantly different in the two sectors was the depth of the nest (t-impaired : t=-0.293, d.f. =37, $p>0.05$). The mean depth of the nest was 48.2±7.2 cm in the North sector and 48.8±5.3 cm in the West sector. As observed, all the hatchlings did not leave the nest at the same time. The period between the first and the last tracks was similar in the two sectors (t-impaired : t=-0.251, d.f.=37, $p>0.05$). Mean time of the hatchlings’ exit from the nest was 5.2±1.8 days in the North sector and 5.4±3.8 days in the West sector.

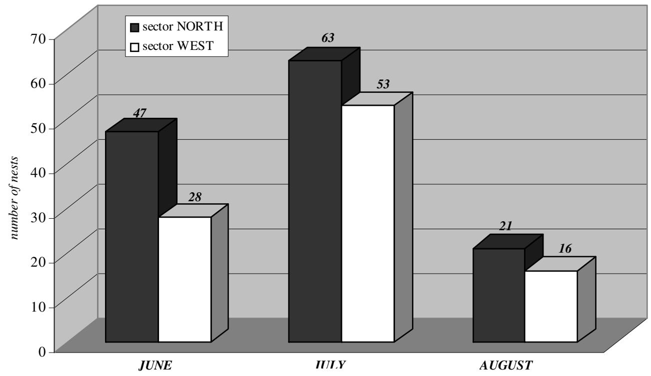

Fig. 2. – Number of nests in the North and West sectors on Marathonissi island (Zakynthos, Greece) during the summer of 1995.

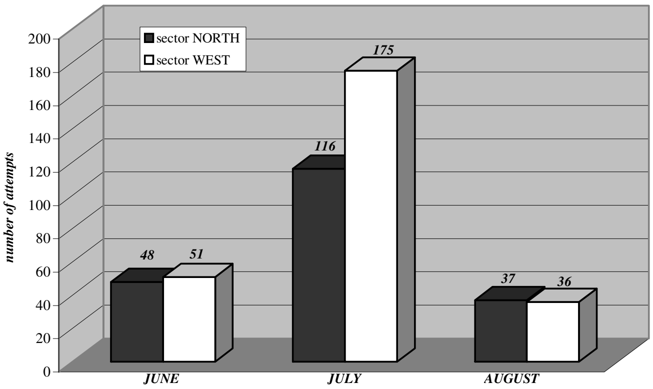

Fig. 3. – Number of attempts in the North and West sectors on Marathonissi island (Zakynthos, Greece) during the summer of 1995.

After nest excavation it was found that the number of eggs per nest was also not significantly different (t-impaired : t=-0.541, d.f. =37, $p>0.05$) in the two sectors. The mean number of eggs per nest was 127.4±19.8 in the North sector and 122.6±33.7 in the West sector. Nevertheless the number of empty eggshells, mark of successful hatching, was greater in the North sector than in the West sector (t-impaired : t=-2.498, d.f. =37, $p<0.05$). Moreover there were more dead embryos in the West sector than in the North sector (t-impaired : t=-2.828, d.f. =37, p<0.05). Finally, the numbers of unfertilized eggs (t-impaired : t=-1.532, d.f. =37, p>0.05), of live embryos (only one, found in the West sector), of live hatchlings (t-impaired : t=0.082, d.f. =37, p>0.05) and of dead hatchlings (t-impaired : t=-1.544, d.f. =37, p>0.05) did not show significant differences between the two sectors.

TABLE 1

Hatching parameters in the North and West sectors on Marathonissi island (Zakynthos, Greece) during the summer of 1995.

	Sector NORTH (n :19)		Sector WEST (n :20)	
	mean±SD	min-max	mean±SD	min-max
Number of eggs per nest	127.4±19.8	88-172	122.6±33.7	76-238
Empty eggshells	97.7±33.6	13-143	70.9±33.3	14-120
Unfertilised eggs	24.3±24.0	0-86	39.3±36.0	0-125
Dead embryos	2.3±2.9	0-10	6.5±7.6	0-28
Dead hatchlings	1.6±2.1	0-7	4.3±7.2	0-26
Live hatchlings	1.5±2.7	0-11	1.4±2.9	0-11

DISCUSSION

Marathonissi island is one of the most important nesting beaches of Zakynthos, where, during the summer of 1995, 228 nests on 350 meters of beach length were observed. During this study the curve length of the adult females *C. caretta* was measured. Such results confirm the hypothesis of the presence of different loggerhead populations in the East Mediterranean Sea. The females of the loggerhead's Cyprus population are larger in size than the Greek ones (Broderick & Godley, 1996). In support of the morphological parameters the same hypothesis was confirmed by the examination of mitochondrial DNA (Bowen et al., 1994; Laurent et al., 1993).

The observations of the present study have shown that the period with the greatest nesting activity was July. Similar data were collected in Cyprus (Demetropoulos & Hadjichristophorou, 1989). However, respective observations on Turkish beaches in Mugla (Erk'akan, 1993) and in Fetihye (Baran & Türkozan, 1996) have demonstrated that the month with the highest nesting activity is June.

The mean number of eggs per nest observed in Marathonissi was 127.4 in the North sector and 122.6 in the West sector. These values were higher than those measured in Kyparisisa (Greece) 117.7 eggs/nest, (Margaritoulis, 1988b), in Israel 82 eggs/nest (Silbersetein & Dmi'el, 1991), in Turkey 82.9 eggs/nest (Baran & Türkozan, 1996) and in Cyprus 61.0 eggs /nest (Broderick & Godley, 1994). Based on bibliographic data, hatchlings show high mortality and it is estimated only 1/1,000 survives to adulthood (Frazer, 1986). It can be assumed that the increased number of eggs/nest in Marathonissi demonstrates a reproductive strategy. Such a hypothesis is enhanced by the percentage of successful hatching in both sectors of Marathonissi (empty eggshells/total of number eggs), being only 65.1%.

Sand temperature is one of the factors that influence the sex ratio and probably the hatchlings' mortality (Mrosovsky & Yntema, 1980). Temperature is also the major factor that affects the incubation period. The two nesting sectors in Marathonissi did not exhibit remarkable differences in the incubation time (Hays et al., 1992). Hatchling emergence, as has been observed in Cephalonia, is an asynchronous phenomenon (Houghton & Hays, 2001). In other nesting areas shorter incubation periods than that in Marathonissi have been observed, such as 55 days in Kiparissia (Greece) (Margaritoulis, 1988), 47.9 days in Cyprus (Broderick & Godley, 1994; Godley et al., 2001), 54 days in Israel (Silbersetein & Dmi'el, 1991) and 55.0 in Turkey (Baran & Turkozan, 1996).

Other studies on the neighboring island of Cephalonia demonstrate a positive linear relationship between the number of clutches into which eggs could be divided and the total time spent by nesting turtles on the beach, and hence a negative relationship between the time invested on the beach per egg and clutch size (Hays & Speakman, 1991). Body size of females was also positively related to the number of eggs laid and clutch volume (Hays & Speakman, 1992).

The current study showed that in both nesting areas in Marathonissi a correlation existed between the number of nests, the number of hatchlings and their mortality. Most likely factors, such as sand granulometry, humidity, presence of rocks and stones e.t.c. influence both nesting choice and successful incubation. Nevertheless, further investigation is required to establish the significance of this correlation, as well as to demonstrate the factors affecting nesting choice and hatching success.

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Marked interannual differences in reproductive parameters and daily egg production of anchovy in the northern Aegean Sea

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ABSTRACT. In the present paper, an overview of the application of the Daily Egg Production Method (DEPM) to the northern Aegean Sea anchovy stock is presented, and reproductive parameters are compared in the framework of ambient oceanographic regimes. The DEPM was applied twice : in June 1993 and June 1995. Data collection was based on bongo-net ichthyoplankton surveys and concurrent adult surveys onboard the commercial fishing fleet. Revised, more precise estimates of the daily egg production are presented based on the inclusion of both eggs and yolksac stages in the estimation procedure (fit of single embryonic mortality curves). Remarkable between-years differences in the daily egg production, batch fecundity and spawning frequency were found. These parameters were significantly higher in June 1993 than in June 1995. In June 1993, waters were colder, less saline and richer in zooplankton compared to 1995. Adult somatic condition and egg size were also higher in June 1993 than in 1995. These findings emphasize the importance of adult prey availability in determining anchovy egg production.

KEY WORDS : *Engraulis encrasicolus*, Aegean Sea, DEPM, Reproduction

INTRODUCTION

The Daily Egg Production Method (DEPM) is an ichthyoplankton-based method for estimating biomass of fish stocks and monitoring trends in fish abundance (Hunter & Lo, 1997). It has been developed for fishes that have indeterminate annual fecundity, like most clupeoids (Lasker, 1985), and has been applied to a variety of anchovy and sardine species and stocks (Alheit, 1993 ; Hunter & Lo, 1997). Besides biomass estimation, the application of DEPM provides regional time series on important biological variables of fish stocks, which can lead to new insights into the reproductive biology of multiple spawning fishes, particularly when such variables can be compared and subsequently related to environmental regimes.

This paper presents an overview of the application of DEPM to the anchovy [*Engraulis encrasicolus* (Linnaeus, 1758)] stock of the northern Aegean Sea (Greece, Eastern Mediterranean). The DEPM has been applied to anchovy stocks in the Western Mediterranean (Garcia & Palomera, 1996), the northern Aegean Sea (Somarakis & Tsimenides, 1997 ; Somarakis et al., 1997 ; Somarakis, 1999), the central Aegean and Ionian Seas (Somarakis et al., 2002) and the Sicilian channel (Quintanilla & Garcia, 2001). The applications in the northern Aegean Sea were carried out in June 1993 and June 1995 and were largely experimental, based on bongo-net larval surveys coupled with concurrent adult surveys onboard the commercial purse seine fleet. Reproductive parameter estimates are compared in an effort to understand the reproductive strategy of the species.

MATERIAL AND METHODS

The biomass model

The spawning stock biomass was estimated according to the model (Lasker, 1985) :

$$B = (\mathrm{k} \cdot P \cdot \mathrm{A} \cdot W)/(R \cdot F \cdot S)$$

where, B = spawning stock biomass in metric tons, k = conversion factor from grams to metric tons, P = daily egg production (number of eggs per sampling unit, m^2), A = total survey area (in sampling units, m^2), W = average weight of mature females (grams), R = sex ratio (fraction of mature females by weight), F = batch fecundity (mean number of eggs per mature females per spawning), and S = fraction of mature females spawning per day (spawning frequency).

Based on the delta method, the approximate variance of the biomass estimate is a function of sample variances and covariances (Lasker, 1985) :

$$VarB \cong \hat{B}^2 (CV(P)^2 + CV(W)^2 + CV(F)^2 + CV(S)^2 + 2COVS)$$

where CV denotes coefficient of variation, and $COVS$ is the sum of terms involving covariances.

Survey description

Two oceanographic surveys were carried out during June 1993 and June 1995 in the northern Aegean Sea (eastern Mediterranean). The sampling scheme was based on transects spaced approximately ten nautical miles apart and stations located at five nautical-mile intervals on each transect (Fig. 1). The same stations (n=111) were sampled in both years. The total survey area was 17396 km^2. Plankton and hydrographic sampling (vertical profiles of temperature and salinity) were performed at each station.

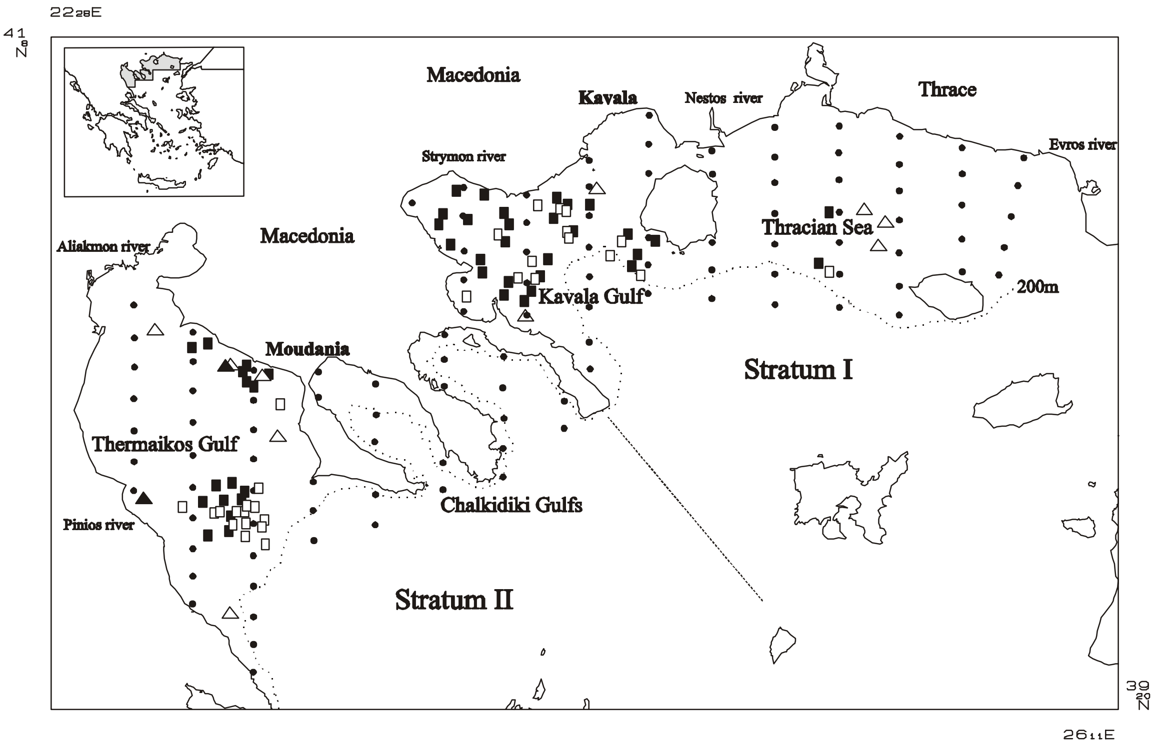

Fig. 1. – Northern Aegean Sea. Map of the surveyed area showing the location of sampling stations. ● : plankton and hydrographic samples. ■ : 1993, purse seine samples. □ : 1995, purse seine samples. ▲ : 1993, pelagic trawl samples. △ : 1995, pelagic trawl samples.

A 60-cm bongo-net sampler was used on both cruises. Mesh sizes on the sampler were 335 and 250 microns. The 0.250-mm mesh net is considered to completely retain anchovy eggs and larvae (Somarakis et al., 1998 ; Somarakis, 1999). Tows were double oblique and the volume filtered was determined by a calibrated flowmeter (Hydrobios) in the mouth of each of the nets. The depth of the sampler could be monitored onboard at any time during the tow by means of a recording depthmeter attached to the sampler. Maximum tow depth and volume of water filtered were subsequently used to standardize catches to numbers per m^2. More details are provided in Somarakis et al. (1998).

Adult samples were collected on board the commercial purse seine fleet of Kavala and Moudania and were representative of the fishing grounds (Fig. 1). Additional samples of hydrated females were obtained by means of a pelagic trawl operated from the research vessel "PHILIA", during the daily spawning interval (21:00-2:00). Fish were fixed onboard immediately after collection, using 15 l jars filled with 10% neutral-buffered formalin. Each sample consisted of random collection of 1.5-2 kg of anchovies.

Laboratory procedures

Anchovy eggs and larvae were sorted from the plankton samples. The eggs were staged using the eleven - stages system of Moser & Ahlstrom (1985). Yolk-sac larvae were staged into larvae with un-pigmented eyes (YSI) and larvae with traces of brown pigment or brownish eyes (YSII). Eggs and yolk-sac larvae at each developmental stage were counted and their abundance standardized to number per m^2. Zooplankton displacement volume (ZDV) was measured for each sampling site from the catch of the 0.250-mm mesh bongo net (Smith & Richardson, 1977). ZDV values were standardized to ml/m^2. At each station, the major and minor diameters of ten anchovy eggs were measured to the nearest 0.02 mm using an ocular micrometer. Egg volumes were calculated using the formula for a prolate spheroid.

Processing of an adult sample in the laboratory consisted of measuring length and weight (both total and gonad free weight), and sexing of all or at least 50 fish per sample. Correction factors were applied to convert formalin-weight to wet weight and the total weight of hydrated females was corrected for the increase in weight due to hydration of the ovaries (Somarakis et al., 2002). Relative condition factor of females (Bolger & Connolly, 1989) was calculated. The gonads of ten females per sample were randomly selected and subjected to histological analysis. All macroscopically detected hydrated or running females were measured and their gonads weighed and preserved in formalin for subsequent histological and batch fecundity analysis. The hydrated oocyte method was used for batch fecundity measurements (Hunter et al., 1985).

Spawning frequency (*S*), i.e., the fraction of mature females spawning per night, was assessed by the postovulatory follicles (POFs) method. The three types of POFs described by Hunter & Macewicz (1985) (Day-0, Day-1, and Day-2+ POFs) were also observed in our histological preparations and were used in classifying ovaries as to the date of spawning (Somarakis et al., 2002). Actively spawning anchovy (hydrated and Day-0 females) are oversampled during the hours of spawning (Somarakis, 1999 ; Somarakis et al., 2002 and references therein). To overcome this problem, we used samples collected outside the daily spawning interval, i.e. after 4 :00 a.m., and calculated spawning frequency based on the composite fraction of Day-0 and Day-1 spawners, to increase precision of the spawning frequency estimates (Quintanilla & Perez, 2000). Fractions of Day-0 and Day-1 spawners had the same statistical distributions after 4:00 a.m. (Wilcoxon paired sample tests, p>0.05).

Parameter estimation

Age of eggs was calculated based on a temperature dependent model of European anchovy developmental rate (Regner, 1985), the station surface temperature (5 m), peak spawning time (midnight ; Somarakis, 1999), and time of tow (Lo, 1985). Procedures of ageing anchovy eggs are described in Somarakis et al. (2002).

The estimation of the daily egg production generally involves the fit of an exponential mortality model to the abundance-at-age egg data set (Picquelle & Stauffer, 1985). A preliminary estimate of the daily egg production for the 1993 survey, based on the egg data set (Somarakis & Tsimenides, 1997) was problematic and highly uncertain because of inadequate numbers of positive egg data. This was mainly due to the effect of high incubation temperatures and corresponding occurrence of only single or two daily cohorts of eggs in the samples. To increase the number of age categories for constructing the mortality curves, we assumed that the mortality rate was the same for eggs and yolk-sac larvae, and we included both in single embryonic mortality curves (Lo et al., 1996 ; Somarakis et al., 2002). The estimate of daily production of eggs was derived by regressing the counts of embryos (eggs and yolk sac larvae) on their age using the exponential mortality model :

$$P_t = Pe^{-Zt}$$

where P_t= number of embryos at age t produced per day per m^2, t = age in days, P = daily egg production per m^2, Z= daily rate of instantaneous embryonic mortality.

