Eur J Wildl Res (2009) 55:301–308
DOI 10.1007/s10344-008-0243-2

ORIGINAL PAPER

Sexual differences in the diet of great cormorants *Phalacrocorax carbo sinensis* wintering in Greece

Vasilios Liordos · Vassilis Goutner

Received: 27 January 2008 / Revised: 30 November 2008 / Accepted: 17 December 2008 / Published online: 14 January 2009

Abstract Sexual differences in the diet of the great cormorant, *Phalacrocorax carbo sinensis*, were studied in four Greek wintering areas, the Amvrakikos Gulf, the Axios and Evros Deltas and the Messolonghi Lagoon, through the analysis of stomach contents. Great cormorants are birds sexually dimorphic in size, with males being generally larger than females. Although similar prey species were found in the stomachs of both sexes in all the studied areas, significant differences were observed with respect to the proportion of species taken. Male birds ate higher proportions of large fish species such as grey mullets, European sea bass, *Dicentrarchus labrax*, and Prussian carp, *Carassius gibelio*, while female birds took higher proportions of smaller species such as big-scale sand smelt, *Atherina boyeri*, and black goby, *Gobius niger*. As a consequence, male great cormorants were found to feed on significantly larger prey than did females by means of fish standard length and body mass. There was no significant difference between the sexes in the mass of food found in stomachs.

Keywords Piscivorous predator · Winter diet · Prey selection by sex

Introduction

The great cormorant, *Phalacrocorax carbo*, is a large-sized fish-eating waterbird with an almost cosmopolitan distribution (Orta 1992). The subspecies *P. c. sinensis* is found in continental Europe and Asia, and its European population, although stabilising recently, has been increasing since the 1970s (Debout et al. 1995; Van Eerden and Gregersen 1995; Marion 2003). This increase has been attributed to the legal protection and increase in fish productivity due to eutrophication of aquatic habitats (Russell et al. 1996). As a consequence, severe conflicts with angling and fisheries interests have been raised in many European countries (Russell et al. 1996; Cowx 2003). Therefore, much research on great cormorant's diet, energetics, impact on fish populations and management has been conducted, especially during the last 10 years (e.g. Keller 1995; Kirby et al. 1996; Grémillet et al. 2003; Lorentsen et al. 2004; Stewart et al. 2005).

The great cormorant numbers have also been increasing in Greece since the 1970s. The breeding population of 550 pairs counted in 1971 (Handrinos and Akriotis 1997) increased to an all-time high, 5,360 pairs in 2002 (Liordos 2004). In addition, over 20,000 birds wintered in Greece in recent years (V. Liordos, unpublished data). The bird's fish-eating habits along with its population explosion also prompted an urgent need for studies on great cormorant's diet and its impact on fish populations and fisheries in Greece. Six studies on the diet of the great cormorant have been carried out in Greece (Goutner et al. 1997; Liordos et al. 2002; Dimitriou et al. 2003; Kazantzidis and Naziridis 2003; Liordos and Goutner 2007a, b). These studies described and compared the diet composition of the great cormorant at several Greek colonies and wintering areas, but they did not investigate the effect of sex on the diet. Great cormorants are sexually dimorphic, with males generally being larger and heavier than females (Cramp and Simmons 1977; Koffijberg and Van Eerden 1995; Liordos and Goutner 2008). The aim of this paper was

Communicated by E. Hadjisterkotis

V. Liordos (✉) · V. Goutner
Department of Zoology, School of Biology,
Aristotle University of Thessaloniki,
GR-54124 Thessaloniki, Greece
e-mail: liordos@yahoo.com

therefore to examine the patterns of prey selection of the great cormorant in relation to sex in four major wintering areas of Greece by analysing stomach content data from Liordos et al. (2002) and Liordos and Goutner (2007a).

Materials and methods

The study was conducted in four major Greek wintering areas, the Amvrakikos Gulf, the Axios and Evros Deltas and the Messolonghi Lagoon (Fig. 1), all of them designated as wetlands of international importance under the Ramsar Convention. The Amvrakikos Gulf (38°59′–39° 11′ N, 20°44′–21°07′ E) covers a total of 405 km^2, 220 of which belong to a variety of wetland habitats (e.g. open and closed lagoons, salt marshes, salt flats, reed swamps) and the rest to open water. The great cormorants roost mainly on the Gaidaros islet, a rocky outcrop of about 1 ha in size located close to the gulf's mouth (Aktion Strait). The Axios Delta (40°27′–40°38′ N, 22°33′–22°52′ E) belongs to a large wetland complex covering a total of 68.7 km^2 situated near the city of Thessaloniki. The great cormorants roosted at sea over water on mussel aquaculture infrastructure. The Evros Delta at the Greek–Turkish border (40°44′–40°51′ N, 25°53′–26°8′ E) is an extensive area (190 km^2) diverse in habitats. The great cormorants roosted on a poplar *Populus* sp. stand on the west bank of the river's east branch. The Messolonghi Lagoon (37°40′–39°40′ N, 20°10′–21°30′ E) belongs to the largest Greek wetland complex and is one of the largest in the Mediterranean basin situated in southwest Greece, totalling 258 km^2. Two winter roosts were used in the area: one at Makropoula, a rocky outcrop, and another at the River Acheloos, on tamarisks *Tamarix* sp.

