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Diet of the Monk Seal (*Monachus monachus*) in Greek Waters

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Abstract

Stomach contents were collected from 27 monk seal carcasses between 1997 and 2008 from different areas along the Greek coast. This sample included nine animals that had been deliberately killed and five accidental deaths due to fisheries interactions. Stomachs from monk seals of both sexes, including adults and subadults, were analysed. A total of 530 prey items from at least 71 prey species was identified, with approximately 74% of prey identified at least to genus, while 2.8% could be identified only to class level (i.e., fish or cephalopods). We found 266 cephalopods (50%), 253 fish (48%), a few non-cephalopod molluscs (1.5%), and two crustaceans (0.4%). Faecal samples were also collected but contained no identifiable prey remains. Octopuses were the most important prey in terms of numbers eaten and contribution to reconstructed prey biomass. The common octopus (*Octopus vulgaris*) (33.9% of prey by number) was around three times as numerous in the diet as the lesser octopus (*Eledone cirrhosa*) (11.1%). Fish of the families Sparidae (28.1%) and, to a lesser extent, Scorpaenidae (2.3%), Congridae (2.5%), and Atherinidae (2.5%) were also frequent in the stomachs. Many of the prey species recorded are of commercial fishery importance. Exploratory multivariate analysis (redundancy analysis [RDA]) indicated weakly significant seasonal, spatial, and interannual variation in diet and also suggested a relationship between diet composition and cause of death. No trends in diet related to sex or age class were identified. Sparids occurred more frequently in animals that had been deliberately killed than those that had died due to other causes, highlighting the interactions taking place between monk seals and fishing activities.

Key Words: monk seal, *Monachus monachus*, Greece, fish, octopus, sparid, fishing interactions

Introduction

The Mediterranean monk seal (*Monachus monachus*) is a critically endangered species (*International Union for Conservation of Nature* [*IUCN*] *Red List*, CMS Appendix I, CITES Appendix I). Presently, fewer than 600 individuals survive, the majority of these living in the eastern Mediterranean Sea on the Aegean and Turkish coasts. The National Marine Park of Alonissos, Northern Sporades, in the northern Aegean Sea was established in 1992 to protect the last viable population of the Mediterranean monk seal. The Hellenic Society for the Study and Protection of the Monk Seal (MOm), in collaboration with the Hellenic Ministry for the Environment, Energy and Climate Change, runs a national rescue and information network in support of the conservation of the monk seal in Greece.

Numbers are thought to be declining (Johnson et al., 2006), and although recent research has investigated topics such as population dynamics (Dendrinos et al., 1994, 1999; Politikos & Tzanetis, 2009); distribution; habitat use and movements (Adamantopoulou et al., 1999; Gücü et al., 2004; Dendrinos et al., 2008); parasites (Papadopoulos et al., 2010); anatomy (Brombin et al., 2009); and effects of human activity, including fisheries interactions (Güçlüsoy, 2008a, 2008b; Karamanlidis et al., 2004, 2008; Gücü, 2010), knowledge of the feeding ecology of this species remains limited.

While the few dietary studies to date point to a varied diet, a high importance of cephalopods, and the likelihood of frequent interactions with fishing gear, almost nothing is known of seasonal or geographic variation in Mediterranean monk seal diet, whether there are differences in diet between males and females, how diet changes over the lifetime of the animal, and whether diet has changed in recent years—information which is needed to understand the monk seal's ecological role. Cebrian et al. (1990) described the stomach contents of one individual bycaught in a trammel net in Greece and identified fish and cephalopods, including bogue (*Boops boops*), angler fish (*Lophius* spp.), octopus (*Octopus* spp.), and cuttlefish (*Sepia* spp.). González (1999) describes the monk seals as an opportunistic predator, with a varied diet consisting of cephalopods (*Octopus, Sepia*, and the squid *Loligo* spp.); fish of the families Mugilidae, Sparidae, and Clupeidae; and crustaceans such as lobsters (*Palinurus* spp.). The author also reported that monk seals feed by taking fish from nets. Salman et al. (2001) examined two monk seal stomachs from the Aegean coast; cephalopods were dominant by weight (94%) in the food remains, and the species found included the cuttlefish (*Sepia officinalis*), the musky octopus (*Eledone moschata*), and the globose octopus (*Bathypolypus sponsalis*). Other items recorded in the stomachs were sponges (*Sarcotragus* sp.) and seagrass (*Posidonia oceanica*). Obtaining further knowledge of the feeding ecology of the Mediterranean monk seal is also important to evaluate threats (e.g., in relation to likely fisheries interactions) and to define future conservation actions. However, some caution is needed in interpreting opportunistically collected dietary data, and it is important to evaluate potential sources of bias—for example, whether the source of samples has influenced the results obtained.

The present study, based on a considerably larger sample size than previous dietary studies, describes the diet of the Mediterranean monk seal along the Greek coast and investigates sources of variation in diet; testing for geographical, temporal, sex-, and age-related variation, and comparing the food in the stomachs of animals from different cause of death categories.