We used both yolk-sac larvae stages (YSI and YSII) and calculated their duration and age from fertilization following methods described in Somarakis et al. (2002). The technique to estimate *P* and *Z* was weighted non-linear least squares regression. Station weighting factors were proportional to the station representative area.

We used the ratio estimator (Picquelle & Stauffer, 1985) for adult parameters *W*, *R*, *F*, and *S*. Data on the number of eggs per batch (F_{ij}) and the ovary free weight (W^*_{ij}) recorded for the hydrated females were used to fit a linear model :

$$F_{ij} = a + bW^*_{ij}$$

The regressions were forced through zero because *a* was not significantly different from zero at the 0.05 level.

RESULTS

The distribution and abundance of eggs and yolk-sac larvae are presented in Fig. 2. Higher egg concentrations were found in the Thracian Sea and Thermaikos Gulf. The surveys did not cover the entire anchovy egg and yolksac distribution. Particularly in the Thracian Sea, a significant fraction of egg and larval production seemed to extend offshore as well as in Turkish territorial waters.

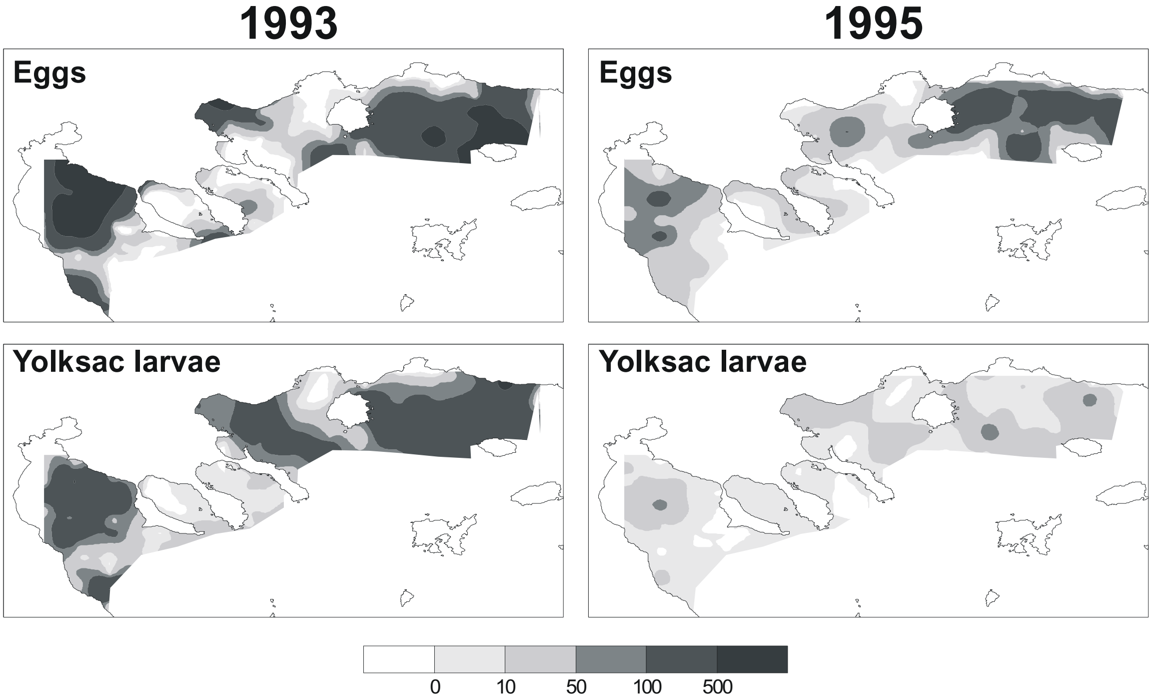

Fig. 2. – Contour maps of anchovy eggs and yolksac larvae abundance (numbers/m2) in June 1993 and June 1995.

On the basis of the egg distribution pattern and regional allocation of adult samples (Fig. 1) the surveyed area was stratified into two sub-regions : the Eastern region (Thracian Sea and Kavala - Stratum I) and the Western region (Thermaikos and Chalkidiki Gulfs - Stratum II). The DEPM was applied separately for the two strata. Statum I covered 9354 km^2 and stratum II 8042 km^2. Parameter and biomass estimates are given in Table 1.

TABLE 1

Biomass and parameter estimates of the DEPM applied to the northern Aegean anchovy stock in June 1993 and June 1995. Stratum I comprised the Thracian Sea and Kavala Gulf. Stratum II comprised the Thermaikos and Chalkidiki Gulfs (see Fig. 1). Coefficients of variation are given in parentheses.

	Stratum I (East)		**Strarum II (West)**	
Parameter	**1993**	**1995**	**1993**	**1995**
Daily egg Production (*P*, eggs/m^2)	109.22	25.71	87.19	19.75
	(0.27)	(0.24)	(0.33)	(0.26)
Instantaneous embryonic mortality rate (*Z*)	0.17	0.52	1.26	0.54
	(0.36)	(0.40)	(0.39)	(0.48)
Average weight of mature females (*W*, g)	24.89	25.65	20.88	22.72
	(0.03)	(0.03)	(0.03)	(0.03)
Weight specific sex ratio (*R*)	0.51	0.51	0.60	0.61
	(0.05)	(0.08)	(0.05)	(0.03)
Average batch fecundity (*F*, number of eggs)	12451	7781	10474	5128
	(0.05)	(0.06)	(0.04)	(0.10)
Fraction of mature females (*S*)	0.29	0.15	0.26	0.13
	(0.21)	(0.11)	(0.20)	(0.23)
Spawning biomass (*B*, metric tons)	14002	10282	9030	8948
	(0.34)	(0.22)	(0.38)	(0.36)

Estimates of the daily egg production (*P*) and adult reproductive parameters (*F, S*) indicated a higher spawning intensity in 1993 than in 1995. Batch fecundity (F_{ij})-on-gonad free weight (W_{ij}^*) relationships were :

<u>Stratum I</u> : 1993 : $F_{ij} = 563\ W^*_{ij}$, $r^2 = 0.63$, n=25

1995 : $F_{ij} = 325\ W^*_{ij}$, $r^2 = 0.22$, n=70

<u>Stratum II</u> : 1993 : $F_{ij} = 558\ W^*_{ij}$, $r^2 = 0.81$, n=43

1995 : $F_{ij} = 242\ W^*_{ij}$, $r^2 = 0.27$, n=15.

Analysis of covariance showed that, for each year separately, the between-strata difference in batch fecundity was not significant (P>0.05). However, the slope of the regression line (relative batch fecundity, eggs/g) was significantly higher in 1993 than in 1995 (P<0.05, Fig. 3). Spawning frequency estimates (Table 1) indicated a mean inter-spawning interval (=1/S) of 3.5 days and 3.9 days, for Stratum I and II respectively, during June 1993, and 6.7 days and 7.7 days for the same areas in June 1995.

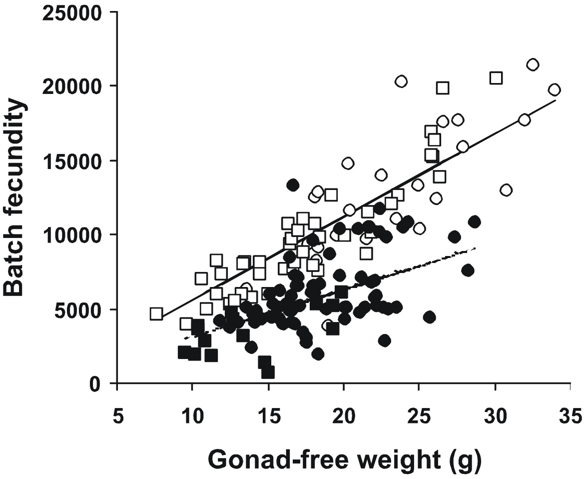

Fig. 3. – Batch fecundity (number of eggs)-on-gonad free weight relationssships. ○ : 1993, Stratum I. ● : 1995, Stratum I. □ : 1995, Stratum II. ■ : 1995, Stratum II. Zero-forces regression lines for 1993 (solid line) and 1995 (broken line) are also drawn.

Mean egg size and somatic condition of adult females were also significantly higher (t-tests, p<0.05) in June 1993 than in 1995 (Fig. 4). Concurrently, waters were colder, less saline and richer in zooplankton during 1993 than in 1995 (p<0.05, Fig. 4).

DISCUSSION

The applications of the DEPM to the northern Aegean Sea anchovy stock were largely experimental, based on data from bongo-net larval fish surveys and opportunistic adult sampling on board the commercial fleet (SOMARAKIS & TSIMENIDES, 1997). A concurrent total biomass survey carried out by acoustic methods during June 1995 (MACHIAS et al., 1997), gave the estimates of 26671 (CV=0.19) and 17929 metric tons (CV=0.15) for the eastern and the western stratum respectively. The surveyed area during the DEPM applications did not cover the entire spawning area of the anchovy stock, thus, the calculated biomass values are underestimates of the total spawning biomass of this stock. However, sampling procedures and subsequent laboratory and analytical methods were identical between 1993 and 1995 and allowed the between-year comparison of the estimated parameters. The robustness of the DEPM to opportunistic adult sampling is discussed elsewhere (SOMARAKIS & TSIMENIDES, 1997).

In comparing the DEPM parameters between 1993 and 1995 in relation to various environmental and fish parameters, we observed that adult food availability (mesozooplankton) was higher in the cooler and fresher waters of 1993 (Fig. 4). Concurrently, female anchovies were in better condition, producing numerous large-sized eggs at a higher spawning frequency (short interspawning interval). These observations are consistent with a ration-related reproductive tactic in anchovy (SOMARAKIS et al., 2000).

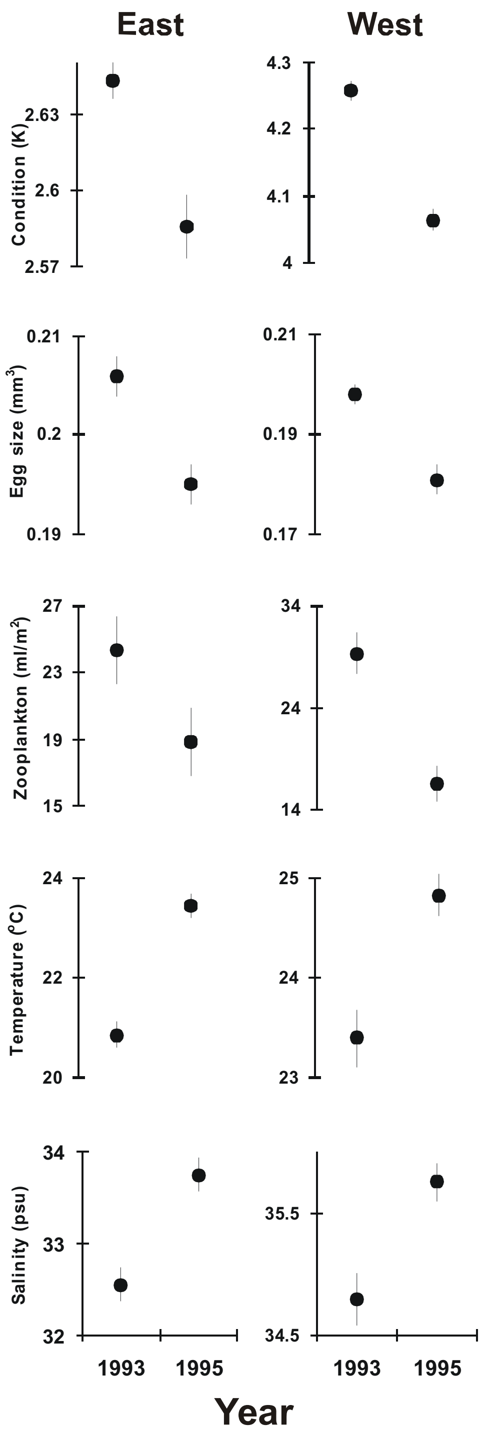

Fig. 4. – Averages and 95% confidence intervals per area (East: Stratum I – West: Stratum II) and year (1993-1995) for relative condition factor (K), mean egg size, zooplankton displacement volume, surface temperature (5 m) and surface salinity (5 m).

In short-living multiple spawning fishes, adults may spawn in direct response to temperature and photoperiod, however, there are examples that minimum forage be required for the onset of spawning, despite ample fat stores (Blaxter & Hunter, 1982). Several studies indicate a ration-related variation in size-specific fecundity or interspawning interval (e.g. Bagenal, 1973 ; Bailey & Almatar, 1989 ; Tsuruta & Hirose, 1989). In south-African pilchard, females spawn an increased number of eggs in response to better fish condition, irrespective of temperature (Le Clus, 1992). Energy allocated to multiple spawnings is derived primarily from feeding rather than from energy reserves in many small pelagic fishes (e.g. Wright, 1990 ; Wang & Houde, 1994). In other cases, spawning is related to both dietary intake and nutritional status of the fish (e.g. Milton et al. 1994). A link between adult forage and spawning is reasonable because of the high energetic cost of frequent spawnings and the fact that areas suitable for planktivorous adults are also suitable for the planktivorus larvae (Blaxter & Hunter, 1982). Recently, Peebles et al. (1996) showed that bay anchovy's egg and subsequent larval production is related to adult as well as larval prey availability. They suggested that hatching larvae are likely to be associated with elevated nauplius densities because of the inherent interdependence between copepod life stages.

Applying the terminology of life history evolution (Stearns, 1992), Somarakis et al. (2000) labeled planktivorous short-lived small pelagic species, such anchovies, as 'income breeder', spawning soon after energy for egg production becomes available. These species are characterized by substantial, ration-related variations in batch fecundity, spawning frequency, and, probably, in egg size. In multiple-spawning fish, batch fecundity does not necessarily increase to compensate for smaller egg sizes (Le Clus, 1992).

The DEPM applications to the northern Aegean Sea anchovy stock are the first to be made in the eastern Mediterranean. The comparison of parameter estimates in relation to environmental regimes highlights the importance of inter-annual variations in the oceanographic habitat in controlling anchovy egg production.

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Some structural and functional characteristics of a soil nematode community from a Mediterranean grassland

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ABSTRACT. This paper refers to the effects of large-scale seasonal fluctuations as well as experimentally induced small-scale variations of soil temperature and moisture on the structural and functional characteristics of a soil nematode community from a Greek Mediterranean grassland. Two levels of soil temperature, with a mean difference of 1.4° C, and two levels of moisture (2.3% difference in water content) were created. The experiment lasted for a six-month period (from July to December).

All nematode community parameters vary significantly with season, with the exception of the environmental constant (C_{env}), which reflects the intensity of competition. The Maturity Index (MI) is affected only by seasonally fluctuating soil conditions, while the Plant Parasite Index (PPI) is affected only by the small-scale differences in soil temperature and moisture. The high value (1.48) of bacterivorous to fungivorous ratio (B/F) indicates mainly bacterial mediated decomposition, resulting in good soil fertility. The B/F ratio is affected both by large and small-scale changes in soil conditions. Diversity and richness show dependence on seasonal variations as well as on small changes in temperature, while no effect of moisture is recorded. The correlations between nematode community parameters, microflora parameters and soil nitrogen pools show independence of nematode parameters from soil N-pools ($N_{organic}$ and $N_{inorganic}$) and parameters relating to microflora, as well as strong dependence on microbially-bounded nitrogen.

KEY WORDS : climatic change, Mediterranean-type ecosystems, functional groups, community structure

INTRODUCTION

Organic matter transformation and nutrient turnover in terrestrial ecosystems involve a large array of soil organisms (Swift et al., 1979). Among them, nematodes play a quite important role in determining soil functioning (Ekschmitt et al., 2001), since the major part of nutrient interchange in soils is due to the activity of microbial-feeding nematodes (Griffiths et al., 1995). Nematofauna has been the target group of different studies aiming to seek effects associated with changes in organic matter input (Armendariz & Arpin, 1996 ; Armendariz et al., 1996 ; Fu et al., 2000 ; Akhtar, 2000), modified microbial productivity (Sohlenius, 1990 ; Griffiths et al., 1994), soil pollution (Ruess et al., 1993 ; Korthals et al., 1996) etc. Moreover, community diversity indices together with indices such as the ratio of bacterivorous to fungivorous nematodes (B/F), the plant parasite (PPI) and the maturity (MI) indices, accounting for both quantitative and qualitative ecological aspects of nematode communities (Bongers, 1990, Porazinska et al., 1999), have been extensively used for bioindication purposes, relating to the degree of human intervention in agricultural systems (Freckman & Ettema, 1993), the soil quality (Yeates & van der Meulen, 1996) and the recovery after perturbation (Urzelai et al., 2000).

In the present work, we used the above mentioned parameters of a nematode community in order to assess the impact of climatic changes on soil dynamics. Indeed, data regarding the effects of the foreseen global climatic changes on soil ecosystem components, especially at a local scale, are missing (Bakonyi & Nagy, 2000). Our work was carried out in a Mediterranean grassland and constitutes a part of our contribution to an EU-project, entitled «Diversity Effects in Grassland Ecosystems of Europe (DEGREE)» focusing on climatic change effects on soil nematodes, microbial processes and nutrient transformation patterns. The soil microclimate at each European grassland included in this project was experimentally manipulated, according to a common design for all partner countries. The microclimatic changes obtained by temperature and moisture manipulations in our field site, were of a small-scale and could be considered similar to those predicted by some climate change scenarios for the Mediterranean region (Osborne & Woodward, 2001). The effects of those small-scale microclimatic changes on the structural and functional characteristics of the nematode community were explored and compared to the effects of the seasonal changes of temperature and humidity. These latter climatic changes were considered of a large-scale, since the mediterranean climate exhibits a clear-cut seasonality, characterised by hot-dry summers and mild-wet winters. Furthermore, though a full list of the nematode taxa recorded in our filed site has already been given in Nagy & Stamou (1998), information associating the nematode community characteristics with soil biochemical parameters is missing. Thus, in this paper we also tried to correlate the nematode community parameters with parameters relating to soil microflora and nitrogen pools.