Under licence by the Ministry of Agricultural Development and Food, 22 birds were collected in collaboration with hunters at the Amvrakikos Gulf (February 2002), 13 in the Axios Delta (October 2001), 28 in the Evros Delta (December 1999) and 16 at the Messolonghi Lagoon (February 2002). Spatial variation in diet has previously been found to be significant (Liordos and Goutner 2007a), and data therefore could not be pooled together.

Marquiss and Carss (1997) analysed stomach contents by recording only intact items and by also including items identified by key bones and found that large fish were recorded with similar frequency by both methods, but smaller fish were more likely to be recorded from key

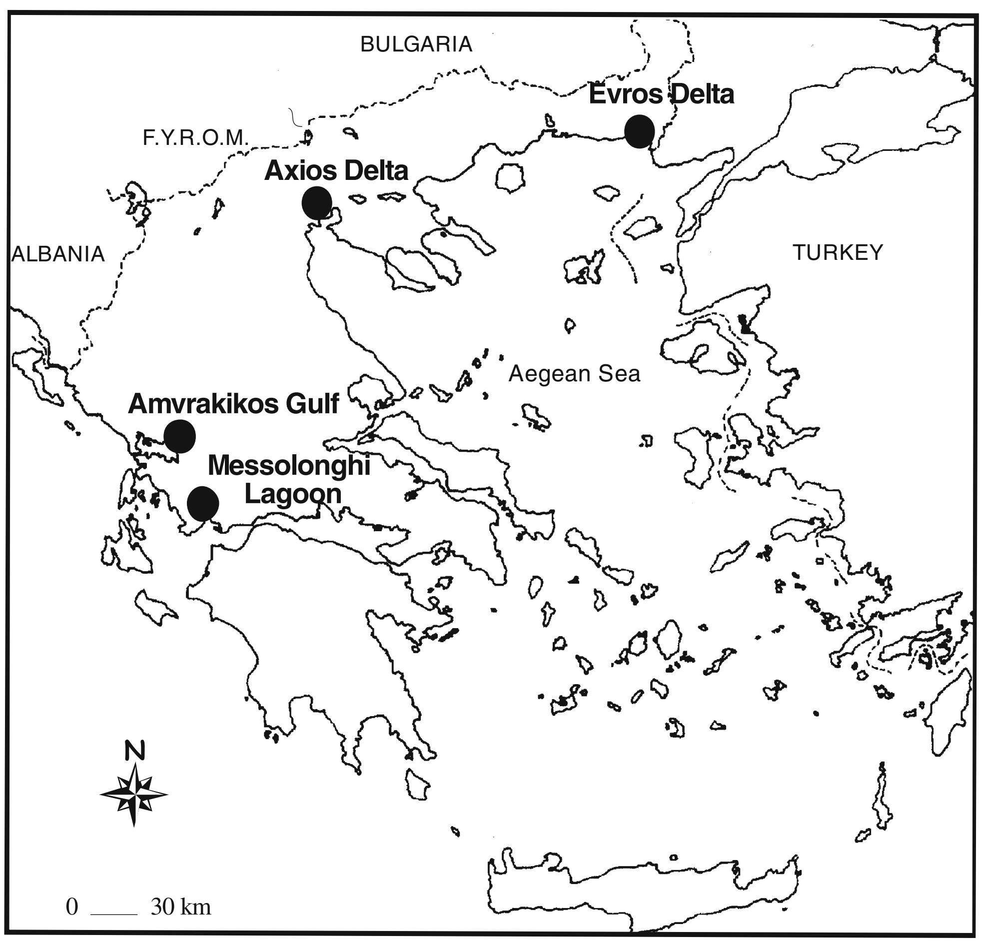


Fig. 1 The study areas in Greece

bones than intact. Therefore, in order to derive as much information as possible from the samples, whole fish were first identified and measured, and then hard key bones, mainly otoliths and chewing pads, were extracted and appropriately identified and measured according to Carss et al. (1997). Fish length and body mass were subsequently calculated using regression equations found in literature or constructed by the authors (see Liordos and Goutner 2007a and references therein). For a more detailed description of the methods of bird collection, storage, dissection and prey identification and measurement, please refer to Liordos et al. (2002) and Liordos and Goutner (2007a). The sex of each bird was identified by gonadal inspection.