Materials and Methods

Study Area and Samples

Stomach contents of 27 stranded monk seals—10 subadult males, five adult males, seven subadult females, and five adult females—were analysed. In addition, 14 faecal samples collected from haulout sites were examined. The samples were collected in different areas of the Greek coast by members of MOm from 1997 to 2008 (Figure 1). The stomachs collected from 1997 to 2005 were

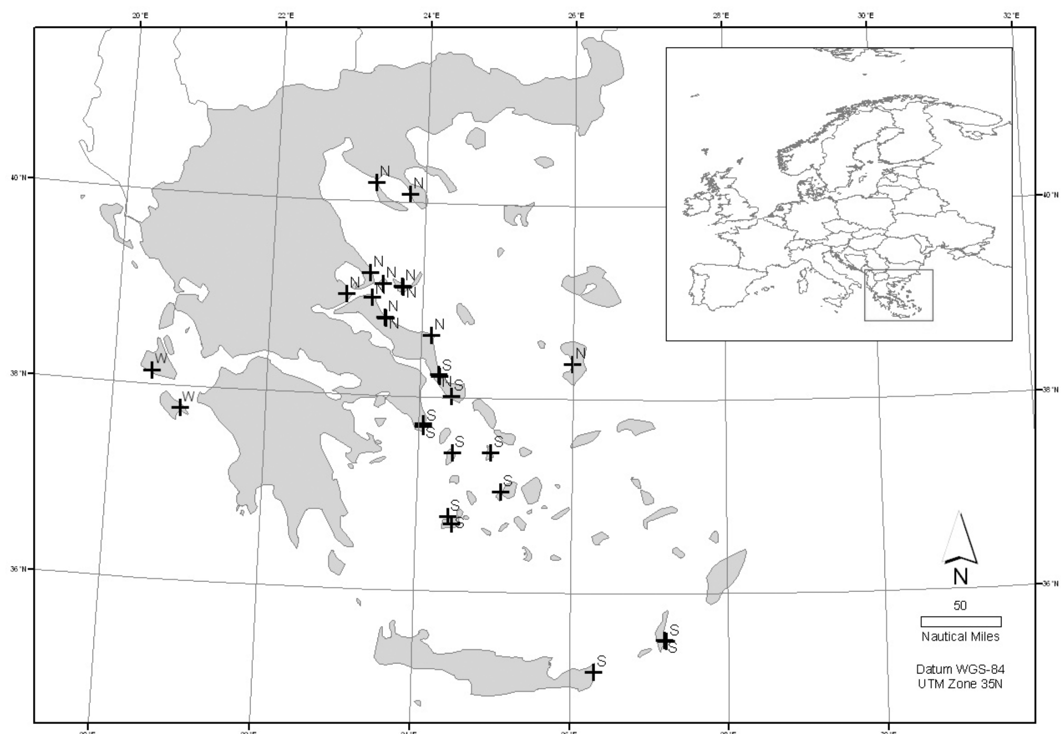

Figure 1. Map showing the stranding locations along the Greek coast of the monk seal carcasses for which stomachs were examined in this study; the letters indicate the classification of sites into geographical areas: north (N), south (S), and west (W).

immersed and stored in 37% formalin, while stomachs collected from 2006 to 2008 were stored frozen (-20º C) until further analysis. The faecal samples were also stored frozen (-20º C).

Stomachs and faeces were washed through a series of sieves (the smallest mesh size being 0.250 mm), and prey remains were transferred to 70% alcohol for sterilization. Fish bones and otoliths, as well as mollusc shells, were then stored dry while other prey items were stored in 70% alcohol.

Prey Identification and Quantification

All prey remains were identified to the lowest possible taxon. Identification made use of reference collections of fish and cephalopod material held at the University of Aberdeen, augmented by fish material collected from a fish market in Athens and a research cruise survey by the Hellenic Centre for Marine Research (HCMR) in July 2008, and by published guides (Clarke, 1986; Härkonen, 1986; Watt et al., 1997; Tuset et al., 2008).

Any intact prey items were weighed and measured (total length for fish; dorsal mantle length for cephalopods). All fish otoliths, cephalopod beaks, and crustacean remains were sorted into species categories and standard measurements (fish otolith length or width and cephalopod lower or upper beak length) were taken using a binocular microscope fitted with an eyepiece graticule or using a digital calliper (0.01 mm), depending on the size of the remains. Measurements were also taken from identifiable fish jaw bones. Fish and cephalopod lengths were then calculated from these measurements using published regressions (e.g., Clarke, 1986). When no regression was available, we used either a regression from a similar species or the average length of reference specimens and length/weight relationships from FISHBASE (www.fishbase.org). Fish and cephalopod weight was similarly obtained (see Appendix 1). Other prey items, such as crabs, shrimps, and non-cephalopod molluscs, were found in very low amounts, and they were grouped for subsequent analysis.

Overall diet was described using three standard indices: (1) % frequency of occurrence, (2) % number, and (3) % reconstructed weight for each prey category.

Statistical Analysis

Redundancy analysis (RDA) was used to detect relationships between diet and the various explanatory variables, which described the location and time of sample collection (area, 4-y period, season), the monk seals (age-class [adult or subadult], sex), and the source of the samples (cause of death category). Three main areas were identified: (1) northern Aegean Sea, (2) southern Aegean Sea, and (3) west coast/Ionian Sea. The study was divided into three time periods (1997-2000, 2001-2004, and 2005-2008); seasons were defined (*sensu strictu*) as Winter—21 December to 20 March; Spring—21 March to 20 June; Summer—21 June to 20 September; and Autumn—21 September to 20 December. Cause of death was classified into four groups: (1) non-human induced death, (2) deliberate killing (including the use of dynamite, harpoon, and shooting), (3) accidental death (nets), and (4) unknown causes. Due to the varying degree of taxonomic resolution that was possible when identifying the prey, we explored several ways of coding the response variable (i.e., diet composition)—for example, grouping according to taxonomic groupings or habitat types (Table 1). Due to the relatively high number of zeros, all prey occurrence data were converted to 0-1. Patterns in the data were identified from examination of bi-plots and the significance of explanatory variables was determined using permutation tests. Where a pattern relating to a particular prey type was discernible, this was further explored using binary Generalised Linear Models (GLM), using presence or absence of the particular prey type as the response variable and the same set of explanatory variables as used in the RDA. All statistical analysis was carried out using *BRODGAR* software (Highland Statistics Limited, Newburgh, UK).