MATERIAL AND METHODS

Site description

The research site lies at an altitude of 210-215m, 55km south-east of Thessaloniki (40° 20' N latitude, 23° 12' E longitude), and has a south-easterly orientation. It lies on a limestone block of Kimmeridgian-Portlandian age, surrounded by Miocene-Pliocene deposits. The soil is shallow, discontinuous and generally not more than 10 cm deep. The profiles are classified as lithic leptosols (FAO) with a gravely and stony clay-loam texture. Soil particles bigger than 2 mm represent 69.46% of fresh weight of soil. Soil organic carbon varies from 4.01 to 5.32% and total amount of organic matter from 6.89 to 9.18% dry matter of soil. The pH (H_2O) and pH (KCL) is 7.7 and 6.6 respectively.

According to previous data (Diamantopoulos et al., 1996), the climate of the region is characterized as Mediterranean with small amounts of rainfall during the hot summer months. The dry period lasts from mid June to mid October. Mean annual air temperature and precipitation is 16.03° C and 435.53 mm, respectively.

Experimental design and sampling

The experiment lasted for a six-month period, from July to December, during which soil microclimate was manipulated in 12 adjacent field plots (1x1m), covered by the grasses *Stipa bromoides* (L) Dorf., *Aegilops geniculata* (Roth.), *Aegilops triuncialis* (L.), *Avena sterilis* (L.), *Brachypodium distachyum* (L.) Beauv., *Bromus tectorum* (L.) and *Dactylis glomerata* (L.) among others (Dalaka 2001). In order to modify soil temperature conditions, we used vertical windshields and horizontal transparent greenhouse roofs (cutting off also precipitation). Soil water content was manipulated by weekly irrigation. The experimental set-up of the whole DEGREE project, common for all partner countries, aimed at obtaining different combinations of soil temperature and water content in the field plots, and superimposing them on the local seasonal variations of these climatic variables. A detailed description of DEGREE's experimental design is given in Ekschmitt et al. (1999) as well as in Bakonyi & Nagy (2000).

The within plots microclimatic conditions were quantified by measuring soil temperature and soil water content on a monthly basis for the 6-month experimental period. Temperature was measured by min-max thermometers placed 5 cm below surface and left in the field plots for the whole month, while soil water content at each plot was determined by drying 5g of soil at 104° C for 24h and estimating evaporation loss.

Finally, the experimental manipulations of microclimate resulted in a full factorial scheme of two temperature (warm, cold) x two moisture (wet, dry) levels. Each treatment, i.e. each temperature x moisture combination comprised three plots. Average temperature for the whole sampling period was 23.6° C and 25° C in cold and warm plots respectively. A t-paired test showed that this difference (1.4° C on average) was statistically significant ($p<0.05$). Regarding moisture levels, the average difference between dry and wet plots was 2.3% d.w., and this difference was highly significant ($p<0.01$). Thus, although the experimental modifications of moisture and temperature were of small scale, they were not masked by the seasonal variations of those variables, which were of a larger scale.

Soil sampling was conducted on a monthly basis for the 6-month experimental period. On each sampling occasion, three random soil cores were taken from the top 8 cm of soil of each field plot with a steel cylinder (7 cm diameter). The three cores from each plot were unified in one composite sample, packed in polythene bags, transported to the laboratory and stored at 4° C for further analyses. The composite samples taken from plots of each treatment were grouped as replicates. In total, 12 composite samples (3 replicate plots x 4 treatments) were taken each month.

Nematode analyses

A portion of 100g fresh weight was separated from the composite soil sample from each plot for the purposes of nematode extraction. Nematodes were isolated using Cobb's sieving and decanting method (s'Jacob & van Bezooijen 1984). Nematode extraction through a double layer of cotton wool filters lasted for two days. After total numbers of specimens were counted, nematodes were fixed in 4% formalin. Expert assistance was offered by the Hungarian partners of DEGREE for the identification of nematodes to genus level and their classification to feeding types following Yeates et al. (1993). The group of plant-feeders was separated into epidermal and roothair feeding nematodes and plant parasites.

Maturity Index (MI) and Plant Parasite Index (PPI) were calculated according to Bongers (1990), while diversity (Shannon-Weaver index) together with evenness and richness were calculated according to Pielou (1975). The assessment of genera biomass was based on average body dimensions and was calculated via the formula of Andrassy (1984). For the assessment of nematode activity, a model developed by Ekschmitt et al. (1999) was used. For the construction of the model, data concerning abundance of nematode genera and body dimensions were used. Activity was expressed as released carbon mass per hour and g dry mass soil.

The environmental constant (C_{env}), which reflects the intensity of competition, was estimated from the rank/abundance plots, as proposed by May (1975) and Motomura (1932). In a geometric series, the abundance of genera ranked from most to least abundant is :

$$n_i = N\, C_{env}\, (1- C_{env})^{i-1}\, [1-(1- C_{env})^{s}]^{-1}$$

where n_i= nb. of individuals in the ith genus, N= total nb. of individuals, s= total nb. of genera and C_{env}= environmental constant.

Biochemical analyses

Ergosterol was used as an index of active fungal biomass. It was estimated from 5 g fresh mass soil by means of quantitative HPLC analysis after ethanol extraction (Djajakirana et al., 1996). For the determination of soil microbial-C the fumigation-incubation method of Jenkinson & Powlson (1976), with the modifications recommended by Ross (1990) for grassland soils, was used. N-microbial was measured by the method of Brookes et al. (1985). Soil respiration was measured by absorption in alkali (1 N KOH) followed by titration with 0.1 N HCL after incubation for three days at 10° C (Isemeyer 1952). Bacterial substrate utilization, which reflects the functional diversity of the bacterial community, was estimated in Gram-negative plates by a modified BIOLOG method (Vahjen et al., 1995). Inorganic-N (NO_3^- and NH_4^+) was determined by distillation, while organic-N was assessed by the Kjeldahl method (Allen, 1974).

RESULTS

In total 39 nematode genera with an overall mean density of about 16 $ind.g^{-1}$ were sampled during the six-month period. In Table 1 mean values of different nematode community parameters are presented. Parameters related to phenology and activity exhibited the higher variation (from 55 to 69%), whereas the opposite held for parameters related to diversity.

TABLE 1

Overall mean values of some structural and functional characteristics of the nematode community as well as some indices relating to life history strategies. Values for 95% confidence limits, minimum, maximum and estimates for the coefficient of variation are also given

Variable	Mean	Min.	Max.	CV%
Abundance (ind./g d.w.)	16.00±2.08	3.01	53.50	55.23
Richness (nb. genera)	21.26±0.70	16.00	27.00	14.11
Diversity	2.56±0.04	2.21	2.97	7.03
Evenness	83.93±0.92	75.41	92.93	4.64
C_{env}	0.21±0.01	0.09	0.59	33.00
Biomass (μg f. w./ g d.w.)	12.18±1.83	2.77	41.49	63.79
Activity (ng CO_2-C/g d.w.* h)	4.57±0.74	0.75	17.09	68.92
B/F	1.48±0.18	0.18	3.69	53.89
MI	2.33±0.05	2.00	2.92	7.72
PPI	2.47±0.04	2.11	2.94	6.88

TABLE 2

Percentage contribution of the different nematode functional groups to abundance, richness, biomass, activity, MI and PPI.

Variables	Bacterivorous	Fungivorous	Root feeders	Plant Parasites	Predators	Omnivorous
Abundance (ind./g d.w.)	31.36	27.37	17.35	16.52	0.56	6.87
Richness (nb. genera)	32.07	21.67	9.39	20.44	2.55	13.87
Biomass (μg f.w/gd.w.)	18.95	12.06	2.22	5.82	1.10	59.82
Activity (ngCO_2-C/g d.w. * h)	27.00	17.69	4.73	9.20	1.05	40.32
MI	41.40	37.75			1.25	19.55
PPI			41.63	58.19		

TABLE 3

Statistically significant effects of seasonal large-scale fluctuation and experimentally created small-scale variation in soil temperature and moisture conditions on nematode community parameters.

Variables	Season	Moisture	Temperature	Interactive effect
Abundance (ind./g d.w.)	0.01			0.00
Biomass (μg f.w./g d.w.)	0.05	0.01	0.01	0.01
Diversity	0.05		0.00	
Richness (nb. genera)	0.01		0.05	
Activity (ngCO_2-C/g d.w. * h)	0.01			0.05
C_{env}		0.05	0.00	0.05
MI	0.00			
PPI		0.00		0.00
B/F	0.05			0.00

In Table 2, the percentage contribution of the different feeding groups to nematode biomass, activity, richness, density, MI and PPI is displayed. Omnivorous nematodes contributed most to biomass and activity, whereas their contribution to MI value was quite important. Among the remaining groups, bacterivorous and fungivorous nematodes contributed more to total density and richness followed by plant-parasite and root-hair feeders. Finally, predacious nematodes had the lowest contribution to all community parameters.

In order to explore the effect of the large-scale seasonal changes of soil temperature and moisture as well as the small-scale effect of our experimental manipulations on the nematode community, we analysed data from the whole sampling period by a Two-way ANOVA. The experimental temperature and moisture levels were the grouping variables, while the month of sampling, which accounts for the effect of seasonality, was the blocking one. The seasonal effect was significant for all parameters except C_{env} and PPI (Table 3). Higher values for nematode abundance, biomass and activity occurred in September in dry-cold samples (Fig. 1). The ratio B/F displayed a significant temporal pattern and was significantly affected by small-scale differences in soil temperature and moisture (Table 3, Fig. 2). Bacterivorous

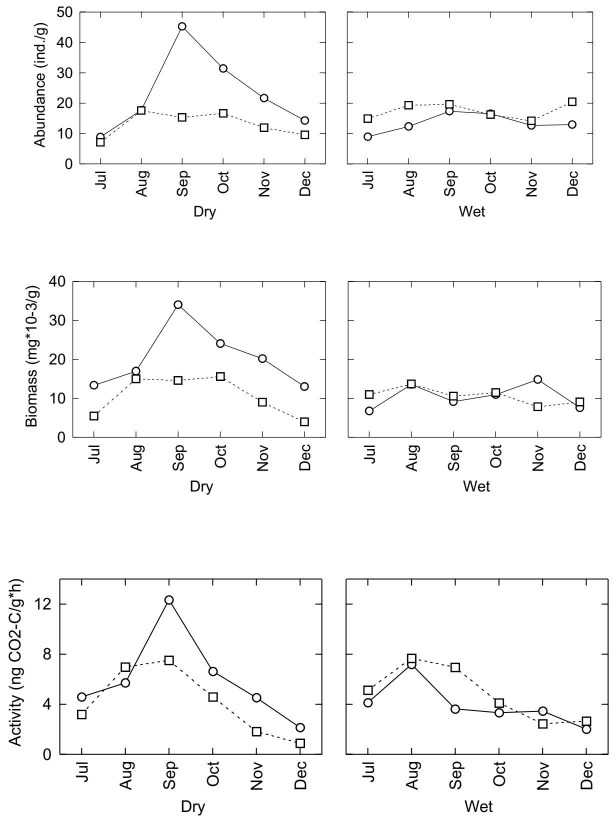

Fig. 1. – Abundance, biomass and activity of nematodes in relation to time and moisture conditions. Circles and squares correspond to cold and warm samples respectively.

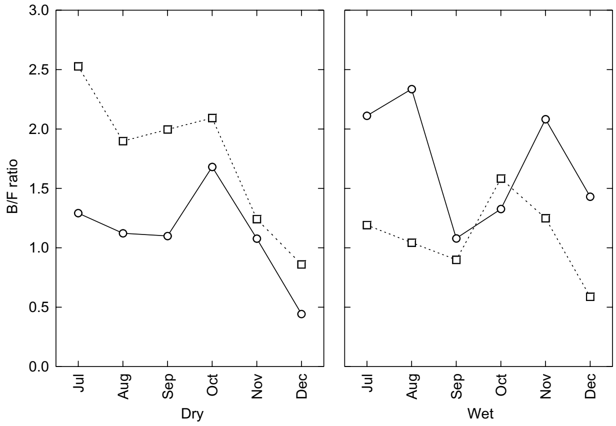

Fig. 2. – Ratio bacterivorous to fungivorous nematodes in dry and wet samples plotted against time. Circles and squares correspond to cold and warm samples respectively.

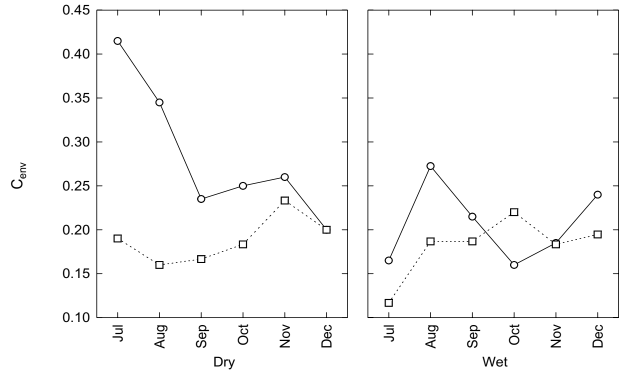

Fig. 3. – Estimates of the environmental constant in dry and wet samples plotted against time. Circles and squares correspond to cold and warm samples respectively.

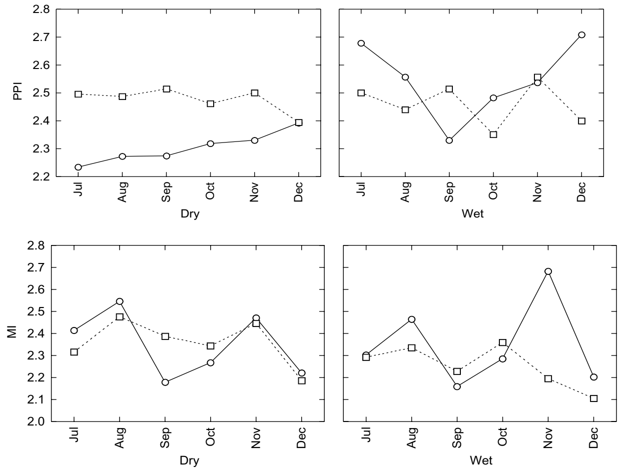

Fig. 4. – PPI and MI values in dry and wet samples plotted against time. Circles and squares correspond to cold and warm samples respectively.

nematodes dominated over fungivorous during almost the whole sampling period especially in dry-warm and in wet-cold samples. Values of C_{env} were controlled by small-scale changes in temperature and moisture. Higher C_{env} values were recorded in wet than in dry and in warm than in cold samples (Table 3, Fig. 3). For PPI, the independent effect of small-scale changes in moisture as well as the interactive effect of temperature x moisture were highly significant (Table 3, Fig. 4). Higher PPI values were recorded in wet than in dry and in dry-warm than in dry-cold samples. MI was the only parameter that exhibited only seasonal fluctuations with higher values in August and November (Table 3, Fig. 4). For richness and diversity, beyond the seasonal effect, the independent effect of small-scale differences in temperature was also significant. Higher values occurred in the middle of the sampling period in warm samples (Table 3, Fig. 5).

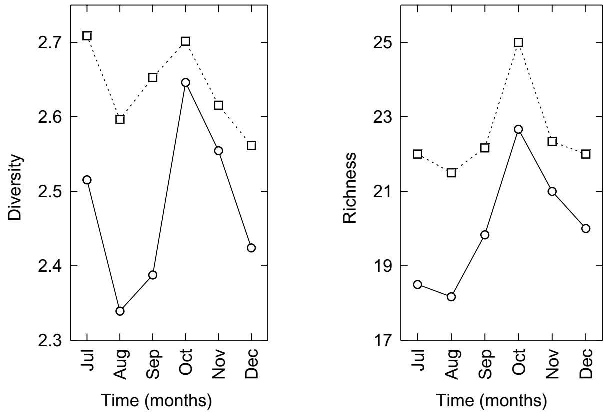

Fig. 5. – Shannon diversity and Richness plotted against time. Circles and squares correspond to cold and warm samples respectively.

No correlation between nematode community parameters and parameters associated with soil nitrogen pools was revealed (Table 4). Among microbial community parameters, only N-microbial was correlated positively with nematode abundance, richness, biomass and activity.

TABLE 4

Correlation of nematode community parameters with parameters relating to soil microflora and nitrogen pools. Only significant values are figured.

Variables	CO_2 (mgC/g d.w. *h)	Biolog (Ext.650/g d.w.)	C-mic (mgC/g d.w.)	N-mic (mgN/g d.w.)	Ergoster. (µg/g d.w.)	N-NO_3 (mgN/g d.w.)	N-NH_4 (mgN/g d.w)	N-org (mgN/g d.w.)
Abundance (ind./g d.w.)			0.34	0.50				
Richness (nb. genera)		-0.24		0.31				
Diversity								
MI					-0.26			
PPI								
Biomass (µg f.w./g d.w.)				0.45				
Activity (ngCO_2-C/g d.w. * h)	0.37			0.33				
C_{env}								

DISCUSSION

The number of nematode genera recorded in the mediterranean grassland of our study is comparable with that of other European grasslands (Cook et al., 1992 ; Freckman & Ettema, 1993 ; Hanel, 1996 ; Bongers, 1998 ; Bongers et al., 1998 ; Nagy, 1998), while nematode density is much lower than that recorded in Hungarian and Germany grasslands subject to similar experimental treatments (Nagy 1998, Bongers et al., 1998). MI is lower and PPI is similar to those recorded in a Spanish Mediterranean grassland (Urzelai et al., 2000), while they are lower than those recorded in Australian and New Zealand soils (Yeates, 1996 ; Yeates & van der Meulen, 1996). Concerning diversity, its value is comparable to data reported by Freckman & Ettema (1993) ; Yeates (1996) and Urzelai et al. (2000).

The composition of nematode community is typical of a dry mediterranean soil. As in Spanish mediterranean grasslands (Urzelai et al., 2000), predators represented a small proportion of the community. Bacterivorus and fungivorus nematodes had a good contribution to overall density, a feature commonly shared by nematode communities from dry soils (Griffiths et al., 1995). Contrary to coniferous forests where this ratio is much lower than unit (De Goede et al., 1993), the mean value of the B/F ratio in our site showed bacterial predominance, probably reflecting good soil fertility (Popovici & Ciobanu, 2000). Omnivorous feeders made a good contribution to biomass, activity and MI. Obviously, it is due to weighty persisters with high metabolic rate.