Prey types found in the stomachs of male and female great cormorants were quantified by (1) relative abundance by numbers (*N*%), as the percentage of each prey type out of all prey types found in the sample, (2) relative abundance by biomass (*B*%), as the percentage of the biomass of each prey type out of the estimated total biomass of the sample and (3) frequency of occurrence (*F*%), which is the percentage of samples that contained each prey type (Duffy and Jackson 1986). The above parameters were used to provide an index of relative importance (IRI) and IRI% for each prey type (*i*; Pinkas et al. 1971; Sanger 1987; Martin et al. 1996; Mariano-Jelicich et al. 2007) as:

$$\mathrm{IRI}_i = F_i\% \times (N_i\% + B_i\%),\ \text{and}$$

$$\mathrm{IRI}_i\% = (\mathrm{IRI}_i \times 100)/\mathrm{IRI}_{total}.$$

Variation in diet composition between the sexes was assessed by comparing numbers (*N*) of fish prey taken by each sex with *G* tests (Zar 1999). IRI% was then used to identify the most important prey (Hart et al. 2002). Number of fish per stomach, total estimated fish biomass per stomach and fish standard length (SL) and body mass (BM) for each sex class were estimated and compared by sex using Mann–Whitney (M–W) *U* tests (Zar 1999). Median and range are presented for each variable.

Table 1 Common and scientific names of the fish species found in the diet of male and female great cormorants wintering in Greece during 1999–2002

Common names	Scientific names
Atherinidae	
Big-scale sand smelt	*Atherina boyeri*
Blenniidae	
Peacock blenny	*Salaria pavo*
Carangidae	
Horse mackerel	*Trachurus* spp.
Clupeidae	
Twaite shad	*Alosa fallax*
European pilchard	*Sardina pilchardus*
Round sardinella	*Sardinella aurita*
Cyprinidae	
Bleak	*Alburnus alburnus*
Prussian carp	*Carassius gibelio*
Common carp	*Cyprinus carpio carpio*
Roach	*Rutilus rutilus*
Engraulidae	
European anchovy	*Engraulis encrasicolus*
Gobiids	Gobiidae
Black goby	*Gobius niger*
Moronidae	
European sea bass	*Dicentrarchus labrax*
Grey mullets	Mugilidae
Thicklip grey mullet	*Chelon labrosus*
Golden grey mullet	*Liza aurata*
Thinlip mullet	*Liza ramado*
Leaping grey mullet	*Liza saliens*
Flathead mullet	*Mugil cephalus*
Mullidae	
Red mullet	*Mullus barbatus barbatus*
Sparidae	
Gilthead sea bream	*Sparus aurata*
Syngnathidae	
Pipefish	*Syngnathus* spp.
Zeidae	
John dory	*Zeus faber*

Common and scientific names are taken from FishBase online (www.fishbase.org)

Results

The common and scientific names of the fish taxa found in the stomachs of male and female great cormorants from all the areas studied are given in Table 1. Twenty-four fish taxa belonging to 13 families (see Tables 1 and 2) were identified.

Differences between the sexes in numerical diet composition were significant at the Amvrakikos Gulf (G=35, df=8, p<0.001; Table 2). European sea bass, *Dicentrarchus labrax*, and grey mullets were the most important prey for males, with IRI% 29.3% and 28.3%, respectively. Big-scale sand smelt, *Atherina boyeri*, was the most important prey for females, accounting for the 52.7% of the diet, followed by gobiids (18.1%). The median number of fish found in the stomachs did not vary significantly between the sexes (males: median 3 fish, range 1–10 fish; females: 3.5 fish, 1–86 fish; M–W Z=−0.52, df=6,16, p=0.606). Differences on fish prey biomass per stomach were also not significant (males: median 234 g, range 49–431 g; females: 196 g, 4–385 g; M–W Z=0.59, df=6,16, p=0.555). In contrast, between-sexes differences in the sizes of fish prey consumed were observed (Fig. 2a, e). Male great cormorants tended to feed on significantly longer (median SL 105.0 mm, range 54.0–277.2 mm) and heavier (median BM 18.1 g, range 0.9–

Table 2 Differences in the diet of male and female great cormorants wintering in four major Greek wetlands