Results

Composition of the Samples and Diet Composition

Of the 27 monk seal stomachs that were analysed, 12 were from females (7 subadults and 5 adults) and 15 from males (10 subadults and 5 adults). More than half of the stomachs were collected during spring and early summer. Fourteen monk seals had died as a direct result of human activity, either deliberately killed (9; ⅓ of the sample) or bycaught in fishing gear (5). Cause of death could not be established in seven cases. Deliberate killing was recorded throughout the study area, from Karpathos in the southeast to Marmaras (Chalkidiki) in the north. These animals had been killed by harpoon, shooting, or dynamite. Four out of five accidental deaths due to fisheries interactions were on the eastern mainland coast (two in Lavrion [Attika], two in Madouthi [Evia]), while the fifth was on the west coast (Zakynthos).

No identifiable hard prey remains were found in the faeces. In total, 530 prey items from at least 71 species were recorded in the stomachs, with ~74% of prey identified at least to genus and only 2.8% identifiable only to class level (i.e., fish or cephalopods). We found remains of 253 (47.7%) fish, 266 (50.2%) cephalopods, eight (1.5%) non-cephalopod molluscs, and two (0.4%) crustaceans (Table 2). Although monk seals feed on a wide range of prey, octopuses were the most important prey category numerically and in terms of reconstructed biomass. *Octopus vulgaris* made up 34% of prey by number,

Table 1. List of response and explanatory variables used in the redundancy analysis (RDA); to form the response variables, prey were grouped in several ways according to taxonomy and ecology.

(a) Response variables

General categories	Specific categories	Codes
Grouping I (Main taxonomic groups)	Fish, cephalopods, others	--
Grouping II (Simple habitat)	Demersal species	DEM
	Non-demersal species	NDEM
Grouping III (Detailed habitat)	Non-demersal species	Ndm
	Sandy/muddy areas	Sm
	Sandy/muddy areas with seagrass	Smg
	Rocky areas	Rc
	Any substrate (nonspecific)	any
Grouping IV	*Atherina hepsetus*	ATH
(Taxonomic, benthopelagic species only)	*Oblada melanura*	SBS
	Diplodus spp.	SRG
	Sparids (Unknown species)	SBX
	Pagellus spp.	PAX
	Carangids	CAR
	Gadids	GAD
	Spondylosoma cantharus	BRB
Grouping V (Benthopelagic prey: Sparidae and others)	Sparids	SBX
	Non-sparids	N-SBX
Grouping VI	Benthopelagic species	BEP
(Taxonomic and habitat)	Demersal species	DEM
	Flatfish species	FLAT
	Other fish species*	ANG
	Scorpaenids	SCS
	Non-identified fish	UNK
	Octopodidae	OCT
	Sepia spp.	CTC
	Squid	SQU
	Other invertebrate	OTH

*Other fish species included Anguilliformes, Trichiuridae, and monkfish

(b) Explanatory variables

General categories	Specific categories	Codes
Monk seal age and sex	Age: Subadult or adult	Y, A
	Sex: Male or female	M, F
Location	Areas: North Aegean Sea	N
	South Aegean Sea	S
	West coast of Greece	W
Temporal variables	Years: 1997-2000, 2001-2004, 2005-2008	Y1, Y2, Y3
	Seasons: 21 Dec-20 March	W1
	21 March-20 June	Sp1
	21 June-20 Sept	Su1
	21 Sept-20 Dec	A1
Cause of death	Non-human induced death	NHID
	Deliberate killing (dynamite, harpoon, shooting)	DK
	Unknown cause of death	U
	Accidental death (drowned in nets)	AD

Table 2. Frequency, total numbers, and estimated biomass of prey items found in monk seal stomachs: %F = percentage frequency, %N = percentage by number, %W = percentage by weight; the mean and range of prey sizes (length, weight) is also given.

Taxon	%F	%N	%W	Length (cm) Mean	Length (cm) Range	Weight (g) Mean	Weight (g) Range
Chondrichthyes							
Batoids	7.4	0.6	0.3	32.3	20.0-56.8	336.7	30.6-358.7
Scyliorhinus spp.	7.4	0.4	0.2	35.0	35.0	130.3	130.3
Osteichthyes							
Anguilliformes							
Eel	18.5	1.1	1.4	71.9	48.0-113.5	983.7	204.7-3,251.3
Congridae							
Conger conger	29.6	2.5	6.9	78.7	56.0-127.5	926.3	221.3-3,289.7
Muraenidae							
Muraena helena	3.7	0.2	<0.1	37.0	37.0	77.8	77.8
Gadiformes							
Unknown gadoid	7.4	0.4	<0.1	25.8	25.8	184.3	184.3
Merlucidae							
Merluccius merluccius	3.7	0.2	0.2	40.6	40.6	522.0	522.0
Phycidae							
Phycis blennoides	7.4	0.4	0.5	14.0	6.2-21.8	419.1	184.3-563.9
Phycis phycis	3.7	0.2	0.2	18.0	18.0	366.4	366.4
Perciformes							
Moronidae							
Dicentrarchus labrax	3.7	0.6	9.3	79.7	71.5-88.0	197.5	3,730.2-6,954.3
Serranidae							
Serranus spp.	3.7	0.2	<0.1	10.3	10.3	17.3	17.3
Serranus hepatus	3.7	0.2	<0.1	15.6	15.6	67.0	67.0
Carangidae	3.7	0.2	<0.1	18.3	18.3	45.6	45.6
Trachurus spp.	3.7	0.2	<0.1	18.3	18.3	45.6	45.6
Mullidae							
Mullus spp.	3.7	0.2	<0.1	21.5	21.5	105.2	105.2
Sparidae							
Unknown sparid	29.6	20.2	6.3	12.8	5.6-3.1	102.7	14.8-147.5
Pagrus pagrus	3.7	0.2	0.6	20.0	20.0	123.4	123.4
Pagellus spp.	3.7	0.2	<0.1	20.4	20.4	100.4	100.4
Pagellus acarne	3.7	0.6	0.1	18.7	15.8-22.6	86.6	49.0-140.3
Pagellus bogaraveo	3.7	0.4	0.9	38.5	35.7-41.3	875.0	674.2-1,075.7
Pagellus erythrinus	7.4	1.1	0.4	22.4	14.8-26.4	139.8	41.4-205.1
Lithognathus mormyrus	3.7	0.2	<0.1	35.7	35.7	537.3	537.3
Diplodus spp.	7.4	0.6	0.3	18.9	16.6-21.9	103.6	70.8-149.8
Diplodus annularis	7.4	1.3	0.2	16.0	14.2-17.7	64.3	46.8-83.7
Boops boops	3.7	0.4	<0.1	20.7	19.8-21.5	89.6	79.4-99.9
Oblada melanura	14.8	2.8	0.5	16.6	6.0-22.0	71.3	3.6-138.0
Spondyliosoma cantharus	3.7	0.2	0.2	33.8	33.8	575.8	575.8
Centracanthidae							
Spicara spp.	7.4	0.9	0.2	18.5	17.8-19.1	76.52	65.3-82.9
Spicara flexuosa	3.7	0.4	<0.1	18.2	18.2-18.2	72.72	72.4-73.1
Spicara maena	3.7	0.8	0.2	23.5	17.9-18.7	190.7	69.8-78.3
Labridae							
Coris julis	3.7	0.2	<0.1	13.9	13.9	34.8	34.8
Scaridae							
Sparisoma cretense	3.7	0.2	0.1	22.0	22.0	158.2	158.2