Concerning the effects of seasonality, most nematode indices exhibited temporal fluctuations. This is in agreement with data referring to Netherlands grasslands (Verschoor et al., 2001). However, as with data from a semi-arid zone in West-Africa (Pate et al., 2000), crucial parameters regarding the structure of the nematode community remained rather invariable in time. Indeed, our results showed temporal constancy of C_{env} and slight temporal variations of MI (in the range 2.20-2.47). Following Porazinska et al. (1999) and Bongers & Ferris (1999) we can infer that presumably, large seasonal variations of soil temperature and moisture do not stimulate microbial activity and consequently no changes either in dominance or in the ratio persisters/opportunists occur.

The effect of the experimentally created small-scale changes in soil temperature and moisture was variable. Moisture manipulations proved inadequate to induce significant changes in MI. This is opposite to suggestions of Porazinska et al. (1998) for positive correlation between nematode MI and irrigation levels. By contrast, C_{env} was significantly affected by such differences. Thus, this parameter proved efficient for indicating effects of small-scale microclimatic changes, analogous to those of climate change scenarios. Microclimatic manipulations significantly affected most other parameters. The temperature effect on nematode community appeared much more pronounced in dry than in wet plots. In dry-cold samples higher values of nematode abundance, biomass and respiration were recorded accompanied by low C_{env} values. Interpreted in terms of competition, these latter values indicate non-effective exploitation of resources. Taking into account that under these conditions PPI values are lower, it is inferred that increased phenological and activity parameters in dry-cold samples result from increased abundance of all nematode groups except persister plant feeding nematodes. Finally, concerning diversity, it is remarkable that beside temporal variation, diversity components are sensitive also to small-scale changes in temperature, a fact that was also reported by Bakonyi & Nagy (2000) for Hungarian soil nematodes. Pate et al. (2000) argued that changes in diversity parameters might reflect changes in ecological resilience related to the quality of soil conditions. Thus, we may infer that in our study site most favorable temperature conditions for resilience occurred in the middle of the sampling period in warm plots.

Small-scale changes in temperature and moisture also influenced the ratio B/F and consequently the outcome of the decomposition processes (Wasilewska, 1979 ; Hendrix et al., 1986). Bacterial feeders dominated over fungal feeders in samples from dry-warm and wet-cold plots. Following Porazinska et al. (1999) the dominance of bacterial feeders might be related to the quick turnover of the available organic matter in these samples. Moreover, changing soil conditions result in a switch to a fungal pathway probably accompanied by slow rate of decomposition. In dry-warm samples higher PPI values were also recorded. Changes in PPI relate to changes in the soil nutritional status following modifications in the dynamics of vegetation (BONGERS et al., 1997). The higher PPI values in dry-warm samples compared to dry-cold ones could be probably attributed to the development of more diverse or more favorable, in terms of nutrients, ground vegetation (VERSCHOOR et al., 2001).

Analysing DEGREE's data from a geographical-climatic cross-gradient (from Greece to Sweden), EKSCHMITT et al. (2001) reported significant correlation between nematode abundance, biomass, activity and soil nitrogen pools. This is not the case with data from the Mediterranean grassland of our study. Furthermore, EKSCHMITT et al. (2001) reported richness as the only nematode parameter that was correlated with soil microflora parameters. Again, this fact is not supported by our results. By contrast, this paper shows a remarkable correlation between N-microbial and the majority of the nematofauna parameters such as biomass, density, activity and richness. Moreover, it shows no effect of the microflora characteristics (biolog, ergosterol) on nematode community. Non correlation between microbivorous nematodes and microflora is often recorded (WARDLE *et al.* 1995) and it is generally attributed to non-linear trophic interactions (ETTEMA *et al.* 1999). According to ANDERSSON (1995), linear trophic synchronization follows environmental disturbances. If this holds true, we may infer that the experimentally induced changes in soil temperature and moisture conditions cannot be considered serious disturbance for the Mediterranean grassland. Besides, previous studies (STAMOU 1998) showed limited significance of much more pronounced disturbances, such as fire and overgrazing on the structure and functioning of soil biota in Mediterranean areas.

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The avifauna of the western Rodopi forests (N. Greece)

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ABSTRACT. The composition of the avifauna in the upland forests of western Rodopi (North Greece) was investigated during spring and summer of 1997 and 1998. A total of 109 species were detected in the area, while 93 of them (85.3%) are regarded as breeders. Ten-minute counts in 260 points in plots of the most representative forest stands produced 3 418 bird sightings of 42 species (13.14 individuals/ point, $\bar{x} = 6.2$ species/ point). Bird density in different forest habitats ranged from six to 34 birds/ 10 ha ($\bar{x}= 19$ birds/ 10 ha). The greatest figure was recorded in oak woods and conifer forests dominated by mature Norway spruce (*Picea abies*) and the lowest in pinewoods. Species diversity was also greater in Norway spruce and broadleaf forests. Species richness should be attributed to the geographical position of the area, and the differences in bird density to the vegetation structure in the various forest habitats.

KEY WORDS : Forest birds, species richness, bird density, Rodopi.

INTRODUCTION

In Greece very few studies have looked at forest bird communities (CATSADORAKIS, 1991, 1997 ; SFOUGARIS et al., 1998), and for species inhabiting commercially exploited forests relevant published accounts are even scarcer. In the Rodopi region (North Greece) special climatic and geomorphologic conditions as well as sociopolitical events have produced widespread woodlands with low human pressure and very few settlements (0.01%). Forested areas cover about 1 180 km^2, which represents 68% of the region. The forests of the area are the most productive in the country and one the most intensively commercialized. Logging usually extracts 187 000 m^3 of wood per year, a figure that represents 30% of the annual timber production in Greece and gives the highest annual forestry revenue at the national level (DAFIS & SMIRIS, 1981; GATZOGIANNIS, 1999). The ecological value of the area lies in its homogenous forests, some of them at the edge of their European distribution, and a great variety of habitats that result in a high degree of biodiversity (SMIRIS, 1987 ; BAUER, 1986).

The aim of this study was to increase the knowledge on the distribution of certain bird groups (i.e. birds of prey, grouses) in the vegetation zones of the region and to provide preliminary information on their breeding status. An attempt was also made to evaluate the significance of the different forest habitats for the avifauna by estimating bird species richness and density.

MATERIAL AND METHODS

Study area

The study area is located in the western Rodopi region in the Drama prefecture, North Greece (Fig. 1) and encompasses the southern slopes of the Rodopi mountain chain whose highest peaks are located in Bulgaria. Its altitude ranges from 300 to 1 600 m a.s.l and covers approximately 1 400 km^2. The climate is transitional from the sub-Mediterranean type to central European with a strong continental character. Mean annual temperature is 11.4° C while the mean annual precipitation is about 1 200 mm distributed through out the year in 100-130 days (MAVROMATIS, 1980 ; Sidironero-Drama & Leivaditis-Xanthi Meteorological Stations : 1978-1989). Forests cover 83% of the study area with 65% of them containing dense forest stands (i.e. 50-75% coverage). In the southern part 100,339 ha (61%) of oak woodland cover the hilly country, adjacent to the valley of the Nestos river and comprise the sub-Mediterranean zone (300-600 m a.s.l). Moving up to the north the beech-spruce zone spreads over 34 500 ha (21%) dominated by beech (*Faqus sylvatica*), Macedonian fir (*Abies borisii-regis*), black pines (*Pinus nigra*), and silver birch (*Betula pendula*). Between the two previous zones black pine forests occupy 6700 ha (4%) only in 6.5% of pure stands, but mainly in mixtures with beech, Scots pine and oaks (e.g. *Quercus frainetto, Quercus pubescens* and *Quercus dalechampii*). Further north the conifer-broadleaf zone extends up to the Greek-Bulgarian border (1600 m a.s.l) and covers 23 400 ha (14%) of dense woodland dominated by Scots pine (*Pinus sylvestris*) (78%), Norway spruce (*Picea abies*) and silver birch (ATHANASIADIS et al., 1993 ; TSIAOUSSI, 1996 ; GATZOGIANNIS, 1999). Basic human activities include apiculture, cattle raising, lumbering and agriculture. Grassland and farmland cover 8.9% and 5.8% respectively of the total area. The greater region is almost void of habitations and human density is about three people per square kilometer (GATZOGIANNIS, 1999).

Fig. 1. – Location of the study area in Northern Greece.

Field techniques and statistics

Bird surveys were carried out in May-July 1997 and 1998. In 1997 most of the fieldwork was spent collecting quantitative data on the species distribution and breeding status. During 11:00 am-15:00 pm observations were made from vantage points and by road surveys with a mean speed of travel of 35 km/h, investigating for birds of prey. All raptors sighted with the unaided eye were identified by the use of binoculars (8x50) and plotted on 1 :50.000 scale maps in an effort to delineate their territories (Woffinden & Murfhy 1977, Bilstein 1978, Fuller & Mosher 1987). The distribution of owl species was surveyed by the playback method by eliciting calls from 20:30h till 23:30h (Falls 1981). Voice imitations started with the smallest species gradually proceeding to the larger ones (Call 1978). A search for the abundance of the Capercaillies (*Tetrao urogallus*) was also undertaken by following 35 transects of 42 km total length, all above the 1000-m contour line. As the species is quite cryptic and very reluctant to fly counts were made within a 10m belt walking in a zigzag manner or throwing stones in order to flush any close-sitting individuals.

In 1998 the relative abundance and density of passerines was censused by point counts (Bibby et al., 1992). Thirteen sample plots were selected from maps of a landscape analysis by the use of a geographic information system in such a manner as to comprise of homogeneous forest stands in terms of age (DBH>30 cm), tree condition and canopy closure (50-75%). Forest stands were selected to be large enough (>60 ha) and dominated by the main tree species of the area. Transient areas among the four vegetation zones were avoided apart from those encompassing oaks with black pines and Scots pines with beech as these tree species intermix a lot in the area. Line transects were firstly followed in order to determine the width of the full-detection strip. Ten transects of about one km each were followed and every bird cue was tallied in five meters strips on either side of the route. The full-detection strip was estimated as the one where the number of birds (regardless of species) dropped below 20% of the average number of the five meters strips closest to the observer (Emlen 1977). Twenty sample points per plot were established by making stops at 150-m intervals along a straight line by using a prismatic compass. The centre of the sample point was checked by a densiometer for the right percentage of canopy closure. All sample points were situated within the forest away from openings in order to minimize the edge effect. The duration of each count was ten minutes starting about five minutes after arrival, allowing the birds to recover from any disturbance. At each sample point the highest count for each bird species was taken at ranges 0-*r* m and 0 m to infinity. The pre-selected radius *r* was equal to the length of the full-detection strip produced by the transect lines' count. Densities were estimated by assuming that the probability of detecting a bird declines with distance from the observer. The general shape of this decline follows a half normal function, exp $[-(x/a)^2]$ where x is the distance from the observer and a is a constant equivalent to the effective radius of the census depending on the circumstances (Jarvinen & Vaisanen 1975). Given that the detectability function has this shape and certain assumptions are met (Buckland 1984), the constant a and the bird density D can be calculated directly by the formula : $D= \log_e (n/n_2)$ x $n/m(pr^2)$ where n = total number of birds detected, n_2 = number outside the fixed radius (r) and m= the number of points. Standard errors of bird density estimates were calculated by using the jackknife method (Miller 1974, Krebs 1989). Differences in bird abundance between sample plots were evaluated using one-way ANOVA (F statistic). The Shannon index of diversity (H') and a heterogeneity index (H'/ H' max) were calculated (Magurran 1988) per sample plot based on the mean number of individuals counted within the fixed detection radius in the point counts. Statistical comparisons were made using the student's t-test with α= 0.01 (Zar, 1984).

RESULTS

Signs of breeding activity and suitable nesting habitat accounted for 93 (85.3%) species out of a total of 109 that belong to 29 families (Appendix 1).

Diurnal raptors were poorly represented with only ten species. The buzzard (*Buteo buteo*) was the commonest raptor distributed equally in all forest habitats and vegetation zones. Twenty eight territories were located over an area of about 300 km^2 producing a density of one pair per 10.7 km^2. Honey buzzards (*Pernis apivorus*) were recorded in oak forests and mixed stands of conifers with deciduous trees up to the conifer-broadleaf zone where no more than five territories were detected. In addition four territories of short-toed eagle (*Gircaetus gallicus*) were delineated at middle and low altitude (<600 m), all in oak forests and marginally in the transient zone between the oaks and the birch-fir forests. The golden eagle (*Aquila chrysaetos*) was located in the Greek-Bulgarian border with one active territory. The breeding distributions of the Levant sparrowhawk (*Accipiter brevipes*), the sparrowhawk (*Accipiter nisus*) and the goshawk (*Accipiter* *gentilis*) were sparse and restricted to the upper zone of the conifer-deciduous forests. The hobby (*Falco subbuteo*) occurred in the lowlands (<400 m) in open oak forests and grasslands with scattered shrubs. Two kestrel pairs (*Falco tinnunculus*) were spotted in rocky outcrops within oak stands well below the 800 m contour line. Moreover a flock of Eleonorae's falcon (*Falco eleonorae*) comprising 20-30 individuals was present in the area, roosting in oaks in the sub-mediterranean zone and hunting flying insects in forest openings or along riverside vegetation just before dusk. In the day time the falcons dispersed further north in the Bulgarian part.

As far as nocturnal raptors are concerned five species were detected. The tawny owl (*Stix aluco*), was found in all forest habitats and constituted the commonest owl species. It showed strong preference for open stands in mixed beech-spruce forests and exhibited the highest density in mature forests (e.g. five different responses in a single voice imitation). The Tengmalm's owl (*Aegolius funereus*), was restricted in the upper conifer zone (>1400 m a.s.l) showing high densities in mature mixed stands of Norway spruce and fir (e.g. four different responses in a single voice imitation). The long-eared owl (*Asio otus*), exhibited an irregular distribution up to the beech-spruce zone, always heard near small openings within the forests. The little owl (*Athene noctua*) and the scops owl (*Otus scops*) were heard near settlements and cultivation in middle altitude areas (<700 m) or in open shrub land and degraded oak forests that are used as rangelands. The highest altitude at which the little owl was heard was 900 m.

The Rodopi forests constitute the only place in Greece where all tetraonids can be found, namely the Capercaillie (*Tetrao urogallus*) the hazel grouse (*Bonasia bonasia*) and the black grouse (*Tetrao tetrix*) although the breeding status of the latter remains unclear (HANDRINOS & AKRIOTIS 1997). In the present study four individuals of Capercaillie were recorded in the 0.42 km^2 belt giving an estimate of 9.5 individuals/km^2. Moreover, in random walks around the forests the species was recorded 11 times in small groups or individual birds (mostly females). All Capercaillie observations were made in forest stands dominated by Norway spruce and Scots pine or in mixed forests of beech and conifers along the Greek-Bulgarian border. The group size was one male and one female or one male with two females although this figure should be regarded as minimum since the survey did not cover displaying males in leks. The species' population density has been estimated at 10-16 individuals/ km^2 (POIRAZIDIS, 1990). The hazel grouse was common in the area. Most of the sightings took place in pure conifer forests or mixed forests of Norway spruce/ Scots pine with beech as well as forests dominated by silver birch.

A full detection strip in point counts was determined as equal to 30 m, and this figure was appointed as the fixed radius in each sample point, thus bird counts were made at ranges 0-30 m and 0 m to infinity. Excluding raptors and grouses, a total of 3,418 birds belonging to 42 species were detected in 260 point counts ($\bar{x}$= 6.2 species and 13.14 individuals/ point). Twelve species (29%) were recorded within the 30m radius in more than 50% of the plots, and 15 species (36%) at a distance of more than 30 m (Table 1). Thirteen species, robin (*Erithacus rubecola*), coal tit (*Parus ater*), chaffinch (*Fringla coelebs*), marsh tit (*Parus pallustris*), blue tit (*Parus caeruleus*), wren (*Troglodytes troglodytes*), nuthatch (*Sitta europaea*), goldcrest (*Regulus regulus*), great tit (*Parus major*), bullfinch (*Phyrrula phyrrula*), hawfinch (*Coccothraustes coccothraustes*), chiffchaff (*Phylloscopus collybita*) and blackbird (*Turdus merula*) constituted 85% of the bird community in terms of numbers, while the first three species accounted for almost half of the bird numbers (48%) in point counts (Table 1).

By comparing the most common species (those recorded in more than 50% of the sample points) to the most numerous ones (species with densities over 5 individuals/ 10 ha) 11 species were equally distributed in high densities, e.g. chaffinch, robin, great tit, blue tit, marsh tit, coal tit, wren, nuthatch, blackbird, chiffchaff and goldcrest. Four species, cuckoo (*Cunculus canorus*) great spotted woodpecker (*Dendrocopos major*), jay (*Garrulus glandarius*) and blackcap (*Sylvia atricapilla*), were widespread but in low densities, and two species (bullfinch and hawfinch) exhibited dense but localized populations. Species richness ranged from eight to 18 species ($\bar{x}$=14 species) in different forest habitats, and bird density from six to 34 birds/ 10 ha ($\bar{x}$ = 19 birds/ 10 ha) and differed significantly (F_{12}=8.35, P<0.01). Greatest bird density was detected in oak woods and mixed conifers dominated by mature Norway spruce (Table 2). Black pine stands had the lowest bird densities and the least number of species. Beech forests showed an intermediate situation, having relatively low bird densities and species richness (average). Pure conifers and silver birch forests accommodated many bird species but in rather low densities. Species diversity was greater in Norway spruce and broadleaved forests than in pine forests, although these differences were not all statistically significant (Table 2). Considering heterogeneity (H'/max H'), bird species were represented more equally in broad-leaf than in conifer forests especially those encompassing Scots pines (Table 2).