Fish taxa	Male				Female			
	N%	*B*%	*F*%	IRI%	*N*%	*B*%	*F*%	IRI%
Amvrakikos Gulf[a]								
Grey mullets	8.3	40.1	33.3	28.3	0.9	15.1	12.5	4.8
Thicklip grey mullet	–	–	–	–	3.8	22.1	18.8	11.5
Thinlip mullet	8.3	14.0	16.7	6.5	3.3	12.7	18.8	7.2
Leaping grey mullet	–	–	–	–	1.4	8.7	6.3	1.5
Flathead mullet	8.4	21.5	16.7	8.7	–	–	–	–
Big-scale sand smelt	37.5	1.3	16.7	11.3	75.6	12.6	25.0	52.7
European sea bass	16.7	16.7	50.0	29.3	1.4	9.4	6.3	1.6
Gobiids	20.8	6.4	33.3	15.9	9.4	14.8	31.3	18.1
European pilchard	–	–	–	–	4.2	4.6	12.5	2.6
Total fish	*n*=24	1,482 g			*n*=213	3,368 g		
Axios Delta[b]								
Grey mullets	15.2	24.7	25.0	19.6	14.7	30.1	60.0	46.4
Golden grey mullet	39.1	16.2	37.5	40.7	–	–	–	–
Black goby	–	–	–	–	61.9	21.6	20.0	28.9
Round sardinella	26.1	31.1	25.0	28.1	2.9	7.9	20.0	3.7
Twaite shad	2.2	0.3	12.5	0.6	8.8	29.8	20.0	13.3
Red mullet	4.3	9.7	12.5	3.4	–	–	–	–
Big-scale sand smelt	8.7	0.7	12.5	2.3	–	–	–	–
John dory	2.2	2.7	12.5	1.2	–	–	–	–
Horse mackerel	2.2	14.6	12.5	4.1	–	–	–	–
Peacock blenny	–	–	–	–	2.9	1.0	20.0	1.3
Pipefish	–	–	–	–	8.8	9.6	20.0	6.4
Total fish	*n*=46	2,184 g			*n*=34	961 g		
Evros Delta[c]								
Prussian carp	60.0	64.5	80.0	88.8	51.1	68.2	80.0	84.7
Grey mullets	10.8	23.9	26.7	8.3	3.3	8.9	15.4	1.7
Big-scale sand smelt	8.6	0.9	6.7	0.5	35.8	7.2	30.0	11.4
European pilchard	12.5	5.8	6.7	1.1	–	–	–	–
Roach	5.3	3.2	13.3	1.0	3.3	3.9	15.4	1.0
Bleak	1.4	0.5	6.7	0.1	–	–	–	–
Round sardinella	1.4	1.2	6.7	0.2	–	–	–	–
European anchovy	–	–	–	–	4.9	3.9	7.7	0.6
Common carp	–	–	–	–	1.6	7.9	7.7	0.6
Total fish	*n*=69	3,893 g			*n*=61	2,459 g		
Messolonghi Lagoon[d]								
Grey mullets	64.2	60.7	80.0	82.7	36.3	78.9	72.7	80.4
Big-scale sand smelt	17.9	0.4	20.0	3.0	58.3	3.4	27.2	16.1
European sea bass	3.6	8.6	20.0	2.0	1.8	7.7	18.2	1.7
Horse mackerel	10.7	19.2	40.0	9.9	1.8	5.0	18.2	1.2
Gilthead sea bream	3.6	11.1	20.0	2.4	–	–	–	–
Gobiids	–	–	–	–	1.8	5.0	9.1	0.6
Total fish	*n*=28	1,582 g			*n*=113	3,370 g		

Data are presented by percent relative abundance by numbers (*N*%), biomass (*B*%), frequency of occurrence (*F*%) and index of relative importance (IRI%). Total fish numbers (*n*) and biomass (g) per sex and number of birds are also given