Taxon	%F	%N	%W	Length (cm) Mean	Length (cm) Range	Weight (g) Mean	Weight (g) Range
Gobidae							
Gobius spp.	3.7	0.2	<0.1	15.9	15.9	55.6	55.6
Gobius bucchichi	3.7	0.2	<0.1	11.3	11.3	17.7	17.7
Atherinidae							
Atherina hepsetus	3.7	2.5	<0.1	7.4	6.8-8.2	2.9	2.2-3.9
Trichiuridae	7.4	0.38	0.2	75.0	75.0	223.4	223.4
Scleropaei							
Scorpaenidae							
Unknown Scorpaenid	3.7	0.2	<0.1	13.4	13.4	41.9	41.9
Scorpaena spp.	3.7	0.2	<0.1	27.7	27.7	345.2	345.1
Scorpaena porcus	11.1	0.9	0.2	14.7	11.3-19.1	59.8	26.1-118.2
Scorpaena scrofa	18.5	0.9	0.5	20.3	12.7-34.9	260.1	25.0-758.5
Pleuronectiformes							
Unknown flatfish	3.7	0.2	<0.1	27.2	27.2	223.6	223.6
Bothidae							
Arnoglossus spp.	3.7	0.2	<0.1	11.3	11.3	11.6	11.6
Citharidae							
Citharus linguatula	3.7	0.2	<0.1	16.3	16.3	25.4	25.4
Soleidae							
Synapturichthys kleinii	3.7	0.2	0.2	19.3	19.3	60.6	60.6
Lophiiformes							
Lophius spp.	7.4	0.8	1.8	28.7	20.9-51.00	995.6	375.3-2,610.7
Unknown fish	29.6	2.6	--	--	--	--	--
Cephalopods							
Octopoda							
Octopodidae							
Octopus vulgaris	74.1	34.0	56.0	--	--	748.3	34.5-4,525.2
Eledone spp.	18.5	7.4	3.2	--	--	195.5	20.5-669.9
Eledone cirrhosa	18.5	2.1	1.2	--	--	251.5	73.2-378.7
Eledone moschata	14.8	1.7	0.6	--	--	150.5	68.2-299.0
Sepiidae							
Sepia officinalis	33.3	2.1	4.2	14.5	8.2-31.8	913.5	29.3-6,641.3
Theuthida							
Omastrephidae	3.7	0.2	<0.1	--	--	157.7	157.7
Loliginidae							
Loligo spp.	7.4	2.6	2.5	26.2	19.9-34.0	429.3	186.3-834.9
Unknown cephalopod	3.7	0.2	--	--	--	--	--
Other Mollusca							
Bivalvia							
Veneridae	3.7	0.2	--	--	--	--	--
Unidentified clam	7.4	0.4	--	--	--	--	--
Pectinoida							
Pectinidae	3.7	0.2	--	--	--	--	--
Gasteropoda							
Archaeogastropoda							
Haliotis spp.	3.7	0.2	--	--	--	--	--
Unknown snail	11.1	0.6	--	--	--	--	--
Crustaceans							
Penaeidae							
Shrimp	3.7	0.2	--	--	--	--	--
Brachiura							
Crab	3.7	0.2	--	--	--	--	--
Others							
"Eggs"	3.7	0.2	--	--	--	--	--

while *Eledone* spp. contributed a further 11%; in total, the family Octopodidae made up 47% of the total number and 61% of the total weight of all prey items (Figure 2). Fish of the families Sparidae (28% by number) were the second most important category by number and weight in the overall diet, while the next most frequent fish categories were Scorpaenidae (3%), Congridae (2.5%), and Atherinidae (2.5%) (Table 2). Many of the prey species recorded were also of commercial fishery importance. One of the stomachs contained a piece of net, but the cause of death of this animal was classified as a non-human induced death (NHID).