TABLE 1

Frequency of observations, numbers counted and estimated bird species densities (mean number of individuals/ 10 ha) from 260 sample points in western Rodopi forests

Species	**Frequency**		**No. of individuals**		**Density**	**S.E.**
	0-30	**All**	**0-30**	**All**		
Coal Tit (*Parus ater*)	237	77	238	477	44.86	11.33
Chaffinch (*Fringila coelebs*)	253	139	216	694	35.22	7.76
Robin (*Erithacus rubecula*)	169	148	184	474	31.70	2.73
Marsh Tit (*Parus palustris*)	47	27	87	123	20.57	7.55
Blue Tit (*Parus caeruleus*)	66	54	81	124	17.87	8.83
Wren (*Troglodytes troglodytes*)	66	46	79	194	13.81	2.26
Nuthatch (*Sitta europaea*)	56	29	72	156	13.14	4.24
Goldcrest (*Regulus regulus*)	53	60	57	106	11.13	5.80
Great Tit (*Parus major*)	39	91	53	111	9.81	4.42
Bullfinch (*Pyrrhula pyrrhula*)	10	16	34	44	8.87	6.26
Hawfinch (*Coccothraustes coccothraustes*)	7	8	32	43	7.89	6.26
Chiffchaff (*Phylloscopus collybita*)	31	50	44	259	6.56	2.01
Blackbird (*Turdus merula*)	31	43	33	110	5.34	1.29
Long-tailed Tit (*Aegithalos caudatus*)	5	30	20	30	4.49	1.89
Great Spotted Woodpecker (*Dendrocopos major*)	23	50	24	80	3.88	1.42
Crossbill (*Loxia curvirostra*)	35	7	20	57	3.35	2.45
Blackcap (*Sylvia atricapilla*)	14	37	15	40	2.56	1.02
Mistle Thrush (*Turdus viscivorus*)	8	13	9	19	1.66	0.71
Jay (*Garrulus glandarius*)	8	25	10	31	1.64	0.45
Crested Tit (*Parus cristatus*)	7	6	7	16	1.25	1.35
Water Pipit (*Anthus spinoletta*)	4	4	4	5	1.10	1.21
Rock Bunting (*Emberiza cia*)	2	3	5	8	1.07	0.83
Cuckoo (*Cuculus canorus*)	7	81	7	113	0.98	0.55
Cirl Bunting (*Emberiza cirlus*)	3	7	5	11	0.91	0.57
Red-backed Shrike (*Lanius collurio*)	3	7	3	7	0.53	0.34
Syrian Woodpecker (*Dendrocopos syriacus*)	2	1	2	3	0.45	0.40
Nutcracker (*Nucifraga caryocatactes*)	3	13	3	34	0.43	0.38
Black Woodpecker (*Dryocopus martius*)	2	4	2	7	0.32	0.29
Short-toed Treecreeper (*Certhia brachydactyla*)	1	2	1	2	0.19	0.17
Woodpigeon (*Columba palumbus*)	1	4	1	4	0.16	0.14
Hooded Crow (*Corvus corone cornix*)	1	4	1	4	0.16	0.14
Song Thrush (*Turdus philomelos*)	1	1	1	7	0.15	0.13
Black Redstart (*Phoenicurus ochruros*)	1	8	1	11	0.14	0.13
Green Woodpecker (*Picus viridis*)	0	1	0	1		0
Middle Spotted Woodpecker (*Dendrocopos medius*)	0	1	0	1		0
Tree Pipit (*Anthus trivialis*)	0	2	0	2		0
Black-headed Wagtail *(*Motacilla flava*)*	0	17	0	2		0
Firecrest (*Regulus ignicapillus*)	0	1	0	1		0
Sombre Tit (*Parus lugubris*)	0	1	0	2		0
Lesser Spotted Woodpecker (*Dendrocopos minor*)	2	2	2	2		0
Ring Ouzel (*Turdus torquatus*)	0	6	1	1		0
Wood Warbler (*Phylloscopus sibilatrix*)	0	61	2	2		0
Total			1 356	3 418		

TABLE 2

Bird density, number of species, bird species diversity and homogeneity indices in the forest stands of western Rodopi.

Sample plots/ dominant tree species	Ind./ 10 ha	S*	S	H’	H'/ max H'
1. *Picea abies- Picea abies* (2,5,8,9,12,13)*	20.29	17	24	2.26	0.531
2. *Pinus sylvestris- Picea abies* (1)	14.52	9	16	1.68	0.598
3. *Picea abies - Pinus sylvestris* (1,2)	34.40	11	17	4.97	0.624
4. *Fagus sylvatica – Picea abies* (2,3)	13.44	15	19	2.27	0.595
5. *Fagus sylvatica – Pinups sylvestris* (1,3,4)	13.13	10	17	1.68	0.622
6. *Pinus sylvestris - Fagus sylvatica* (2,3,5)	11.58	12	14	2.08	0.657
7. *Quercus frainetto - Pinus nigra (2,3,5,6)*	32.17	16	18	2.35	0.453
8. *Pinus nigra - Pinus nigra* (1,3,4,6,7)	6.37	8	15	1.75	0.679
9. *Betula pendula - Pinups sylvestris* (1,2,3,5,6,7,8)	17.90	16	26	2.48	0.612
10. *Fagus sylvatica - Fagus sylvatica* (2,3,5,8)	18.88	17	28	2.37	0.495
11. *Quercus frainetto - Quercus frainetto (2,3,5,8)*	32.33	18	24	2.28	0.453
12. *Pinus sylvestris - Pinus sylvestris* (1,3,4,7,9,10,11)	13.28	11	22	1.79	0.559
13. *Betula pendula - Betula pendula* (1,2,3,5,6,8,11,12)	14.04	18	20	2.52	0.470
Average	18.64		20		

S* : *Number of species detected within the 30m-fixed radius from the observer*
S : Total number of species detected
H' : Shannon-Wiener diversity index
Max H' : maximum diversity
H'/ max H' : Heterogeneity index
() Forest stands with statistical differences in species diversity*

DISCUSSION

Overall the Rodopi forests seem to host both central European and Mediterranean species and could be classified as a transitional zone between the lowest part of temperate forest and the highest part of the Mediterranean one. The composition and structure of the vegetation in the area is typical of montane forests, dominated by broadleaved species at lower elevations and conifers at higher altitudes (Tucker & Evans, 1997). However in the sub alpine coniferous zone, which is dominated by Norway spruce and Scots pine some of the species recorded are typical of boreal forests such as the willow tit, the nutcracker (*Nucifraga caryocatactes*), the ring ouzel (*Turdus torquatus*), the bullfinch, and the Capercaillie which are considered to be rare in Greece. Meanwhile in the temperate forests, dominated by beeches and oaks, the bird community included typical species of broadleaved forests, some of them rather common in many parts of the country (e.g. honey buzzard, short-toed eagle, goshawk, sparrowhawk, tawny owl and a variety of chats, tits and warblers). This pattern is expected in woodland habitats dominated by central European species at the edge of their distribution due to the fact that some of the mountain parts in intermediate zones of the Balkans have been moderately affected by the glacial and interglacial periods. It has also been suggested that mountain regions facing south, east and southeast (such as the mountains of the study area) act as “refugia” for the mediterranean fauna (Matvejev, 1976).

Species diversity and density in point counts coincide with and confirm general conclusions in the existing literature. Considering woodland structure it has been shown in many studies that forests with mature trees, standing dead timber, small open areas and many layers of foliage exhibit a higher ecological value in terms of bird species richness and abundance (MacArthur & MacArthur, 1961; Moss, 1978, Smart & Andrews, 1985; Andrews, 1986; Avery & Leslie, 1990).

Regarding tree species composition, it is generally accepted that spruce carries more bird species than pine (Newton 1986), as spruce woodland provides birds with greater amounts of food (e.g. insects) and better shelter for nests. Birch forests support greater densities of birds than pines (Newton & Moss 1977) while oak woods maintain greater densities than both (French et al., 1986). Pure conifer forests in the study area are rather dark with closed canopy and for this reason field layers are mostly absent or poorly developed. As a result their avifauna is less diverse but the species are quite characteristic. These forests are heavily exploited for timber production and subsequently the bird communities often follow the man-induced succession of the forest. On the contrary mixed forests dominated by oaks exhibit greater development of understory growth and a higher diversity of vascular plants thus supporting a much richer avifauna. In addition, broadleaves often experience an outbreak of foliage-feeding caterpillars, which leads to the defoliation of the canopy branches. This feature was most pronounced in the pure oak woods of the Sub-Mediterranean zone where the young oak trees, although they had a very low foliage profile, attracted insectivorous passerines from adjacent forest habitats.

Beech and silver birch forests are multi-layered but they are dominated by more homogeneous stands with less horizontal heterogeneity and exhibited an intermediate situation regarding bird abundance and density. Above all, the mixed stands of Norway spruce with Scots pine proved of exceptionally high ornithological value. These forests supported a great structural and floristic diversity and offer ample feeding and nesting opportunities to a relatively high number of birds. Similarly pure Norway spruce forests where large amounts of dead wood and small openings were present supported forest birds with many different types of food and nesting sites. Breeding and foraging habitat are mostly suitable for these species that are insectivorous and hole nesting. Woodpeckers largely acquired their food in open conifer stands with many snags, and in areas where intense logging takes place they preyed upon insects thriving in the stools. On the contrary, in beech stands they foraged in mature trees with DBH of 30-50 cm. The diverse avifauna detected in silver birch forests should be attributed to the variety of habitats and microhabitats occurring within certain sampling plots (e.g. mature trees, rocky outcrops, freshwater streams and an understory vegetation rich in shrubs).

On the other hand the low density of diurnal birds of prey is the most striking case of low human intervention on the upland forests. The area seems to sustain atypical habitat for many raptors. The lack of suitable breeding sites for cliff nesters and the scarcity of foraging areas must have had a critical impact on many Greek-Mediterranean species. The extensive area was inhabited by an ancient Greek race (Sarakatsani) that practiced traditional stock raising till late '50s (PSYHOGIOS & PAPAPETROU, 1995). However nomadic flocks were eliminated almost completely during the first two decades after World War II. The reduction of extensive grazing has resulted in regeneration of the forest, which was also enhanced by depopulation of the area and abandonment of agricultural land for political and social reasons (e.g. Greek civil war, GIANNATOS, 1997). As a result forest openings became scarce and foraging habitat for hunting raptors has been substantially reduced.Nevertheless forest management may counterbalance some of the differences detected in bird species richness and abundance. Conifer stands are quite intact as they are managed by group felling or selective thinning and are restocked by natural regeneration from shelter wood. On the contrary oak woods are normally under severe forestry operation such as clear cutting or coppicing on a 10-year rotation cycle, and natural regrowth comes mostly from the stumps. The impact has been most severe in the lowlands close to villages where oak woods are used as pastureland and fuelwood production.

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APPENDIX 1

Breeding status of bird species detected in the western Rodopi forests

1 : Suitable nesting habitat
2 : Territorial defense/ Aerial display/ Courtship behaviour
3 : Nest with chicks found
4 : Adult feeding chicks/ carrying food to the nest
5 : Fledglings observed
6 : Data insufficient

Species	**Breeding status**
***FAMILY*: Accipitridae**	
Pernis apivorus (Linnaeus)	2, 4
Circaetus gallicus (Gmelin)	3, 4
Accipiter brevipes (Severtzov)	1, 2
Accipiter nisus (Linnaeus)	1, 2
Accipiter gentiles (Linnaeus)	1, 2
Buteo buteo (Linnaeus)	2, 4
Aquila chrysaetos (Linnaeus)	1, 2
***FAMILY*: Falconidae**	
Falco tinnunculus (Linnaeus)	2, 2
Falco subbuteo (Linnaeus)	1, 2, 4
Falco eleonorae (Cene)	6
***FAMILY*: Tetraonidae**	
Bonasia bonasia (Linnaeus)	1, 5
Tetrao urogallus (Linnaeus)	1, 5
***FAMILY*: Columbidae**	
Columba palumbus (Linnaeus)	1, 4
Streptopelia turtur (Linnaeus)	1, 2, 5
***FAMILY*: Cuculidae**	
Cunculus canorus (Linnaeus)	1, 2
***FAMILY*: Strigidae**	
Otus scops (Linnaeus)	1
Athene noctua (Scopoli)	1
Asio otus (Linnaeus)	1, 2
Stix aluco (Linnaeus)	1, 2
Aegolius funereus (Linnaeus)	1, 2
***FAMILY*: Caprimulgidae**	
Captimulgus europeus (Linnaeus)	1
***FAMILY*: Apodidae**	
Apus apus (Linnaeus)	6
Apus melba (Linnaeus)	6
***FAMILY*: Meropidae**	
Merops apiaster (Linnaeus)	1
***FAMILY*: Coracidae**	
Coracias garrulous (Linnaeus)	1
***FAMILY*: Upupidae**	
Upupa epops (Linnaeus)	1, 4
***FAMILY*: Picidae**	
Picus canus (Gmelin)	1, 2
Picus viridis (Linnaeus)	1, 2
Dryocopus martius (Linnaeus)	1, 5
Dendrocopos major (Linnaeus)	1, 3
Dendrocopos syriacus (Hemprich-Ehrenberg)	1, 2
Dendrocopos medius (Linnaeus)	1, 3
Dendrocopos leucotos (Bechstein)	1
Dendrocopos minor (Linnaeus)	1, 3
Picoides tridactylus (Linnaeus)	1
***FAMILY*: Alaudidae**	
Melanocorypha calandra (Linnaeus)	1
Caladrella brachydactyla (Leisler)	1
Galerida cristata (Linnaeus)	1
***FAMILY*: Hirundidae**	
Pryonopogne rupestris (Scopoli)	6
Hirundo rustica (Linnaeus)	6
Delichon urbica (Linnaeus)	6
***FAMILY*: Motacillidae**	
Anthus trivialis (Linnaeus)	1
Anthus spinoletta(Linnaeus)	1, 2
Motacilla flava (Linnaeus)	6
Motacilla cinerea (Tunstall)	6
Motacilla alba (Linnaeus)	6
***FAMILY*: Cinclidae**	
Cinclus cinclus (Linnaeus)	1
***FAMILY*: Troglodytidae**	
Troglodytes troglodytes (Linnaeus)	5
***FAMILY*: Turdidae**	
Erithacus rubecola (Linnaeus)	1, 5
Luscinia megarhynchos (Brehm)	1, 2
Phoenicurus ochruros (Gmelin)	5
Phoenicurus phoenicurus (Linnaeus)	1
Saxicola rubetra (Linnaeus)	5
Saxicola torquata (Linnaeus)	6
Oenanthe isabellina (Temminck)	6
Oenanthe oenanthe (Linnaeus)	1
Turdus torquatus (Temminck)	3, 5
Turdus merula (Linnaeus)	5
Turdus philomelos (Brehm)	5
Turdus viscivorus (Linnaeus)	5
***FAMILY*: Sylvidae**	
Hippolais pallida (Hemprich-Ehrenberg)	1
Sylvia cantillans (Pallas)	1
Sylvia melanocephala (Gmelin)	2
Sylvia communis (Latham)	1,1
Sylvia atricapilla (Linnaeus)	3, 5, 4
Phylloscopus bonelli (Vieillot)	1, 2
Phylloscopus sibilatrix (Bechstein)	1, 2
Phylloscopus collybita (Veillot)	1, 2
Regulus regulus (Linnaeus)	1, 2
Regulus ignicapillus (Temminck)	1
***FAMILY*: Muscicapidae**	
Muscicapa striata (Pallaas)	1
Ficedula parva (Bechstein)	1
***FAMILY*: Aegithalidae**	
Aegithalos caudatus (Linnaeus)	5
***FAMILY*: Paridae**	
Parus lugubris (Temminck)	2
Parus palustris (Linnaeus)	1, 5
Parus montanus (Conrad)	1
Parus cristatus (Linnaeus)	5
Parus ater (Linnaeus)	5, 4
Parus caeruleus (Linnaeus)	5
Parus major (Linnaeus)	5

Species	Breeding status
***FAMILY*: Sittidae**	
Sitta europaea (Linnaeus)	5
Sitta neumayer (Michahelles)	1
***FAMILY*: Certhiidae**	
Certhia familiaris (Linnaeus)	1
Certhia brachydactyla (Brehm)	1
***FAMILY*: Oriolidae**	
Oriolus oriolus (Linnaeus)	1
***FAMILY*: Laniidae**	
Lanius collurio (Linnaeus)	5
Lanius minor (Gmelin)	1
Lanius senator (Linnaeus)	2
***FAMILY*: Corvidae**	
Garrulus glandarius (Linnaeus)	1, 2, 5
Nucifraga caryocatactes (Linnaeus)	1, 5
Corvus corone (Linnaeus)	1
Corvus corax (Linnaeus)	6
***FAMILY*: Passeridae**	
Passer domesticus (Linnaeus)	4
Passer montanus (Linnaeus)	1
***FAMILY*: Fringilidae**	
Fringila coelebs (Linnaeus)	5
Serinus serinus (Linnaeus)	5
Carduelis chloris (Linnaeus)	5
Carduelis carduelis (Linnaeus)	5
Carduelis spinus (Linnaeus)	1
Carduelis cannabina (Linnaeus)	5
Loxia curvirostra (Linnaeus)	5, 4
Pyrrhula pyrrhula (Linnaeus)	5, 4
Coccothraustes coccothraustes (Linnaeus)	5
***FAMILY*: Emberizidae**	
Emberiza citrinella (Linnaeus)	6
Emberiza cirlus (Linnaeus)	1, 2
Emberiza cia (Linnaeus)	5
Emberiza hortulana (Linnaeus)	6
Emberiza melanocephala (Linnaeus)	6
Milaria calandra (Linnaeus)	6

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A review and reappraisal of research in some previously unsurveyed Mediterranean marine turtle nesting sites, 1990-2001

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ABSTRACT. One of MEDASSET's main objectives has been the assessment of coastal areas on a pan-Mediterranean scale in a search for potential nesting sites of *Caretta caretta* (loggerhead turtle) and *Chelonia mydas* (green turtle), the only two marine turtle species known to reproduce in the Mediterranean. The specific characteristics of each coastal region were logged, as turtles cannot be successfully protected unless all their reproductive habitats are known. If any important turtle nesting sites were found, recommendations for implementation of protective measures were made to the States involved, followed by efforts towards the implementation of protective legislation and conservation measures. These surveys took place in Sardinia, Italy (1990 & 1991), the North Aegean (mainland and islands), Greece (1991), the western part of the Egyptian Mediterranean coast (1993), Syria (1991), Libya (1995 & 1998) and Lebanon (2001). This review sums up data resulting from these pioneering studies and re-evaluates it in the light of more recent information regarding marine turtle nesting and conservation in the Mediterranean.

KEY WORDS : marine turtles, Mediterranean, coastal assessment, conservation, nesting beach

INTRODUCTION

The Mediterranean region hosts breeding populations of two of the seven marine turtle species that occur in the world : *Caretta caretta* (L., 1758) (Reptilia : Cheloniidae) nests widely within the eastern basin and North Africa, whereas the green turtle *Chelonia mydas* (L., 1758) (Reptilia : Cheloniidae) nests in a more restricted range, mainly comprising Turkey and Cyprus. In the early '90s both species were reported as declining (GROOMBRIDGE, 1990) with the Mediterranean green turtle population being reported recently as "critically endangered" (HILTON-TAYLOR, 2000).