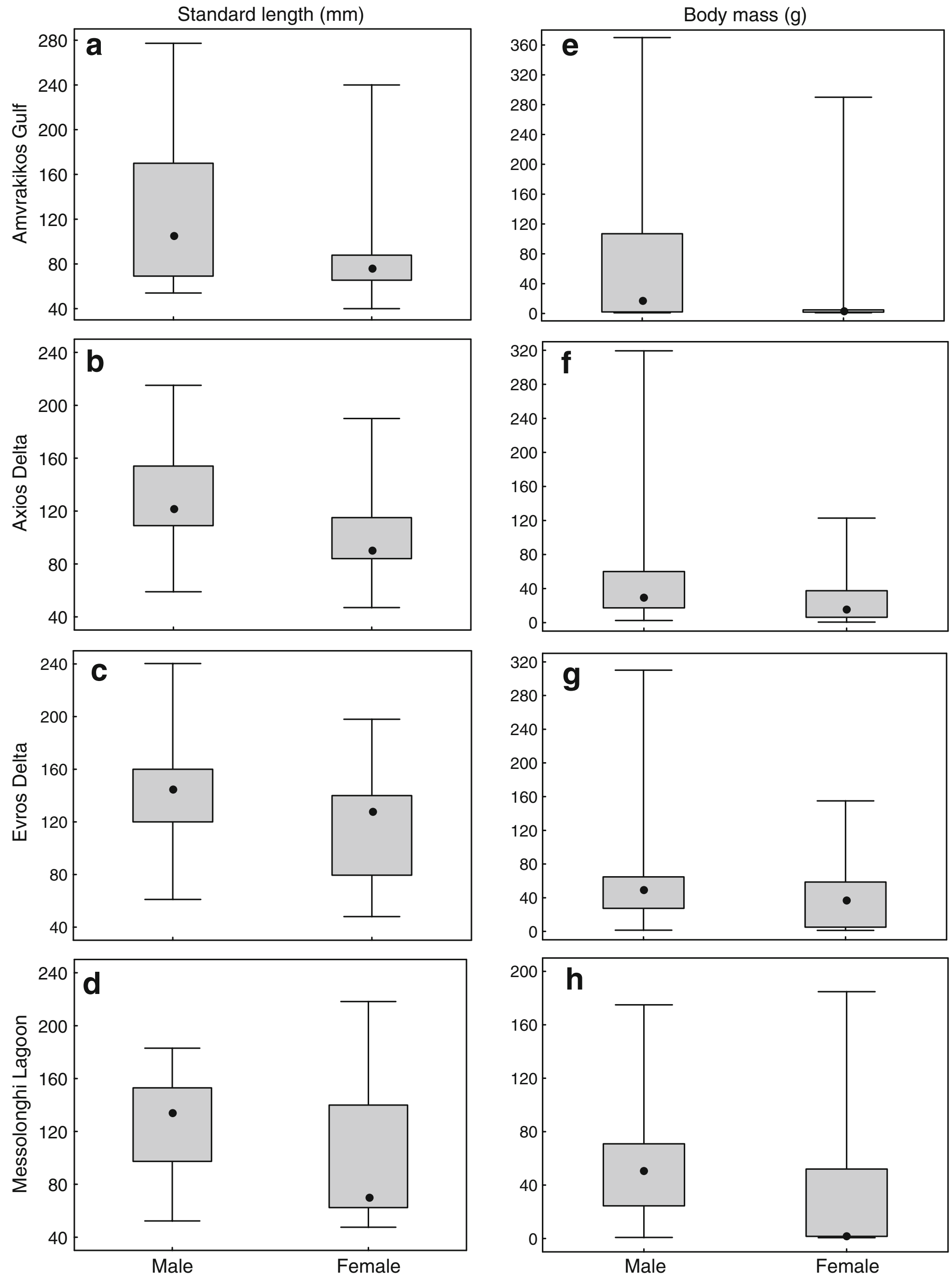
[a] Six males, 16 females

[b] Eight males, five females

[c] Fifteen males, 13 females

[d] Five males, 11 females

Fig. 2 Comparison of standard length (**a**–**d**) and body mass (**e**–**h**) of fish prey in the diet of male and female great cormorants wintering at the Amvrakikos Gulf (**a**, **e**), Axios Delta (**b**, **f**), Evros Delta (**c**, **g**) and Messolonghi Lagoon (**d**, **h**). Indicated are the median (*dot*), 25–75% quartiles (*boxes*) and range (*whiskers*). See Table 2 for sample sizes



370.0 g) fish than female ones (median SL 75.9 mm, range 40.0–240.0 mm, M–W Z=2.52, df=24,213, p=0.012; median BM 3.0 g, range 1.0–290 g, M–W Z=2.60, df=24,213, p=0.009).

The composition of the diet by numbers also presented a significant sexual variation in the Axios Delta (G=81, df=10, p<0.001; Table 2). Golden grey mullet, *Liza aurata* (IRI% 40.7%) and round sardinella, *Sardinella aurita* (28.1%), were the most important fish taken by the males. Grey mullets were the most important prey regarding the females (46.4%), followed by black goby, *Gobius niger* (28.9%). The median number of fish per stomach did not vary significantly between males (median 5 fish, range 3–13 fish) and females (median 2 fish, range 1–25 fish; M–W Z=1.32, df=8,5, p=0.183). The median fish prey biomass per stomach was 251 g (range 71–589 g) for males and 123 g (range 81–362 g) for females (M–W Z=0.88, df=8,5, p=0.380). Fish of different sizes were selected by the sexes (Fig. 2b, f). Male birds consumed significantly larger prey (median SL 122.0 mm, range 59–215.1 mm; median BM 30.5 g, range 2.5–319.4 g) than female ones (median SL 90.7 mm, range 47.0–190.0 mm, M–W Z=3.68, df=46,34, p=0.0002; median BM 16.5 g, range 0.7–122.8 g, M–W Z=2.30, df=46,34, p=0.021).

Significant sexual differences in diet composition by numbers were also detected in the Evros Delta (G=35, df=8, p<0.001; Table 2). Prussian carp, *Carassius gibelio*, was the most important prey species for both sexes (with IRI% 88.8% and 84.7% for males and females, respectively) followed by grey mullets (8.3%) in males and big-scale sand smelt (11.4%) in females. The median number of fish per stomach for male great cormorants was four fish (range 2–11 fish) and the median fish prey biomass per stomach 177 g (range 35–640 g). On the other side, the median number of fish per stomach for female birds was four fish (range 1–11 fish) and the median fish prey biomass per stomach 205 g (range 19–442 g), but differences between the sexes were not significant (M–W Z=−0.16, df=15,13, p=0.871, number of prey per sample; M–W Z=0.81, df=15,13, p=0.420, prey biomass per sample). The size of fish prey consumed by each sex was different (Fig. 2c, g). Male birds selected significantly longer (median SL 145.4 mm, range 61.0–240.3 mm) and heavier (median BM 49.1 g, range 1.4–310.1 g) prey than female ones (median SL 128.0 mm, range 48.0–198.0 mm, M–W Z=3.75, df=69,61, p=0.0002; median BM 37.0 g, range 1.2–155.0 g, M–W Z=2.18, df=69,61, p=0.029).