Individual cephalopods in the stomachs ranged in estimated weight from as little as 20 g to over 4 kg. Although most of the cephalopod prey items were measured (94%, 250 individual prey), almost half (45%) of the cuttlefish (*Sepia* spp.) could not be measured because the beaks were damaged. Most of the cuttlefish had an estimated weight in the range of 30 to 387 g, but two individuals weighing over 2 kg each were present. The weight of the larger of these, which was the only prey item in the sample in which it was found, was initially estimated as being over 6 kg. This estimate is based on the lower beak hood length (LHL) of 1.4 cm and application of the LHL-body mass regression in Clarke (1986). However, according to the Food and Agricultural Organization (FAO), the maximum size for this species is 4 kg body weight and 45 cm mantle length (see www.fao.org/fishery/species/2711/en). The estimated mantle length for our specimen was approximately 32 cm, suggesting that Clarke's regression is not accurate for larger individuals. Applying a length-weight regression from Manfrin Piccinetti & Giovanardi (1984) for cuttlefish in the Mediterranean, an animal with 32 cm ML would weigh around 3.2 kg. Slightly over 90% (133) of the measured *Octopus* weighed less than 1 kg, while only four (2.7%) were over 2 kg. In the case of the *Eledone* species, over 96% (54) of the individuals ingested were estimated to weigh less than 500 g (Table 2; Figure 2).

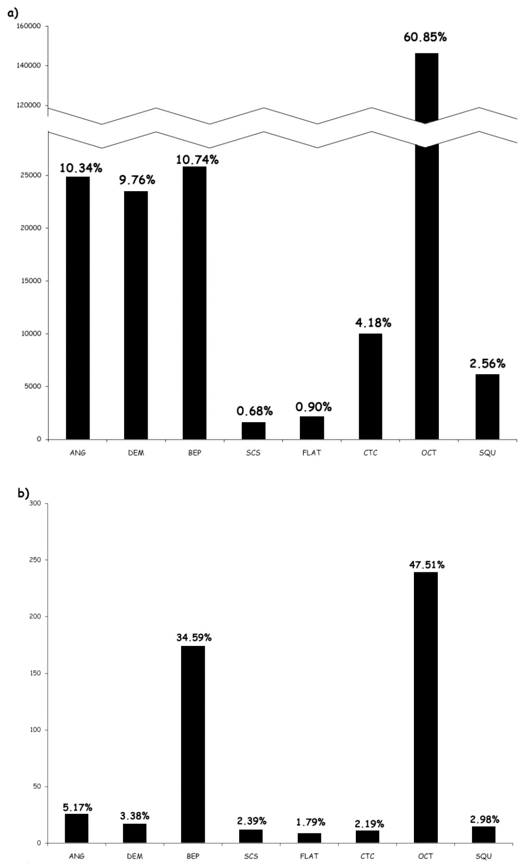

Figure 2. Monk seal diet composition (a) weight in g and (b) number of individual prey; prey are grouped by taxonomic and habitat-based categories (Grouping VI; see Table 1 for explanation of variables).

Estimated individual fish weights ranged from as little as 2 g to almost 7 kg. Weight could not be estimated for 14 (5.6%) fish prey items. Sparids were the most important fish prey group numerically (28.1% by number; 9.6% by weight) although two other groups were of similar importance in terms of biomass: anguilliform species (*Muraena* spp. and *Conger* spp.; 8.3% by weight, 3.8% by number) and sea bass (9.3% by weight, 0.6% by number).

Crabs, shrimps, and non-cephalopod molluscs were found in low amounts (totalling 2.8% of prey by number). Parasites (*Anasakis, Taenia,* and isopod ectoparasites) were found in seven (26%) stomachs. Isopods were identified as the only parasite in three of the samples. *Anasakis* and *Taenia* occurred in young animals in the southern Aegean Sea. One stomach was found to be full of these parasites and did not contain food items.

Patterns in Diet Composition

Results from the RDA are summarised in Table 3 for each of the different classifications of the dietary data (see Table 1). It is important to note that the statistical results from RDA indicate which explanatory variables have statistically significant effects on diet composition but do not specify the nature of the effect. Visual examination of bi-plots allows inferences to be made about the nature of the effect, but these inferences require further testing. When analysis was based on the main taxonomic groupings of prey (fish, cephalopods, other), the strongest trend was a negative association between feeding on fish and NHID. There were also significant effects of area, year, and season. In the second analysis, in which prey were classified by broad habitat (demersal and non-demersal) category, results indicated

Table 3. Numerical output of the RDA for different groupings of prey data (see Table 1 for descriptions); analysis is based on prey numbers (PN) or prey presence/absence (PP) as indicated. The table lists eigenvalues for the first and second axes (λ_1, λ_2), the sum of all canonical eigenvalues (Sum), and results of F tests (F and associated probability P) for the significance of effects of individual explanatory variables (only explanatory variables with significant effects are shown).

Response variables	λ_1	λ_2	Sum	Explanatory variables	F	P
Grouping I (Main prey taxa) (PN)	27.16	21.43	0.54	NHID	5.017	0.007
				N	3.438	0.021
				Y2	3.265	0.028
				W1	2.786	0.050
Grouping II (DEM/NDEM) (PN)	32.13	21.61	0.54	DK	3.366	0.032
				Y2	3.332	0.033
Grouping III (Detailed habitat) (PP)	25.18	11.66	0.56	NHID	3.421	0.009
				W1	2.801	0.023
Grouping IV (Benthopelagic prey) (PN)	18.24	12.99	0.50	DK	2.484	0.005
Grouping V (Benthopelagic prey: sparids/non-sparids) (PN)	43.11	6.09	0.49	DK	5.797	0.001
Group VI (Taxonomy and habitat) (PN)	16.19	11.90	0.51	Y3	1.925	0.044

that feeding on non-demersal species was weakly positively associated with monk seals that had been deliberately killed and that an effect of year was also apparent (Figure 3a). The third analysis, using a more detailed habitat classification, highlighted a negative relationship between NHIDs and three habitat categories (non-demersal prey, rocky areas, and sandy/muddy areas with seagrass) as well as indicating seasonal variation in diet (Figure 3b). The next analysis was based on the subset of benthopelagic prey and indicated an association between feeding on sparids and death by deliberate killing. This pattern was confirmed in an analysis in which benthopelagic prey were simply divided into sparids and non-sparids. The last analysis, based on mixed taxonomic and habitat groupings, revealed only a year effect. Therefore, overall, RDA results indicate a statistically significant relationship between diet composition and cause of death, and visual examination of bi-plots suggested an association between deliberate killing and feeding on non-demersal (sparid) fish species. In all cases, statistical significance was relatively weak as might be expected given the small sample size. No variation in diet in relation to age or sex was detected.