Today, comprehensive long-term field data on nesting numbers for *C. caretta* in several Mediterranean areas are not available, although there are some reviews that concentrate on the conservation aspect (MARGARITOULIS et al., 2003 ; LAURENT, 1998). An overall estimation of the population status of *C. mydas* and *C. caretta* in the Mediterranean was recently presented in BRODERICK et al. (2002) and KASPAREK et al. (2001) ; for *C. mydas*, high variation between annual nesting numbers does not seem to indicate any particular trend regarding changes in the nesting population size.

Since its formation in 1988, MEDASSET has been committed to safeguarding the Mediterranean marine turtle populations through scientific research and conservation activities. Following the principle that "….there is no other basis for sound political decisions than the best available scientific evidence…" (BRUNDTLAND 1997), surveys in various Mediterranean countries have been conducted either in order to search for new nesting beaches or to assess the status of known ones, with respect to conservation priorities for marine turtles.

The purpose of this paper is to provide a summary of all research surveys funded or co-funded by MEDASSET in the past 12 years that aimed to locate new nesting beaches. The majority of these projects were also co-funded by the European Community, UNEP-MAP (United Nations Environment Program – Mediterranean Action Plan) and/or others. In the light of more recent information, the importance of past data can now be evaluated more objectively. Knowledge of marine turtle populations in several less-researched Mediterranean areas may thus become more clearly appraised, focusing attention for future research and conservation efforts.

MATERIAL AND METHODS

Data from past surveys funded or co-funded by MEDASSET have been provided from the organisation's archives after reviewing published and, in some cases, unpublished information (Table 1). In order to reappraise this information we next considered accessible published scientific literature originating from more recent surveys conducted within the same geographical area. It became obvious that the fieldwork protocol differed greatly between surveys and/or years, in each case varying according to the particular constraints that researchers faced : however, in all cases "nesting evidence" was standardized to include either direct observations of oviposition and/or indirect signs such as nesting tracks, false tracks, nests, eggs/egg shells and/or hatchlings. It should be emphasised that most of these pioneering projects

TABLE 1

Summary of marine turtle nesting surveys along less explored areas of the Mediterranean, 1991-2001

	Sardinia, 1990	**Sardinia, 1991**	**North Aegean Sea, 1991**	**Syria (entire coastline), 1991**	**Egypt (between Alexandria and El-Salum), 1993**	**Egypt (entire coastline), 1998**	**Libya (NE coastline), 1995**	**Libya (Sirte - Misratah), 1996**	**Libya (NW coastline), 1998**	**Lebanon, 2001**
Length of surveyed coastline	750 km (S. Anna to Murtas with emphasis on the Gulf of Orosei)	70 km (beaches prioritised according to the 1990 results)	2078 km (664 km of sandy beaches surveyed in detail)	193 km (79,5 km of sandy beaches surveyed in detail)	602 km (255 km of sandy beaches surveyed in detail)	616.5 km of sandy beaches	1195 km (141.65 km of sandy beaches surveyed in detail)	209 km (186.3 km of sandy beaches surveyed in detail)	407 km (105.7 km of sandy beaches surveyed in detail)	200 km (30.2 km of sandy beaches surveyed in detail)
Survey season	July–August 1990	July 1991	June–August, 1991	June 1991	June–July, 1993	May-August, 1998	June-July, 1995	summer 1996	July 1998	late spring – summer 2001
Survey duration	13 days (July 24th– August 7th	10 days	28 days	10 days (20th–30th June)	29 days	103 days (20thMay - 1stSeptem.)	21 days (16th June–7th July)		16 days (1st–16th July)	17 days (May – June), 2 days (July), 13 days (23rd July - 5th of August)
Survey type[a]	b, c, fp	fp	fp	fp	fp		c, fp		c, fp	b, fp
Nesting evidence	none	none	1 false track close to Mirina, Limnos	25 tracks (18 nests) between Latakia and Jablah (15.5 km) 2 false tracks between Tartous and the Syrian-Lebanese border (28.5 km)	10 *C. caretta* tracks, apparently evenly distributed over the surveyed area one dead *C. caretta* hatchling	3 *C. caretta* tracks on the northwest coastline several *C. caretta* and *C. mydas* nests on the N.Sinai coast	>300 *C. caretta* tracks (176 nests) (most of them found along Oum-el-Frais, Ras-el-Aweija, East Sirte and N.Bengazi beaches)	66 *C. caretta* tracks 2 dead *C. mydas* hatchlings	15 *C.caretta* tracks	nests/tracks in : El-Mansouri, Qasmiye, Mahmoudiye, Adloun and Damour. In El-Mansouri both *C.caretta* and *C.mydas* were identified as nesting species. additional nesting sites reported by fishermen.
Literature	Venizelos 1993; Whitmore *et al.* 1991	Venizelos 1993; Whitmore *et al.* 1991	Venizelos 1993; Kasparek 1991	Kasparek 1995; Kasparek 1994; Venizelos 1993	Venizelos & Kasparek 1996, Kasparek 1993	Campbell *et al.* 2001 and references therein	Laurent *et al.* 1995	Laurent *et al.* 1999	Laurent *et al.* 1999	Demirayak *et al*, 2003
Project funded by:	MEDASSET under an E.C. Contract No. 6610(90) 4313	MEDASSET under an E.C. Contract No. 6610(90) 4313	MEDASSET under an E.C. Contract No. 6610(90) 4313	MEDASSET, Herpetofauna Conservation International (HCI)	MEDASSET, RAC/SPA (UNEP/MAP), National Institute of Oceanography and Fisheries (Alexandria, Egypt)	Darwin Initiative programme (UK)	RAC/SPA(UNEP/MAP)MEDASSET, TCEP (Libya), Marine Biology Research Centre (Tajura, Libya), WWF International		RAC/SPA(UNEP/MAP), TCEP (Libya), Marine Biology Research Centre (Libya), MEDASSET, WWFInternational	MEDASSET, RAC/SPA(UNEP/MAP), Lebanese Ministry of the Environment

a.b: boat, c: car, fp: foot patrols

intended to survey Mediterranean areas where little or no marine turtle nesting data were available. As a result, researchers were interested in providing primary evidence of nesting – if any – rather than monitoring nesting numbers or producing other quantitative information. Field data on nesting population size or other reproduction parameters are therefore lacking herein.

The non-parametric Spearman rank correlation coefficient was used to assess correlation in temporal variation of *C. caretta* nesting densities along different coastal sections in the Mediterranean (Fig.1, Fig.2 ; Table 2). Data for Kyparissia – Greece were adapted after MARGARITOULIS & REES (2001). Data in Cyprus were adapted after GODLEY et al. (1998) ; BRODERICK et al. (1997) ; GODLEY & KELLY (1996) ; BRODERICK & GODLEY (1995) ; GODLEY & BRODERICK (1994) and BRODERICK & GODLEY 1993. According to GODLEY et al. (1998), the methodology of nest number assessment has changed little through this time period so primary data on nesting numbers is considered as being already standardised. Coastal zone lengths were taken after GODLEY & BRODERICK (1992) ; these zones include virtually the same beaches from one year to the other (BRODERICK & GODLEY, 1993).

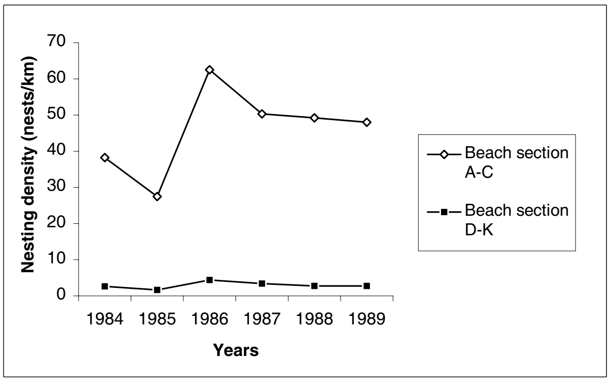

Fig. 1. – Nesting density comparison between adjacent beach sections in Kyparissia, Peloponnisos-Greece (data after MARGARITOULIS & REES 2001).

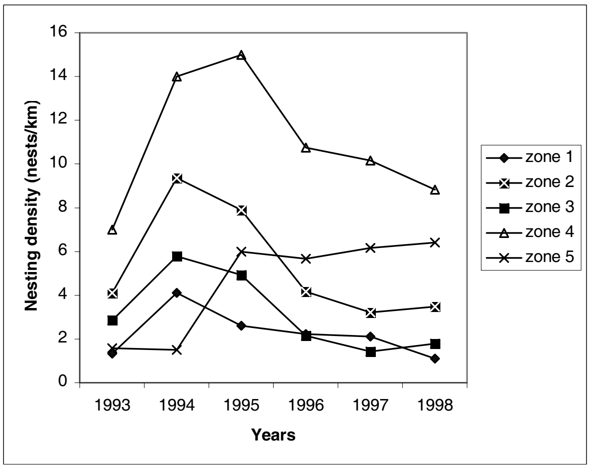

Fig. 2. – Nesting density comparisons between adjacent coastal zones along the northern shore of Cyprus (data after references mentioned in text)

TABLE 2

Spearman rank correlation coefficients r_s for nesting density comparisons between adjacent coastal zones along the northern shore of Cyprus shown in Fig.2. Significant values (n=6, p<0.05) are shaded in grey.

	zone 1	zone 2	zone 3	zone 4	zone 5
zone 1		0.8286	0.715	0.886	-0.6
zone 2			0.99	0.715	-0.714
zone 3				0.543	-0.77
zone 4					-0.2

Application of rank correlation on marine turtle nesting data may raise the point of temporal pseudo-replication, as the compared "replicates" (in this case, nesting densities as estimated in different zones for each year) are not truly independent (KREBS, 1989) ; the fact that individual marine turtles return to nest every 2-3 years to the same geographical zone (MILLER, 1997) gives rise to dependent data along the entire time series. Yet, it is assumed that, as this is a general phenomenon in marine turtle populations, the same bias will be reflected along any time series of marine turtle nesting density data, so the correlation analysis may proceed by ignoring it.

RESULTS

Sardinia - Italy, 1990 and 1991

This short term EC project was undertaken in the absence of any previous comprehensive survey for nesting in Sardinia and in the light of increasing pressures from tourism along the coastline. Past reports had indicated scarce nesting of *C. caretta* in the western part of Sardinia, and in the east within the Gulf of Orosei (GROOMBRIDGE, 1990 and references therein). The survey was repeated in July 1991. No evidence of nesting activity was recorded in either survey despite evaluation of a few beaches (especially in East Sardinia) as potential nesting sites (Table 1). Fishermen confirmed a continuing presence of adult and sub-adult *C. caretta* offshore.

There has been no recent information to confirm *C. caretta* nesting in Sardinia and it is now considered improbable. As individual *C. caretta* recorded in the Gulf of Naples showed movements that extended well over 2000 km, (BENTIVEGNA, 2002), it is possible that turtles observed along the Sardinian coast could be from populations nesting in other parts of the basin. Although turtle nesting in the Western Mediterranean is almost non-existent nowadays, a recent report has indicated nesting activity of *C. caretta* on the Spanish Mediterranean coast (TOMÁS et al., 2003).

Northern Aegean Sea (mainland and islands) 1991

During the summer of 1991, 2078 km of the North Aegean coast were surveyed for *C. caretta* nesting, including the islands of Thassos, Limnos, Lesvos and Samothraki (Table 1). Further surveys were carried out in July and August on beaches considered most suitable for nesting ; dune systems and coastal pollution were also recorded. Despite the presence of potentially suitable sites, the only nesting evidence found was a false track recorded on the island of Limnos: the authors speculated that despite the presence of apparently suitable beaches, unfavourable climatic conditions may deter turtles from nesting. Five young loggerheads (carapace length 20-25 cm) found dead in the area indicated, however, that a nearby shallow water area could be a foraging site for juveniles.

A later survey also reports no indication of *C. caretta* nesting in the Northern Aegean mainland and islands (Margaritoulis et al., 1995 ; Margaritoulis & Dretakis, 1991). Recent estimates of the overall nesting activity of *C. caretta* in Greece contain no reference to nesting in that area (Margaritoulis, 2000). Occasional "diffuse" nesting, however, may occur but on a very small scale.

Syria, 1991

The entire Syrian coast was surveyed for the first time in June 1991 (Table 1). Most evidence of nesting was recorded between Jablah and Latakia. The predation rate was 100%, mostly due to stray dogs and humans. Seaborne plastic garbage contamination was found, as well as raw sewage being piped directly into the sea.

To our knowledge, since the 1991 survey no comparative data have appeared. Information on nesting species in Syria is still speculative.

Egypt (northwest coast), 1993

A comprehensive survey with ground patrols along the western part of the Egyptian Mediterranean coastline took place in June and July 1993 (Table 1). Despite several informal reports by fishermen and others of *C. caretta* occurrence in the sea, nesting evidence was scarce. This research indicated the exploitation of both *C. caretta* and *C. mydas* products in Alexandria and contributed to the formulation of Egypt's first conservation law 4/1994, which includes protection of marine turtles.

The entire Egyptian coastline, including the part between Alexandria and El-Salum, was reassessed for nesting evidence in 1998 (data reviewed in Campbell et al., 2001). Fieldwork confirmed the 1993 survey conclusion, that nesting activity at the north-western part of the Egyptian Mediterranean coast is negligible, whereas most nesting occurs in the area to the east of Port Said (North Sinai) (Table 1).

Enforcement of the law against trade in marine turtle products in Egypt has now increased following a recent campaign by MEDASSET and local NGOs (Venizelos & Nada, 2000).

Libya 1995 & 1998

The north-eastern part of the Libyan coast, between Sirte and the Egyptian border (1195 km) was inspected during June - July 1995, the first survey of the area outside the Kouf National Park (Schleich 1987). The majority of the beaches were inspected only once with evidence of *C. caretta* nesting (Table 1). The authors speculated, after extrapolating from the data collected, that the total annual number of *C. caretta* nests made in Libya could be estimated at around 9000 nests per season (Laurent & Al, 1995). The northwest part of the Libyan coast between Misratah and the Tunisian border was inspected in July 1998 (Table 1). This report also included primary data that had originated from an independent survey undertaken in 1996 between Sirte and Misratah (in Laurent et al., 1999) (Table 1).

The extrapolation method applied in 1995 to deduce marine turtle nesting numbers along the whole Libyan coast (Laurent et al., 1995) has since been criticised (see "discussion"). Three beaches along the eastern part were resurveyed in 1999 (Haddoud & El Gomati, in press).

Lebanon 2001

During summer 2001, an assessment was carried out in order to locate potential nesting sites along the Lebanon coast (Table 1). Evidence of marine turtle nesting was recorded for five sites: On one of these, nesting by both *C. caretta* and *C.mydas* was confirmed. Egg predation especially by canids was heavy at all sites. A number of beaches where past nesting had been reported, were found to be the subject of severe erosion, and in some cases had disappeared completely; sand extraction from beaches, dunes, offshore sand dredging and unplanned sediment removal from river beds for construction and military purposes were seen as definitive causes of erosion along the Lebanese coast. Sea-borne garbage pollution was also recorded in some areas.

DISCUSSION

Through several years of research, we have achieved greater insight into the nesting beaches of *Caretta caretta* and *Chelonia mydas* (Fig. 3). Although Greece and Turkey host a large percentage of the Mediterranean *C. caretta* nesting population (Margaritoulis, 2000 ; Yerli & Demirayak, 1996) and *C. mydas* nesting sites are mainly confined to Cyprus and Turkey (Kasparek et al., 2001), there is now substantial evidence of small nesting populations for both species in other countries of the Mediterranean.

In Sardinia, the absence of any signs of nesting activity suggests that nesting there is improbable although fishermen commonly report

C. caretta by-catch. Nesting in the northern Aegean is equally unlikely. Evidence from Syria is confined to the 1993 data, which is insufficient for adequate classification of the beaches; further research is advisable, especially in view of the encouraging recent discovery of *C. mydas* nesting on the neighbouring Lebanon coast, and the important nesting beaches over the Turkish border. In Egypt, it appears that few turtles nest to the west of Alexandria, and small numbers of *C. caretta* and *C. mydas* breed in Sinai, although offshore populations are reportedly significant.

The situation in Libya remains debatable. Past assessments that employed extrapolation to determine the status of the nesting population of *C. caretta* (Laurent et al., 1995 ; 1999), have attracted criticism as this methodology implies random or regularly spaced nesting in order to give rise to realistic estimations, and opposes the general trend of aggregated emergence and nesting observed in long-term datasets. *C. caretta* for example, displays a highly aggregated distribution of nesting in Kyparissia, Greece (Fig.1) and temporal variation in nesting density correlates positively between beaches, indicating a consistent trend in time and non-random nesting ($r_s = 1$, $p<0.05$). *C. caretta* nesting density comparisons between adjacent coastal zones along the northern shore of Cyprus also indicate a similar trend, although not in all cases (Fig.2, Table 2). Analogous patterns are reported from other geographical areas e.g. Florida, U.S.A. (Mattison et al., 1994) and Turkey (Türkozan & Baran, 1996). Except for some cases of sporadic nesting, we are not aware of any data from within the Mediterranean indicating random or regularly spaced nesting patterns. Therefore, we feel that there is insufficient evidence to employ extrapolation of nesting densities from one beach to another; nesting numbers produced in this way are, in our opinion, unrealistic (see also comments in Margaritoulis & Rees, 2001).