Significant differences in the diet were also found at the Messolonghi Lagoon between male and female great cormorants in terms of numerical abundance (G=21, df=5, p<0.001; Table 2). Grey mullets dominated in the diet of both sexes (with IRI% 82.7% and 80.4% for males and females, respectively) followed by horse mackerel, *Trachurus* sp., in males (9.9%) and big-scale sand smelt in females (16.1%). The median number of prey items contained in the stomachs of male great cormorants was seven fish (range 1–9 fish) and in those of female ones four fish (range 1–74 fish), but differences were not significant (M–W Z=0.68, df=5,11, p=0.497). The median fish prey biomass per stomach also did not differ significantly between the sexes (males: median 302.7 g, range 132–500 g, females: median 253 g, range 105–681 g; M–W Z=0.17, df=5,11, p=0.865). Differences in the size of fish prey consumed by male and female great cormorants were also observed at the Messolonghi Lagoon (Fig. 2d, h). Male birds consumed significantly larger prey (median SL 134.8 mm, range 52.3–183.0 mm; median BM 51.3 g, range 0.8–175.0 g) than female ones (median SL 70.5 mm, range 47.5–218.2 mm, M–W Z=2.53, df=28,113, p=0.011; median BM 2.4 g, range 0.6–184.8 g, M–W Z=2.76, df=28,113, p=0.006).

Discussion

Liordos et al. (2002) and Liordos and Goutner (2007a) compared the diet of great cormorants and found significant differences between four Greek wintering areas. They analysed stomach contents following the guidelines given by Carss et al. (1997), which give information for the full diet of individual birds. However, birds are difficult to collect and sample sizes are often small, as in the present study. Marquiss and Carss (1997) found that variation in the diet of great cormorants increases considerably when samples fell below about ten stomachs. In this study, 50% of the samples are below ten stomachs, and therefore, there could have been larger margins of error in the diet estimates in the smaller samples. In addition, Marquiss and Leitch (1990) analysed grey heron, *Ardea cinerea*, nestling regurgitations and found that there was a strong tendency for the same prey species to occur together, and individual items could not be assumed therefore to occur independently of one another within regurgitations. Given these potential sources of bias, our results revealed significant differences in diet composition between the sexes in all the four wintering areas studied. Patterns of sex-specific prey selection were similar in all the areas. Whilst a few species composed the bulk of the diet of either sex, there were considerable differences in the proportions with which each prey type contributed to the diet of male and female great cormorants. Male birds selected more often larger fish species such as grey mullets, European sea bass and Prussian carp than female birds, which preferred more often smaller fish such as big-scale sand smelt and black goby. Generally, male birds had taken smaller numbers of large fish, whereas female birds took larger numbers of smaller fish. Total mass of food found in stomachs did not differ significantly between the sexes, probably partly offset by the larger numbers of prey taken by the females.

The difference in the selection of prey between the sexes found in this study was consistent with findings from other studies on great cormorants (Koffijberg and Van Eerden 1995; Stewart et al. 2005), king cormorants, *Phalacrocorax albiventer* (Kato et al. 1996), Japanese cormorants, *Phalacrocorax capillatus* (Ishikawa and Watanuki 2002), and double-crested cormorants, *Phalacrocorax auritus* (Anderson et al. 2004). Many seabird species are sexually dimorphic in size (Fairbairn and Shine 1993; Croxall 1995) and male great cormorants are 15–19% heavier than females (Koffijberg and Van Eerden 1995; Liordos and Goutner 2008). A general relation between body mass and foraging behaviour in seabirds seems to exist: Heavier birds are able to dive deeper and for longer periods than lighter ones (Cooper 1986). Great cormorants are deep foragers (Johnsgard 1993), and it may suggest that males can catch larger fish because more are available at deeper depths. Male great cormorants have also on average a 15% deeper (Koffijberg and Van Eerden 1995) and 11% longer (Liordos and Goutner 2008) bill than females. Males should have therefore a better handling performance of larger and more powerful fish than females. Therefore, it seems possible that male birds are able to catch and swallow larger prey than female ones (Koffijberg and Van Eerden 1995).

Bernstein and Maxson (1984) found that blue-eyed shags, *Phalacrocorax atriceps*, exhibit sexual differences in daily foraging patterns: Males forage in the morning and females in the afternoon. This may affect the prey types taken by an individual due to the possibility of variation in prey availability through the day. Great cormorants also use two different foraging techniques: Social fishing (Van Eerden and Voslamber 1995) and solitary fishing (Voslamber et al. 1995). Social fishing involves large flocks of birds that target schools of pelagic fish. The birds can take large numbers of small-sized fish in this manner (Grémillet et al. 1998). In contrast, when fishing solitarily, the birds dive to the seabed and target benthic prey of large size and high nutritional value (Voslamber et al. 1995; Grémillet et al. 1998). It is possible that any difference in foraging habits and skills between the sexes can affect foraging success and/or prey choice of an individual bird. Future research should concentrate therefore on sex-specific differences in foraging patterns and techniques, foraging trip duration, and dive patterns (e.g. depth, duration, frequency of dives).