GLM analysis, in which presence of sparids in the diet was used as a response variable, confirmed a positive association between feeding on sparids and with death by deliberate killing ($p = 0.028$). No other explanatory variables had a significant effect.

Discussion

As previously reported for Mediterranean monk seals (Salman et al., 2001), cephalopods, especially octopuses (*O. vulgaris* and *Eledone* spp.), comprised a substantial part of the diet. Nevertheless, the high number of different prey categories recorded (at least 75 taxa) suggests a generalist, perhaps opportunistic, predator that exploits the most readily available prey. It should be noted that the term *opportunistic predator* is used rather indiscriminately in the literature. Although it implies a lack of selectivity in predation, the only evidence usually available is that the diet is varied. There are few previously published studies about the diet of monk seals in other areas. Studies on the Hawaiian monk seal (*Monachus schauinslandi*) suggest that it is also a generalist predator, although fish appear to be the most important component of its diet (Goodman-Lowe, 1998). Longnecker (2010) reported anguilliform fish species of the families Congridae and Muraenidae to be the most numerous prey of Hawaiian monk seals.

Investigations of food evacuation times in phocids have been carried out since the 1980s; several studies (Staniland, 2002) suggest that cephalopod beaks may be retained in the gut (reflecting low digestibility and their tendency to become lodged in the stomach lining), perhaps resulting in overestimation of the importance of cephalopods relative to fish. However, in the present study, several large individual cephalopods, almost intact, were found in stomach contents, suggesting that the apparent dominance of cephalopods in the stomach contents is a true reflection of diet. It remains possible that some prey groups were underrepresented. The Marine Mammal Commission (MMC) (2001) reported that young Hawaiian monk seals may consume a substantial amount of lobsters, a conclusion based on fatty acid signature analysis of monk seal blubber rather than traditional faecal or stomach contents analysis. The relatively high frequency of fresh prey remains in stomachs of the present study suggests that if large crustaceans

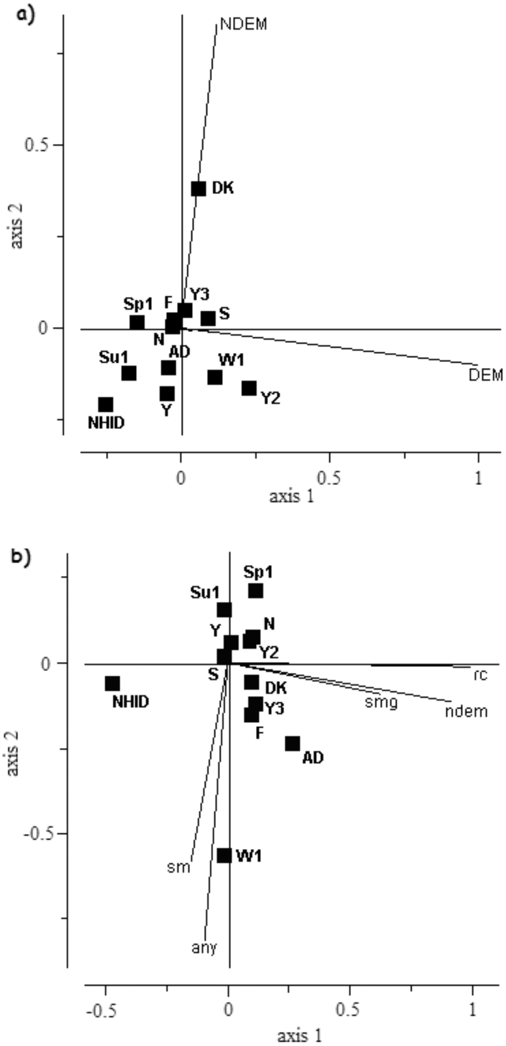

Figure 3. RDA biplots for diet; prey species grouped according to their main habitat: (a) prey numbers for demersal (DEM) and non-demersal species (NDEM) (Grouping II), and (b) prey presence/absence by detailed habitat type (Grouping III). Response variables are represented by thin lines; explanatory variables are represented by squares. See Table 1 for list of abbreviations.

such as lobsters had been eaten by Mediterranean monk seals, evidence would have been found in the stomach contents. Nevertheless, fatty acid studies would be useful to provide confirmation and could also help clarify the relative importance of fish and cephalopods. Since cephalopod flesh digests faster than fish flesh while cephalopod beaks persist longer in stomach contents than do otoliths, results on relative importance could be biased in either direction (Santos et al., 2001).

A large number of small fish was found in two adult monk seals suggesting that they may have been feeding on shoaling fish. The otoliths and bones were from fish of the family Sparidae but were too eroded to identify to species. Although important sparid fisheries occur in the area, we do not know whether monk seals were taking sparids from the vicinity of fishing nets. Many of the prey species of Mediterranean monk seals that were identified in the present study are also of commercial fishery interest in Greece. Indeed, many of the fish prey were identified using a reference collection based on fish bought at the Athens fish market.

Given the presence of large individual fish and cephalopods in stomach contents, there is little doubt that size classes exploited by fishermen and monk seals will overlap, so the scope for competition is clear. We also cannot rule out interactions with aquaculture. Some species of marine mammals are attracted to the vicinity of aquaculture cages by the concentration of wild fish in the vicinity (Díaz López et al., 2005).