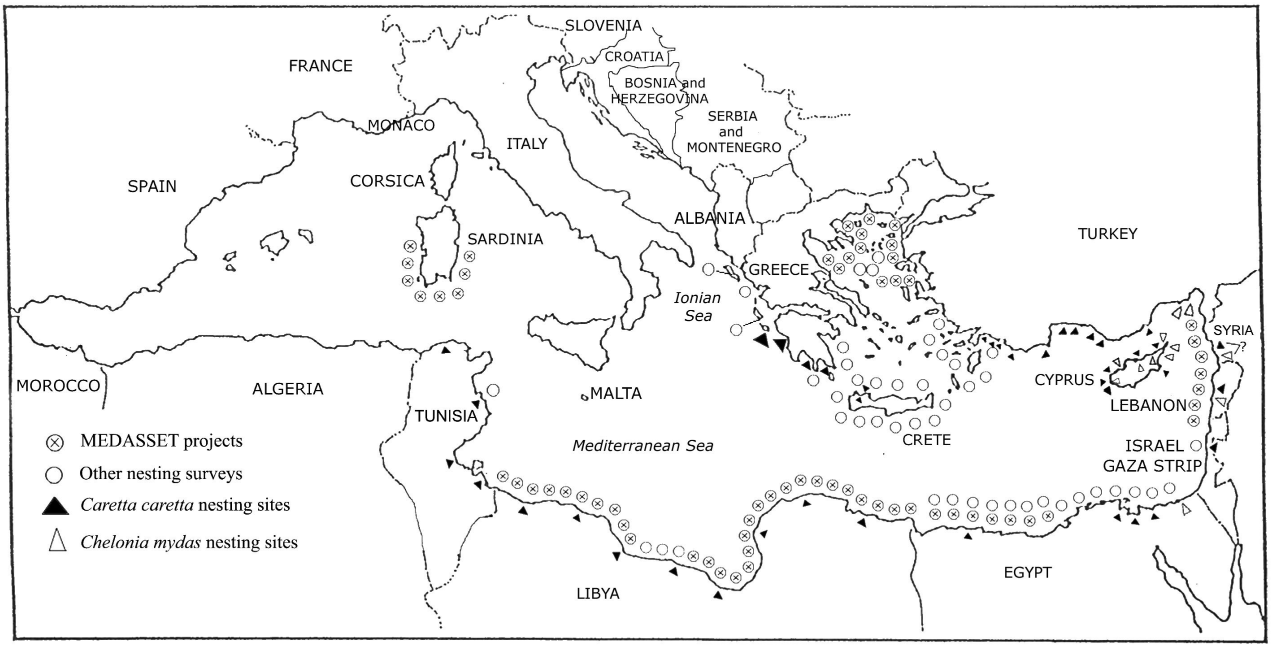

Fig. 3. – Marine turtle nesting surveys in the Mediterranean (drawing not to scale).

With the exception of the major loggerhead nesting sites in Greece, important nesting sites in Cyprus (Broderick & Godley, 1996, Demetropoulos & Hatzihristoforou, 1995) and certain beaches in Turkey (Yerli & Demirayak, 1996), we are aware of only a few long–term projects monitoring marine turtle nesting in the Mediterranean. It is suggested that research should shift towards more elaborate research projects with standardized monitoring procedures for the rest of the significant breeding sites within the basin, with further studies of pelagic populations. Conservation priorities include enforcement of protective legislation, management of nesting areas, protection of foraging and wintering areas and migratory routes, and a limit to the impact of fisheries (Action Plan for the Conservation of Mediterranean Marine Turtles, UNEP/MAP-RAC/SPA). These efforts, however, are undermined by difficulties in the implementation of protective legislation, and lack of knowledge of foraging area ecology and the pelagic stages of these species. It is especially important that international cooperation efforts should go beyond mere protection of nesting beaches : Foraging habitats of the Mediterranean populations are marginally known but recent satellite data agree with older information, mainly derived indirectly from artisanal fisheries by-catch (Venizelos & Nada, 2000), showing that North Africa is probably an important foraging area where turtles may hold distinct home ranges (Godley & Al, 2002).

Although they very rarely change their nesting site, marine turtles are known to occasionally migrate to other nesting beaches as a result of disturbance (Margaritoulis, 1998) or natural causes. Because of the possibility of natural disasters etc. wiping out a nesting area, it is of paramount importance that the future viability of marine turtle populations in the Mediterranean does not solely rely on the few major rookeries, but includes protection of some areas with comparatively low nesting numbers such as the Kuriat Islands in Tunisia, where 13 nests were recorded in 2000 (Jribi et al., 2002). There is an urgent need to establish zones of maximum protection at intervals around the entire Mediterranean coastline on beaches favourable to turtle nesting, and in important pelagic foraging areas. A well-managed international network of protected areas would go a long way towards assuring the survival of all life stages of marine turtles. Currently, an attempt is being made to set up a Mediterranean Sea Turtle Conservation Network in a regional effort to enhance collaboration between sea turtle research and conservation organizations around the Mediterranean.

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Origin and vectors of introduction of exotic molluscs in greek waters

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ABSTRACT. Exotic species of macrophytes, invertebrates and fish have become increasingly prominent in most coastal habitats in the Mediterranean Sea, the Greek waters included, over the last decades. It is well established that the introduction of non-indigenous species has significant ecological as well as economic impact in the Mediterranean Sea. A review of the exotic molluscan records in Greek waters revealed a total of 26 species (16 Gastropoda, 10 Bivalvia). Nine species are of Indo-Pacific and Erythrean origin, and are already well established in the Eastern Mediterranean. The occurrence of these species in the Greek Seas is attributed to progressive penetration through the Suez Canal, the so-called Lessepsian migration. Four species, namely the gastropods *Nerita sanguinolenta, Haminoea cyanomarginata, Melibe fimbriata* and the bivalve *Pseudochama corbieri*, are Red Sea endemic and Indo-Pacific biota, which have been first sighted in Greek waters and to date have a limited distribution in the entire Mediterranean. Another four species, the gastropods *Crepidula fornicata* and *Polycerella emertoni* and the bivalves *Petricola pholadiformis* and *Mya arenaria*, which originate from the Atlantic and occur in ports/lagoons, may have entered via shipping and/or aquaculture. The gastropods *Strombus persicus* and *Rapana venosa* and the bivalves *Anadara demiri* and *Crassostrea gigas* are of Pacific, Indian Ocean or Persian Gulf origin and the vector of their introduction, though not documented, is presumed to be shipping or aquaculture. The rate of molluscan introductions in Greek waters is increasing exponentially with time : 13 out of the 26 species have been recorded since 1990, and further studies may reveal many more.

KEY WORDS : *Mollusca, Exotic Species, Introduction, Greek Seas, Mediterranean*

INTRODUCTION

The vectors of introduction of exotic species to the Mediterranean are diverse : migration through the Suez Canal, thoroughly analyzed by Por (1978, 1990) also termed ‘lessepsian migration’ ; migration through the Gibraltar Straits (Cattaneo-Vietti & Thompson, 1989) ; transport on ship hulls and with ballast waters ; intentional introductions (mariculture) and accidental introductions accompanying intentionally introduced species ; market discards ; escape from aquaria (Zibrowius, 1992). The Suez Canal has been the largest pathway for the entry of invaders in the Mediterranean Sea and more than 300 Erythrean species – principally molluscs, fish, decapod crustaceans, polychaetes and algae - have become established in the Eastern Mediterranean, primarily in the Levantine Basin. The rate of these biological invasions has increased in recent decades, and “they collectively have significant ecological and economic impacts in the Mediterranean Sea” (Galil, 2000).

Given the rate and extent of the phenomenon, some national monitoring projects in countries bordering the Mediterranean have focused on introduced species. The International Commission for the Scientific Exploration of the Mediterranean Sea (CIESM) has published a digital atlas of exotic species in the Mediterranean (fish, crustaceans and molluscs). According to the updated information, the number of exotic molluscan species has increased from 44 (Por, 1978) to 137 (Gofas & Zenetos, 2003).

A review of the Greek marine exotic biota has revealed that molluscs predominate among the 78 exotic species that have been recorded to date (Pancucci - Papadopoulou et al., 2003). The first exotic mollusc reported from the Greek seas is the Erythrean bivalve species *Pseudochama corbieri* (Jonas, 1946) found in Saronikos Gulf in the South Aegean (Ralli-Tzelepi, 1946). The CIESM atlas enumerates 26 exotic molluscs (Zenetos et al., 2003).

The majority of the exotic Gastropod species recorded from the Greek Seas has arrived as Lessepsian invaders (Koutsoubas, 1992). However, other ways of invasion of these species should also be taken into consideration, e.g. invasion through human activities and/or entrance via the Gibraltar Straits (see review by Koutsoubas & Cinelli, 1997). Considering the rate of introduction, an updated inventory is needed of exotic molluscs, to include recent findings and extend the zoogeographical distributions, thus providing further insight to the modes of introduction. Furthermore, and despite intensive research effort into the marine biodiversity in the Greek Seas, especially during the last two decades, which has resulted in reliable molluscan inventories (e.g. Zenetos, 1996 ; Koutsoubas et al., 1997, 2000a, b ; Delamotte & Vardala-Theodorou, 2001) the ecological and economic impacts of the molluscan invaders in the Greek Seas have not been recognized so far.

The present review aims to : 1) present an updated checklist of the exotic mollusc species in Greek Waters, 2) discuss in detail their origins, vectors and their rates of introduction, 3) examine zoogeographical patterns of these species in the Greek Seas and in the Eastern Mediterranean.

MATERIAL AND METHODS

The work is a combined effort to compile all past and recent records of exotic molluscs in the Greek Seas up until April 2002. To this end, part of the information is derived from : the ongoing CIESM ATLAS project (see www.ciesm.org/atlas) ; unpublished data of the authors' research efforts on molluscs in the Greek Seas over the last 20 years ; data originated from the gray literature (e.g. Technical Reports). Of the many terms (aliens, introduced, invaders, exotic, non-indigenous species) currently used to define species introduced from one sea to another via any vector of introduction, we have chosen to adopt the term exotic in the sense used by CIESM. The taxonomy used in this study is that used for Red Sea mollusc species (Oliver, 1992 ; Dekker & Orlin, 2000). In order to define the rate of introduction of the exotic molluscs a special effort was made through the Goulandris Natural History Museum collections, the authors' research collections, and amateur collectors collections available to the authors to trace, to the degree possible, the true dates of appearance of the species in Greek waters. On presenting the zoogeographical distribution of the exotics within the Greek Seas, different physicochemical and dynamic processes were encountered leading to the division suggested by Theocharis et al. (1993) i.e. Ionian Sea, the Sea of Kythira, the Aegean Sea and the Libyan Sea. Given the importance of ports, a more detailed division included Saronikos and Thermaikos Gulfs (in the South and North Aegean correspondingly) where the main Greek ports are situated.

RESULTS

Records and composition of exotic mollusc species in the Greek seas

The examined material in authors' collections along with a review of the relevant literature has revealed that to date 26 exotic mollusc species have been recorded from the Greek Seas. These species are presented in phylogenetic order in Table 1. Very few species, namely the gastropods *Strombus persicus, Bursatella leachi*, *Melibe fimbriata* and the bivalves *Brachidontes pharaonis, Pinctada radiata,* are well established in the Greek Seas. Certain other species i.e. *Crepidula fornicata, Rapana venosa, Bulla ampulla, Anadara demiri* and *Fulvia fragilis* are met in large populations but are locally established. The remaining species have been reported from a single site and usually from a single individual indicating that their presence in the Greek Seas could be considered as accidental.

Origin and vectors of introduction of exotic mollusc species in the Greek seas

Considering the origin of the exotic mollusc species recorded from the Greek Seas (Table 1) the majority are Erythrean ones (five species from Red Sea, three from Indian Ocean and Red Sea, four from Indo-Pacific Ocean and Red Sea), followed by those from the Indo-Pacific oceans (five species). Very few species (four) originate from the Atlantic Ocean.

Many of the Erythrean species, either well established in the Eastern Mediterranean (*Cylichna girardi, Bursatella leachi, Brachidontes pharaoni, Malfuvundus regulus, Gastrochaena cymbium*), or accidental (*Cellana rota, Trochus erythraeus, Murex forskoehli, Pseudochama corbieri*) occur in the Suez Canal and therefore their finding in the Greek coasts should be attributed to progressive penetration through the Suez Canal (Lessepsian migration) (Fig. 1). The same pathway (?Lessepsian) is suspected to be the mode of introduction of another seven mollusc species that are either Red Sea endemics (*Nerita sanguinolenta, Acteocina mucronata, Haminoea cyanomarginata*) or Indo-Pacific species (*Smaragdia souverbiana, Rapana rapiformis, Bulla ampulla, Melibe fimbriata*) (Fig. 1). These species, however, are absent from the Suez Canal and have, to date, a limited distribution in the Eastern Mediterranean. The Indo-Pacific oyster species *Crassostrea gigas* is the most widely distributed oyster introduced word-wide in temperate to tropical seas and its presence in the Greek Seas should be attributed to aquaculture. The opisthobranch Atlantic species *Polycerella emertoni* has been found in the Mediterranean in ports or lagoons close to ports, and shipping is speculated to be the most likely introduction vector. Finally certain species may have followed more than one route. In other cases pathways of introduction remain unknown, even if shipping is assumed to be the most likely vector of their transport since their occurrence is patchy and associated with ports and/or they are fouling organisms on ship hulls or ballast tanks (Fig. 1). The species with a two-mode introduction or introduction via shipping are presented in detail below :

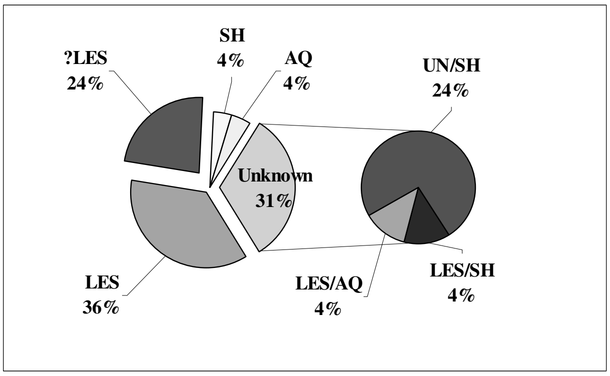

Fig. 1. – Vectors of introduction of exotic mollusc species recorded in Greek Seas. LES = Lessepsian migration ; AQ = Aquaculture ; SH = Shipping ; UN = Unknown

TABLE 1

Findings, Records, Composition and Origin of Exotic Mollusc species in Greek Seas. ^{o} : Species in authors' collections ; * : Additional record in the Greek Seas – this study ; is. = island ; G = Gulf

Exotic Mollusc Species	1st Finding	Citations in the Greek Seas	Sites of Greek Seas Reported	Origin
GASTROPODA				
PROSOBRANCHIA				
NACELLIDAE				
Cellana rota (Gmelin, 1791)	1989	Fountoulakis & Sabelli, 1999	Saronikos G.	IO, RS
NERITIDAE				
Smaragdia souverbiana (Montrouzier, 1863)	1994	Buzzurro & Greppi, 1994	Rhodes is.	IP, RS
Nerita sanguinolenta Menke, 1829	1968	Nordsieck, 1973	Karpathos is.	RS
TROCHIDAE				
Trochus erythraeus Brocchi, 1821	1994	Cosenza & Fasulo, 1997	Crete is.	RS
STROMBIDAE				
^{o}*Strombus persicus* Swainson, 1821	1986	Nicolay, 1986	Rhodes is, **Argolikos G., **Lakonikos G.	PG, AS
CALYPTRAEIDAE				
^{o}*Crepidula fornicata* (Linnaeus, 1758)	1994	Delamotte & Vardala-Theodorou, 1994	Saronikos G., Evoikos G.	WA
MURICIDAE				
Murex forskoehli Roeding, 1798	1966	Settepassi, 1967	Saronikos G.	RS, AS
^{o}*Rapana venosa* (Valenciennes, 1846)	1991	Koutsoubas & Voultsiadou-Koukoura 1991	Thermaikos G.	PO
Rapana rapiformis (Von Born, 1778)	1970	Barash & Danin, 1988/89	Rhodes is.	IP
OPISTHOBRANCHIA				
BULLIDAE				
^{o}*Bulla ampulla* Linnaeus, 1758	1999	Vardala-Theodorou, 1999	Saronikos G., **Argolikos G.	IP
HAMINOEIDAE				
Haminoea cyanomarginata Heller & Thompson, 1983	2001	Gosliner & Mollo *(unpublished data)*	**Korinthiakos G.	RS
CYLICHNIDAE				
Acteocina mucronata (Philippi, 1849)	1997	Storsberg, 1997	Naxos is.	RS
RETUSIDAE				
Cylichna girardi (Audouin, 1826)	1994	Cosenza & Fasulo, 1997	Crete island	IP
APLYSIIDAE				
^{o}*Bursatella leachi* De Blainville, 1817	1986	Barash & Danin, 1986; Koutsoubas, 1992	Chios is., Lesvos is., **Thermaikos G., **Chalkidiki	IP
POLYCERIDAE				
^{o}*Polycerella emertoni* Verrill, 1881	1995	Koutsoubas et al, 2000a	Gialova lagoon	EA
TETHYIDAE				
^{o}*Melibe fimbriata* Alder & Hancock, 1864	1982	Thompson & Crampton, 1984; Koutsoubas & Cinelli, 1997	Astakos G., Kefallonia is., Korinthiakos G., Milos is.	IP
BIVALVIA				
PTEROMORPHIA				
ARCIDAE				
^{o}*Anadara demiri* (Piani, 1981)	**1993	Zenetos, 1994	Thermaikos G.	IO
MYTILIDAE				
^{o}*Brachidontes pharaonis* (Fischer P., 1870)	**1975	Koroneos, 1979; Tenekides, 1989	Rhodes is., Saronikos G., Evoikos G.	IO, RS
OSTREIDAE				
Crassostrea gigas (Thunberg, 1793)	1989	Dimitrakis, 1989	Patraikos G., Korinthiakos G.	PO
PTERIIDAE				
^{o}*Pinctada radiata* (Leach, 1814)	1963	Serbetis, 1963; Nordsieck, 1969; Kallopissis, 1981; Kinzelbach, 1985; Barash & Danin, 1988/89; Zenetos, 1996	Rhodes is., Karpathos is., Saronikos G., Evoikos G., Lesvos is., **Lakonikos G.	IP, RS
MALLEIDAE				
Malvufundus regulus (Forskål, 1775)	2001	Giannuzzi-Savelli et al., 2001	Simi is.	IP, RS
HETERODONTA				
CHAMIIDAE				
Pseudochama corbieri (Jonas, 1846)	1946	Ralli-Tzelepi, 1946	Saronikos G.	RS
CARDIIDAE				
^{o}*Fulvia fragilis* (Forsskål in Niebuhr, 1775)	1999	Vardala-Theodorou, 1999	Saronikos G.	IO, RS
PETRICOLIDAE				
^{o}*Petricola pholadiformis* Lamarck, 1818	1994	Delamotte & Vardala-Theodorou, 1994	Evoikos G.	WA
MYIIDAE				
^{o}*Mya arenaria* Linnaeus, 1758	**1984	Zenetos et al. 2003	Saronikos G.	EA
GASTROCHAENIDAE				
^{o}*Gastrochaena cymbium* (Spengler, 1783)	**1974	Tenekides, 1989	Saronikos G.	IP, RS

Lessepsian migration – Shipping

The Indo-Pacific bivalve *Fulvia fragilis* seems to have followed the typical distribution of a Lessepsian migrant. It has been recorded in the Suez Canal, in the coasts of Israel, Tunisia and S. Turkey (www.ciesm.org/atlas). However, its recent finding in Saronikos Gulf, and in particular in Peiraew port, suggests transport via shipping, as all other areas in the Mediterranean from where it has reported are also in the vicinity of ports.