Acknowledgements We are indebted to all the people who helped us during research: S. Goutner, S. Kazantzidis, P. Menounos, D. Papandropoulos, F. Passios, F. Pergantis, P. Vafeidis, and S. Zogaris. We also thank two anonymous reviewers whose useful comments and suggestions helped greatly improve the manuscript. The performed experiments comply with the current laws of Greece.

References

Anderson CD, Roby DD, Collis K (2004) Foraging patterns of male and female double-crested cormorants nesting in the Columbia River estuary. Can J Zool 82:541–554, doi:10.1139/z04-019

Bernstein NP, Maxson SJ (1984) Sexually distinct daily activity patterns of blue-eyed shags in Antarctica. Condor 86:151–156, doi:10.2307/1367031

Carss DN, Bevan RM, Bonetti A, Cherubini G, Davies J, Doherty D, El Hilli A, Feltham MJ, Grade N, Granadeiro JP, Grémillet D, Gromadzka J, Harari YNRA, Holden T, Keller T, Lariccia G, Mantovani R, McCarthy TM, Mellin M, Menke T, Mirowska-Ibron I, Muller W, Musil P, Nazirides T, Suter W, Trauttmansdorff JFG, Volponi S, Wilson B (1997) Techniques for assessing cormorant diet and food intake: towards a consensus view. Proceedings IV European Conference on Cormorants. Suppl Ric Biol Selvaggina XXVI:197–230

Cooper J (1986) Diving patterns of cormorants Phalacrocoracidae. Ibis 128:562–570, doi:10.1111/j.1474-919X.1986.tb02707.x

Cowx IG (ed) (2003) Interactions between fish and birds: implications for management. Fishing News Books, Blackwell Science Ltd., Oxford

Cramp S, Simmons KEL (eds) (1977) Handbook of the birds of Europe, the Middle East and North Africa. The birds of the western Palearctic, vol. 1. Oxford University Press, Oxford

Croxall JP (1995) Sexual size dimorphism in seabirds. Oikos 73:399–403, doi:10.2307/3545964

Debout G, Røv N, Sellers RM (1995) Status and population development of cormorants *Phalacrocorax carbo carbo* breeding on the Atlantic coast of Europe. Ardea 83:47–59

Dimitriou E, Kapareliotis A, Acovikiotis K, Pergantis F, Perifanos M, Tsagarakis E (2003) Injured fishes due to great cormorants' attacks at Bouka Lagoon. Proceedings of the 11th Pan Hellenic Ichthyologists Conference, Preveza, Greece, pp 215–218 (in Greek with English summary)

Duffy DC, Jackson S (1986) Diet studies of seabirds: a review of methods. Colon Waterbirds 9:1–17, doi:10.2307/1521138

Fairbairn J, Shine R (1993) Patterns of sexual size dimorphism in seabirds of the Southern Hemisphere. Oikos 68:139–145, doi:10.2307/3545319

Goutner V, Papakostas G, Economidis PS (1997) Diet and growth of great cormorant (*Phalacrocorax carbo*) nestlings in a Mediterranean estuarine environment (Axios Delta, Greece). Isr J Zool 43:133–148

Grémillet D, Argentin G, Schulte B, Culik BM (1998) Flexible foraging techniques in breeding cormorants *Phalacrocorax carbo* and shags *Phalacrocorax aristotelis*: benthic or pelagic feeding? Ibis 140:113–119, doi:10.1111/j.1474-919X.1998.tb04547.x

Grémillet D, Wright G, Lauder A, Carss DN, Wanless S (2003) Modelling the daily food requirements of wintering great cormorants: a bioenergetics tool for wildlife management. J Appl Ecol 40:266–277

Handrinos G, Akriotis T (1997) The birds of Greece. Christopher Helm, London

Hart RK, Calver MC, Dickman CR (2002) The index of relative importance: an alternative approach to reducing bias in descriptive studies of animal diets. Wildl Res 29:415–421, doi:10.1071/WR02009

Ishikawa K, Watanuki Y (2002) Sex and individual differences in foraging behaviour of Japanese cormorants in years of different prey availability. J Ethol 20:49–54, doi:10.1007/s10164-002-0053-z

Johnsgard PA (1993) Cormorants, darters, and pelicans of the world. Smithsonian Institution Press, Washington

Kato A, Nishiumi I, Naito Y (1996) Sexual differences in the diet of king cormorants at Macquarie Island. Polar Biol 16:75–77

Kazantzidis S, Naziridis T (2003) The effect of cormorant *Phalacrocorax carbo sinensis* (Linnaeus, 1758) on fishery at Lake Kerkini, Greece. Proceedings of the 11th Pan Hellenic Ichthyologists Conference, Preveza, Greece, pp 235–238 (in Greek with English summary)

Keller T (1995) Food of cormorants *Phalacrocorax carbo sinensis* wintering in Bavaria, southern Germany. Ardea 83:185–192