The fact that a third of the present sample arises from deliberate killing suggests that some fishermen perceive monk seals as a competitor and/or a nuisance due to damage to gear and consumption of fish (e.g., Yediler & Gücü, 1997). Indeed, deliberate killing by fishermen (and by fish farmers) is known to be a significant source of mortality in Mediterranean monk seals (Anonymous, 1999; Tudela, 2004). A study in Turkey found that monk seals could cause considerable damage to fishing gear, although the overall annual economic impact on the artisanal fishery was modest (Güçlüsoy, 2008a). Salman et al. (2001) recorded a piece of gill net in one of two stomachs they examined from monk seals in Turkish waters, while Cebrian et al. (1990) noted that Mediterranean monk seals regularly collect food from fishing gear and often damage nets. We found a piece of net in one of the monk seal stomachs, although the cause of death in this case was diagnosed as NHID.

Despite the small sample size, using RDA, dietary variation was seen to be significantly related to cause of death, area, year, and season. The statistical significance of area, year, and season effects was low, and none of these effects was significant in the subsequent GLM analysis. A larger sample size would be needed to quantify these effects further. The most consistently apparent trend was a relationship between cause of death and diet. This highlights a potential source of bias in the samples (i.e., that the overall picture of diet composition depends on the source of samples) but also has conservation implications. In the UK, studies on the diet of grey (*Halichoerus grypus*) and harbour (*Phoca vitulina*) seals during the 1950s and 1960s (Rae, 1960, 1965, 1968, 1973) were widely criticised for relying on data from seals shot by fishermen (in this case, legally) because the seals had entered coastal salmon nets on the east coast of Scotland. The results suggested a high importance of salmon (*Salmo salar*) in seal diets, something not shown in subsequent studies (e.g., Prime & Hammond, 1990; Pierce et al., 1991). In the UK, predation by seals on salmon is nowadays generally regarded as a localised phenomenon, which may nevertheless have a substantial impact in affected areas (see Carter et al., 2001). However, deliberate (illegal) killing of monk seals was recorded throughout the study area in the present study. Thus, the behaviour of monk seals which led to these fatal interactions with humans is probably relatively widespread, and the results on feeding habits arising from these animals may therefore be considered as representative.

The significant positive association between death by deliberate killing and feeding on sparids may indicate that, where monk seals are feeding on sparids, they have a higher likelihood of coming into contact with, and being perceived to interfere with, fishing activities. However, this requires further investigation as the association, although statistically significant, is based on a small sample size. It is very likely that this association has its root in interactions between monk seals and fishing activities, the importance of which is further emphasised by the fact that five animals in the present study were accidentally caught in fishing gear. Entanglement in fishing gear is an important cause of mortality in Mediterranean monk seals and also results in significant financial losses to fishermen (Johnson & Karamanlidis, 2000; Karamanlidis et al., 2011). Glain et al. (2001) found that 61.5% of fishermen interviewed in Greece consider monk seals to have an adverse effect on their activities.

Given the extreme rarity of the study species and the consequent low likelihood (or desirability) of obtaining a substantially larger sample of stomach contents, attention should be given to alternative means of obtaining dietary data, including faecal analysis and fatty acid analysis of tissue samples. Diet studies on monk seals are often based on analysis of scats collected at haulout sites; however, monk seals on the Mediterranean coast mainly rest in tidal caves that are difficult to access. Given the absence of identifiable hard remains of prey in the 14 faecal samples collected during the present study, an alternative method of prey identification is needed—for example, by identifying the prey DNA (see Reed et al., 1997). Fatty acid analysis of inner blubber from carcasses or biopsies could provide a second useful source of additional dietary data, although a complete library of prey fatty aid signatures would be required to facilitate quantitative interpretation, and this is a major undertaking for a predator with such a varied diet. In addition, obtaining biopsies from a species which hauls out in remote caves and beaches will be logistically difficult and would cause further disturbance to these endangered animals.

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Appendix 1. Regression equations used to estimate fish and cephalopod sizes: TL = total length for fish and dorsal mantel length for cephalopods; W = total weight; OL = otolith length (mm); OW = otolith width; DL = dorsal (dentary) length (from symphysis to the tip of the dorsal limb of the dentary); VL = ventral length (from symphysis to the tip of the ventral limb of the dentary); OF = outer fork length (from symphysis to the outer fork of the dentary); PMXL = total length of the premaxilla; LHL = lower hood length; LRL = lower rostral length. Sources are as follows: Br = Brown & Pierce (1998); Ca = Campillo (1992); Ci = Cicek et al. (2006); Cl = Clarke (1986); Do = D'Onghia et al. (2000); Du = Dulčić & Glamuzina (2006); Fe = Ferreira et al. (2008); Fi = Filiz & Mater (2002); GH = Gema Hernandez-Milian (unpub. data); Ko = Koutrakis & Tsikliras (2003); Kr = Kraljević et al. (2003); Mo = Moutopoulos & Stergiou (2002); Pe = Pereda & Villamor (1991); Pw = Present work; Sa = Santos et al. (2007); So = Sobrino & Gil (2001); Sta = Stergiou & Politou (1995); Stb = Stergiou & Moutopoulos (2001); Tc = Türker-Çakir et al. (2005).