Lessepsian migration – Aquaculture

The pearl oyster *Pinctada radiata* was intentionally introduced to Greece for mariculture purposes, and has since established thriving populations in the sites where it was firstly imported for aquaculture (i.e. Lesvos island, Evoikos Gulf, Saronikos Gulf), but its recent finding in Rhodes island and Lakonikos Gulf, where aquaculture activities are absent, supports the Lessepsian mode of introduction.

Unknown – Shipping

The gastropod *Strombus persicus* from the Persian Gulf and Arabian Sea, was first recorded in the Mediterranean not far from the oil terminal in the south Turkish Bay of Iskenderun. The species has not been recorded from the Red Sea, and its introduction in the Mediterranean could be attributed to ships coming from the Persian Gulf (Oliverio, 1995). However, the species has planktotrophic larvae thus ensuring long-distance dispersal. Galil & Zenetos (2002) argue that the rapid geographic expansion and successful establishment of this species in the Levantine basin is typical of a Lessepsian invader. The slipper limpet *Crepidula fornicata* is assumed to have been introduced in the Mediterranean by shipping related to oyster/mussel commerce for farming. Its occurrence is rather local in the Mediterranean (e.g. French coasts near Toulon, Sicily - Zibrowius, 1992). Presumably there were separate introductions of cultivated bivalves from the French Atlantic coast to the French Mediterranean lagoons, and from unknown origin to the Italian and Maltese sites (Galil & Zenetos, 2002). The species has a broad adaptive ability, extensive period of reproduction with direct fecundation (through piling), together with the absence of specific predators (Blanchard & Erhold, 1999). Its record from Saronikos Gulf and in particular close to Peiraeus port is related rather to shipping, as there is no oyster/mussel farming in the broader area. *Rapana venosa* a gastropod native to the Sea of Japan was introduced in the Black Sea accidentally in the 40s and most possibly independently in the Adriatic in the 70s. It has been speculated that the planktonic larvae of the species arrived through ballast water in commercial ships, but a more likely scenario is that egg masses may have been transported with the products of marine farming i.e. oysters or mussels. Its discovery in the northern Aegean Sea near natural oyster and mussel banks in the bay of Thessaloniki (major port in the North Aegean) in the 90s (Koutsoubas & Voultsiadou - Koukoura, 1991) is most possibly related to shipping but transfer via the Dardanelle's strait should not be excluded. The bivalve *Anadara demiri*, originating from the China Seas, was reported to dominate the degraded benthic ecosystems in Izmir Bay (Demir, 1977) and Thessaloniki Gulf (Zenetos, 1994). The species seems to be well established in these areas but its distribution in the Mediterranean remains spotty. Though shipping seems to be the most likely vector of introduction since the species, at least in the Aegean, had been found in ports, its recent finding in the Central Adriatic does not exclude other introduction modes. *Petricola pholadiformis* and *Mya arenaria* are bivalves imported for mariculture in Mediterranean lagoons. However, their occurrence in Greek waters should be rather attributed to shipping since the records of the species are from areas near ports and away from areas where marine farms are located.

Rate of introduction of exotic mollusc species in the Greek seas

Thirteen out of the 26 exotic mollusc species have been recorded in the Greek Seas in the last decade (50% of the total number of exotic molluscs recorded so far from these seas) thus implying an exponential rate of introduction of these species in the Greek waters (Fig. 2). It is worth mentioning that only during last year two species, namely the gastropod *Haminoea cyanomarginata* and the bivalve *Malvufundus regulus,* have been recorded from the Greek Seas (Gosliner & Molo unpublished data and Giannuzzi-Savelli et al., 2001 correspondingly).

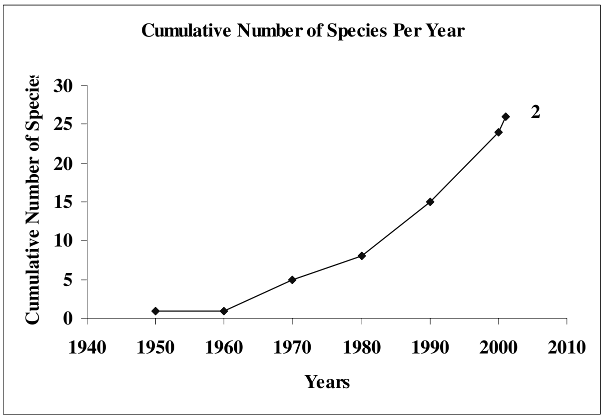

Fig. 2. – Rate of introduction of exotic mollusc species in the Greek Seas.

Comparing the appearance of the exotic mollusc species in the Greek Seas *vs* the Mediterranean Sea, we note that six species (*Smaragdia souverbiana, Nerita sanguinolenta, Rapana rapiformis, Haminoea cyanomarginata, Melibe fimbriata, Pseudochama corbieri*) are Red Sea endemic and Indo-Pacific biota that have been firstly sighted in Greek waters and then in the rest of the Mediterranean Sea. With the exception of *Melibe fimbriata*, these species have a limited distribution in the entire Mediterranean to date. On the contrary some of the very first exotic mollusc species in the Mediterranean Sea that entered that sea via the Suez Canal, colonized its eastern part and became locally abundant in the Levantine basin i.e. Lessepsian migrants, such as *Murex forskoehli, Brachidontes pharaonis, Pinctada radiata* and *Malvufundus regulùs* then later appeared in Greek waters after a time lapse of 60 to 98 years.

Zoogeographical patterns of the exotic mollusc species in the Greek seas

Twenty one exotic mollusc species have been recorded from the Aegean Sea, four from the Ionian Sea, two from the Sea of Kythira and one from the Libyan Sea (Fig. 3). Within the Aegean, the southern part is richer (19 species), and two major centres can be distinguished there : a) the Saronikos and Argolikos Gulfs, which are in the route of many ships towards Peiraeus (the biggest Greek port), where 11 species have been recorded and b) the Dodekannese islands, which are located close to the Levantine basin, the main area of distribution of exotic species within the Mediterranean, where seven species have been recorded. Also in the North Aegean, two major centres can be seen ; a) Thermaikos Gulf (three species) and b) Evoikos Gulf (four species), which are both areas where major ports are located.

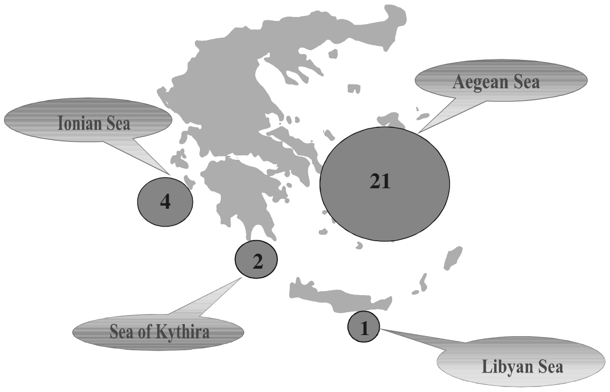

Fig. 3. – Number of exotic mollusc species recorded from the different Greek Seas

DISCUSSION

Twenty six exotic molluscan species (16 Gastropoda and 10 Bivalvia) have been collected in the Greek Seas during the last decades. These comprise less than 2.4% of the total number of mollusc species recorded so far in Greek Waters (1095 species – DELAMOTTE &. VARDALA-THEODOROU, 2001).

The majority of the exotic mollusc species in Greek waters (61%) originate from the Indo-Pacific region or are distributed in these oceans and the Red Sea. The next major component are Red Sea endemics (19%). This is also the case for other marine taxa with exotic representatives in the Mediterranean (POR, 1978). A major problem when dealing with exotic mollusc species is to dismiss the Mediterranean species that occur also in the Indo-Pacific region, as 'tethyan relicts' (CATTANEO-VIETTI & THOMPSON, 1989). A review of the palaeontological records shows that none of the exotic mollusc species reported so far from the Greek waters were present in the area during the Pleistocene. Were the aforementioned species present in the Mediterranean at earlier geological periods, they should be found as fossils either under the recent mean sea level, if they lived during the last glaciation, or above mean sea level, if they lived during warm periods. On reviewing the literature referring to the Upper Pleistocene marine fossil Mollusca, from the warm periods of Tyrrhenian-Eutyrrhenian and Neotyrrhenian in Greek Seas, the aforementioned species did not occur as fossils (VARDALA-THEODOROU, 1999). This implies that the exotic mollusc species found so far in the Greek Seas are not relicts of the past.

Only four out of the 26 exotic molluscs in the Greek Seas (*Crepidula fornicata*, *Polycerella emertoni, Petricola pholadiformis* and *Mya arenaria*) are species originating from the Atlantic, which have extended their distribution via different pathways into the Mediterranean. This point strengthens the statements of previous authors that although the major pool of exotic species invading the Mediterranean is Erythrean biota, the discovery of each species new to the inventory of the exotic flora and fauna species should be interpreted with caution and its origin be carefully examined (ZIBROWIUS, 1992 ; GALIL, 2000).

Molluscs are one of the 'leading' groups of the Lessepsian migration, together with decapod crustaceans and fishes (POR & DIMENTMAN, 1989). OLIVERIO (1995) has discussed the use of the term "Lessepsian migration" and concluded that this should not be used indiscriminately for any species of Indo-Pacific origin found in the Mediterranean. A sensible use of the term is for species that have worked their way through the Suez Canal and then spread progressively into the Mediterranean. It is in this sense that almost 35% of the Greek exotic mollusc species (*Cellana rota, Trochus erythraeus*, *Murex forskoehli*, *Cylichna girardi, Bursatella leachi, Brachidontes pharaoni, Pseudochama corbieri, Malvufundus regulus, Gastrochaena cymbium*), which are also successful in the Canal itself, could be considered as true Lessepsian migrants. Another seven Erythrean origin species (*Nerita sanguinolenta, Acteocina mucronata, Haminoea cyanomarginata*, *Smaragdia souverbiana*, *Rapana rapiformis, Bulla ampulla, Melibe fimbriata*) are suspected to have penetrated via the same pathway, but because of no up-to-date records in the Suez Canal and their limited distribution in the entire Mediterranean, they are classified as suspected Lessepsian migrants.

Besides introduction through the Suez Canal, the next major vectors of introductions of exotic marine biota in the Eastern Mediterranean are shipping and then aquaculture (GALIL & ZENETOS, 2002). This pattern is also valid for the exotic molluscs recorded in Greek waters, although to be able to draw the line further investigation is needed. Shipping has been considered the vector of introduction for the opisthobranch mollusc *Polycerella emertoni* and aquaculture for the bivalve species *Crassostrea gigas*. However, transport via shipping routes and mariculture are considered to be the most likely vectors of introduction of exotic mollusc species in the Greek waters in certain cases for which a two-mode introduction scheme has been assumed, where the true vector is still unknown. Even if these two vectors are not the true vectors of introduction of exotic mollusc species in different parts of the Greek Seas, they may have been involved in combination with other pathways of introductions. For *Strombus persicus* and *Fulvia fragilis* Lessepsian migration has been suggested by PASSAMONTI (1996), GALIL & ZENETOS (2002) and shipping by OLIVERIO (1995). Although in the present study their vector of introduction has been characterized as unknown, *Crepidula fornicata, Rapana venosa, Anadara demiri, Petricola pholadiformis* and *Mya arenaria* were sampled in areas close to major ports, therefore shipping should be considered as the true vector of their introduction in the Greek waters. The pearl oyster *Pinctada radiata* has been imported in Greek waters for aquaculture (KALOPISSIS, 1981) and viable populations have successfully established in the wild, but progressive penetration through the Suez Canal should not be excluded as the species has been recorded in other areas of the Eastern Mediterranean ; recently it was found in Rhodes island in the South Aegean where aquaculture is absent. To further extend the discussion on the subject, new findings suggest caution even when dealing with species that have been considered without doubt as true Lessepsian migrants. For example the small mussel *Brachidontes pharaonis*, a species that originates from the Indian Ocean and is widely spread throughout the Red Sea (Oliver, 1992), was among the first migrants noticed in the Eastern Mediterranean. Based on the origin of the species and its present distribution, progressive penetration through the Suez Canal was considered obvious and hence its characterization as a Lessepsian migrant was not questioned. However, preliminary results of molecular studies have shown that although Red Sea genotypes are present in the Mediterranean Sea, non-Red Sea genotypes are fairly common in that sea also, and the frequency of the latter increases as we get further from the Suez Canal (Abelson, pers. commun.). This suggests that ship transport from elsewhere may have occurred for this species rather that natural migration through the Suez Canal. The importance of these two vectors and in particular shipping in introduction of mollusc species in an area of the Greek seas extends beyond the issue of exotic species, since these vectors may have also contributed to spread of species originally native in a restricted part of the Mediterranean. Such a case is that of the pulmonate gastropod *Siphonaria pectinata* (Linnaeus, 1758), originally restricted to the Alboran Sea and the Western coasts of Algeria and now thriving in Saronikos gulf in the South Aegean (Gofas & Zenetos, 2003).

The rate of invasion of exotic mollusc species in the Greek waters has increased in recent decades, in agreement with data for the rate of biological invasions in the whole Mediterranean (Galil, 2000). The increased rate of invasion in the Greek Seas could be the result of a synergy of different reasons, the most important of which are the following : a) the intensive research on the marine biota of the Greek Seas during the last 20 years and especially after 90s, which led to the discovery of many molluscs not reported previously in this area of the Mediterranean, b) the increased anthropogenic activities in the Greek Seas over the last decade such as aquaculture and tourism (contributing factors to increase of maritime traffic).

Among the Greek Seas, the Aegean and in particular the South Aegean is the area where the majority of the exotic mollusc species is distributed. This difference between the two parts of the Aegean should be attributed to : (i) the prevailing environmental conditions (e.g. higher temperatures and salinities in relation to the North Aegean - Poulos et al., 1997), which are favourable for the distribution and settlement of these species, (ii) the vicinity of the South Aegean with the Levantine Basin in connection with the hydrological regime within the Eastern Mediterranean i.e. sea currents running from the coasts of Egypt anticlockwise south of the Turkey coasts up to Rhodes island and then to the South Aegean. The influx of the Levantine Intermediate Water in the South Aegean through the Kassos straits and then to the other Greek Seas (Kontoyiannis et al., 1999) certainly enriches these waters with elements of Indo-Pacific and/or Red Sea origin, which have already been established in the Levantine Basin. (iii) the more intensive research carried out in the South Aegean. Despite the fact that the number of exotic mollusc species in the North Aegean has increased over the last decade, it seems that the Lessepsian migration – the major vector of introduction of exotic mollusc species in the Greek Seas – has not yet proceeded to that part of the Aegean Sea. Only two out of the seven species recorded in the North Aegean i.e. the opisthobranch gastropod *Bursatella leachi* and the bivalve *Brachidontes pharaonis* could be considered as true Lessepsian migrants, while the presence of the other species in this area is in most cases connected with anthropogenic activities i.e. shipping and/or aquaculture. The scarcity of Lessepsian migrants in the North Aegean Sea has also been noticed for other benthic groups such as anthozoans (Vafidis et al., 1994) and crustaceans (Koukouras et al., 1992).

The number of exotic mollusc species recorded from the Greek Seas is moderate when compared with that recorded from other areas of the Eastern Mediterranean. The areas with the largest number of exotic species are the Israeli coasts (95 species), the coasts of SE Turkey (68 species), Cyprus (32 species), the coasts of Egypt (31 species) and the coasts of Lebanon and Syria (29 species). All these areas are located in the Levantine Basin, which constitutes a separate subsystem in the Eastern Mediterranean (Por & Dimentman, 1989). It has been assumed that the prevailing environmental conditions in that basin i.e. high temperature and salinity, make this area unsuitable for many western Mediterranean species (Sara, 1985) and presumably species of Atlantic origin as well. Consequently this area of the Mediterranean is a favourable place for the tropical species that arrive there, since there are few ecological obstacles to prevent their establishment (Galil, 2000). Indeed the Erythrean biota, coming mainly through the Suez Canal in that sea, accentuates its subtropical character (Tortonese, 1985). Por (1978) was the first to suggest that Lessepsian migrants represent at least 10% of the species inventory of the Levantine Basin, while a similar ratio (9.4%) has been suggested by Barash & Danin (1986) for the molluscs. Similarly, the introduction of exotics has increased by about 10% the biodiversity of molluscs along the Lebanese coasts where out of 298 recorded species 29 are exotics (Bitar & Kouli-Bitar, 1999, 2001) and SE Turkey coasts where from a restricted area (Tasuçu area) out of 371 mollusc species 40 belong to exotics (Buzzurro & Greppi, 1996). In Cyprus however, the exotic molluscs contribute only 5% to the malacofauna diversity. Out of the 627 species known to date (Cecalupo & Quadri, 1996 ; Buzzurro & Greppi, 1997) only 32 are exotics (www.ciesm.org/atlas).

Another reason that has been suggested for the low number of exotic mollusc species in other areas than the Levantine Basin of the Eastern Mediterranean (Koutsoubas, 1992), is the restricted period of life for the molluscan planktonic larvae – when referring to their natural spreading capacities – which restricts the distribution of such species over long distances. Areas isolated (due to deep trenches) from the continental coasts, such as islands, are difficult for non-indigenous species to approach.

It is well documented that the presence of exotic species in the Mediterranean has significant ecological and economic impacts in that sea (Por & Dimentman, 1989 ; Zibrowius, 1992 ; Galil, 2000). Tom & Galil (1991) have pointed out the impact of certain exotic mollusc species, which have entered the Mediterranean via Lessepsian migration, on benthic communities in the Israeli coasts. Of the exotic mollusc species distributed in the Greek Seas, the prosobranch gastropod *Rapana venosa* first established in Thermaikos Gulf (Koutsoubas & Voultsiadou-Koukoura, 1991), and has since spread out. According to the local Fisheries and Aquaculture Associations it has become a considerable nuisance in the oyster and mussel beds in the area in a similar way to what has been reported for the Black Sea where the species was first noticed and progressively established (Zibrowius, 1992). The bivalve *Anadara demiri* has been reported to dominate the degraded benthic ecosystems in Thessaloniki Gulf (Zenetos, 1994), a fact strengthening the opinion of Galil (2000) that polluted or physically degraded environments are more prone to invasion than are pristine sites. However, in order to precisely track and better understand the changes in the Greek marine biota, and in particular Mollusca, both its autochthonous and allochthonous components should be further investigated.

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