Kirby JS, Holmes JS, Sellers RM (1996) Cormorants *Phalacrocorax carbo* as fish predators: an appraisal of their conservation and management in Great Britain. Biol Conserv 75:191–199, doi:10.1016/0006-3207(95)00043-7

Koffijberg K, Van Eerden MR (1995) Sexual dimorphism in the cormorant *Phalacrocorax carbo sinensis*: possible implications for differences in structural size. Ardea 83:37–46

Liordos V (2004) Biology and ecology of great cormorant (*Phalacrocorax carbo* L. 1758) populations breeding and wintering in Greek wetlands. PhD dissertation, Aristotle University of Thessaloniki (in Greek with English summary)

Liordos V, Goutner V (2007a) Spatial patterns of winter diet of the great cormorant in coastal wetlands of Greece. Waterbirds 30:103–111, doi:10.1675/1524-4695(2007)030[0103:SPOWDO]2.0.CO;2

Liordos V, Goutner V (2007b) Diet of the great cormorant (*Phalacrocorax carbo* L. 1758) at two Greek colonies. J Biol Res 7:51–57

Liordos V, Goutner V (2008) Sex determination of great cormorants (*Phalacrocorax carbo sinensis*) using morphometric measurements. Waterbirds 31:203–210, doi:10.1675/1524-4695(2008)31[203:SDOGCP]2.0.CO;2

Liordos V, Papandropoulos D, Zogaris S, Alivizatos C, Vrettou E, Arapis T (2002) Great cormorant at Amvrakikos Gulf—research on the conflict between fish-eating birds and fishermen. Intermediate Report, LIFE project, p 75 (in Greek)

Lorentsen SH, Grémillet D, Nyomen GH (2004) Annual variation in diet of breeding great cormorants: does it reflect varying recruitment of gadoids? Waterbirds 27:161–169, doi:10.1675/1524-4695(2004)027[0161:AVIDOB]2.0.CO;2

Mariano-Jelicich R, Madrid E, Favero M (2007) Sexual dimorphism and diet segregation in the black skimmer *Rynchops niger*. Ardea 95:115–124

Marion L (2003) Recent development of the breeding and wintering population of great cormorants *Phalacrocorax carbo* in France—preliminary results of the effects of a management plan of the species. Vogelwelt 124(supplement):35–40

Marquiss M, Carss DN (1997) Methods of estimating the diet of sawbill ducks *Mergus* spp. and Cormorants *Phalacrocorax carbo*. Proceedings IV European Conference on Cormorants. Suppl Ric Biol Selvaggina XXVI:247–258

Marquiss M, Leitch AF (1990) The diet of grey herons *Ardea cinerea* breeding at Loch Leven, Scotland, and the importance of their predation on ducklings. Ibis 132:535–549, doi:10.1111/j.1474-919X.1990.tb00277.x

Martin GR, Twigg LE, Robinson DJ (1996) Comparison of the diet of feral cats from rural and pastoral Western Australia. Wildl Res 23:475–484, doi:10.1071/WR9960475

Orta J (1992) Family Phalacrocoracidae (cormorants). In: del Hoyo J, Elliot A, Sargatal J (eds) Handbook of the birds of the world, vol 1. Lynx Editions, Barcelona, pp 326–353

Pinkas L, Oliphant MS, Inverson ILK (1971) Food habits of albacore, bluefin tuna, and bonito in Californian waters. Fish Bull (Wash, DC) 152:11–105

Russell IC, Dare PJ, Eaton DR, Armstrong JD (1996) Assessment of the problem of fish-eating birds in inland fisheries in England and Wales. Report to the Ministry of Agriculture, Fisheries and Food, project number VC0104. MAFF, London

Sanger GA (1987) Trophic levels and trophic relationships of seabirds in the Gulf of Alaska. In: Croxall JP (ed) Seabirds: feeding, ecology and role in marine ecosystems. Cambridge University Press, Cambridge, pp 229–257

Stewart DC, Middlemas SJ, Gardiner WR, Mackay S, Armstrong JD (2005) Diet and prey selection of cormorants (*Phalacrocorax carbo*) at Loch Leven, a major stocked trout fishery. J Zool (Lond) 267:191–201, doi:10.1017/S0952836905007387

Van Eerden MR, Gregersen J (1995) Long-term changes in the northwest European population of cormorants *Phalacrocorax carbo sinensis*. Ardea 83:61–79

Van Eerden MR, Voslamber B (1995) Mass fishing by cormorants *Phalacrocorax carbo sinensis* at lake Ijsselmeer, The Netherlands: a recent and successful adaptation to a turbid environment. Ardea 83:199–212

Voslamber B, Platteeuw M, Van Eerden MR (1995) Solitary foraging in sand pits by breeding cormorants *Phalacrocorax carbo sinensis*: does specialised knowledge about fishing sites and fish behaviour pay off? Ardea 83:213–222

Zar JH (1999) Biostatistical analysis, 4th edn. Prentice Hall International, Upper Saddle River, NJ