Fish species	Estimated prey length (mm)	Source	Estimated prey weight (g)	Source
Batoids	See Notes 1 & 2		W = 0.0016*TL^3.2914	Fi
Dogfish (*Scyliorhinus* spp.)	See Note 1		W = 0.0016*TL^3.1804	Fi
Eel (*Anguilla anguilla*)	See Note 1		W = 0.0003*TL^3.470	Ko
Conger (*Conger conger*)	See Notes 1 & 2		W = 0.00054*TL^3.225	Stb
Moray eel (*Muraena helena*)	See Note 2		W = 0.00048*TL^3.32	Fe
Hake (*Merluccius merluccius*)	TL = 7.2823+9.7814*DL	GH	W = 0.00516*TL^3.111	Stb
Greater forkbeard (*Phycis blennoides*)	TL = 1.555*OL^1.285	Pe	W = 0.0156*TL^2.843	Me
	TL = 2.7274+2.7897*PMXHH	Pw	--	--
Forkbeard (*Phycis phycis*)	See Note 3	Pe	--	Me
Gadoid	TL = -54.35+76.582*OW	Sa	W = 0.016042*TL^2.8752	Sa
Sea bass (*Dicentrarchus labrax*)	TL = 0.62+0.102*OF	Pw	W = 0.0079*TL^3.065	Du
Serranus spp.	See Note 3	--	--	--
Brown comber (*Serranus hepatus*)	TL = -0.43543+0.91961*VL	Pw	W = 0.0091*TL^3.24	Du
Scad (*Trachurus* spp.)	TL = -27.02+34.939*OL	Br	W = 0.00339*TL^3.273	Stb
Mullet (*Mullus* spp.)	See Note 1	--	W = 0.01772*TL^2.832	Mo
Sparidae	See Note 4	--	--	--
Red porgy (*Pagrus pagrus*)	See Note 5	--	W = 0.152*TL^3.005	Mo
Seabream (*Pagellus* spp.)	See Note 6	--	--	--
Axillary seabream (*Pagellus acarne*)	TL = -1.44342+2.26977*OL	Pw	W = 0.01501*TL^2.933	Mo
Blackspot seabream (*Pagellus bogaraveo*)	TL = 24.25+1.12*OL	So	W = 0.007*TL^3.209	Ca
Common pandorac (*Pagellus erythrinus*)	TL = -2.3896+2.5229*OL	Pw	W = 0.0231*TL^2.778	Mo
	TL = 1.6436+1.8606*OF	Pw	--	--
Sand steenbras (*Lithognathus mormyrus*)	See Note 5	--	W = 0.0094*TL^3.063	Kr
Diplodus spp.	See Note 7	--	--	--
Annual seabream (*Diplodus annularis*)	See Note 1	--	W = 0.0365*TL^2.695	Mo
Bogue (*Boops boops*)	See Note 5	--	W = 0.01467*TL^2.877	Mo
Saddle seabream (*Oblada melanura*)	TL = -0.7102+1.618*VL	Pw	W = 0.02185*TL^2.831	Mo
Black seabream (*Spondyliosoma cantharus*)	See Note 5		W = 0.01772*TL^2.951	Mo
Spicara spp.	TL = 10.6544+1.1366*OL	Pw	See Note 3	Mo
	TL = 6.89+1.7815*OF	--	--	--
Spicara flexuosa	See Note 3	--	See Note 3	--
Spicara maena	TL = 6.436+1.858*OF	Pw	W = 0.0356*TL^2.627	Mo
Rainbow wrasse (*Coris julis*)	See Note 5	--	W = 0.0047756*TL^3.38	Mo
Parrotfish (*Sparisoma cretense*)	See Note 2	--	W = 0.00568*TL^3.311	Mo
Gobius bucchichi	TL = -0.4332+3.5852*OL (see Note 8)	Pw	W = 0.03045*TL^2.89	Sta
Sand smelt (*Atherina hepsetus*)	TL = 0.67948+1.1319*PMXL	Pw	W = 0.0074*TL^2.972	Ko
Trichiuridae	See Note 9	--	W = 0.0004*TL^3.065	Do
Scorpaenidae/*Scorpaena* spp.	TL = -0.44858+0.75472*DL	Pw	W = 0.02356*TL^2.887	Mo

Fish species	Estimated prey length (mm)	Source	Estimated prey weight (g)	Source
Black scorpionfish (*Scorpaena porcus*)	TL = -5.1919+2.9983*OL	Pw	W = 0.02356*TL^2.887	Mo
	TL = -3.74449+0.88154*DL	Pw	--	--
Red scorpionfish (*Scorpaena scrofa*)	TL = -2.876+2.616*OL	Pw	W = 0.1692*TL^2.999	Mo
	TL = 1.15437+0.69321*DL	Pw	--	--
Pleuronectiform	TL = -25.95*53.274*OL	Sa	W = 0.009923*TL^3.036	Sa
Scaldfish (*Arnoglossus* spp.)	See Note 5	--	W = 0.008*TL^3.007	Ci
Spotted flounder (*Citharus linguatula*)	See Note 1	--	W = 0.003*TL^3.2405	Tc
Klein's sole (*Synapturichthys kleinii*)	See Note 5	--	W = 0.0075*TL^3.04	Ko
Monkfish (*Lophius* spp.)	See Note 1	--	W = 0.03045*TL^2.89	Sta
Cephalopod species	**Estimated prey length (mm)**	**Source**	**Estimated prey weight (g)**	**Source**
Octopus (*Octopus vulgaris*)	--	--	W = 6.17186*LR^3.03	Cl
Octopus (*Eledone* spp.)	TL = 3.38+26.57*LRL	Cl	W = 5.365*LRL^2.85	Cl
Cuttlefish (*Sepia officinalis*)	TL = -2.14+21.89*LHL	Sa	W = 0.123687*LR^4.06	Sa
Squid (*Loligo* spp.)	TL = -42.22+84.274*LRL	Sa	W = 6.19536*LRL^3.242	Sa

Notes:

(1) No regression was available for this species, and length was estimated in comparison with reference material.
(2) Intact animals were found and measured.
(3) No regression was available for this species/genus, and we used the regressions for *Spicara maena*.
(4) The unidentified sparid bones were similar to those from *Oblada melanura*, and a regression from this species was used.
(5) Length was estimated by comparison with Tuset et al. (2008).
(6) We used the regression for *P. erythrinus*, the most common *Pagellus* sp. in the area.
(7) We used the regression for *D. annularis*, the most common *Diplodus* sp. in the area.
(8) No regression was available for this species, and we used the regression for *G. niger*.
(9) The only relevant regression available was for *Lepidopus caudatus* (one the most common species of this group occurring in the area). This was a TL-W regression, and length (TL) was assumed to be half of the maximum length obtained by Du (75 cm).