Habitat and Temporal Variation in Diet of Great Cormorant Nestlings in Greek Colonies

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Abstract.—Diet of Great Cormorant (*Phalacrocorax carbo sinensis*) nestlings was studied during four consecutive breeding seasons (1999-2002) at three Greek colonies (Axios Delta, and Lakes Kerkini and Mikri Prespa) in order to assess variation and commercial value of prey. A variety of fish taxa were found in nestlings' regurgitates in each area and season, but only one or two dominated by numbers or biomass. Black Goby (*Gobius jozo*), Round Sardinella (*Sardinella aurita*) and Twaite Shad (*Alosa fallax*) were the most important prey in the Axios Delta; Bleak (*Alburnus alburnus*), Giebel (*Carassius auratus gibelio*) and Roach (*Rutilus rutilus*) at Lake Kerkini; *Chalcalburnus belvica* and Giebel at Lake Mikri Prespa. Nestling diet varied both seasonally (but only at Lake Kerkini significantly so) and annually (significantly in the Axios Delta and at Lake Mikri Prespa). Temporal changes can be attributed to changes in prey availability and abundance and confirm this bird's opportunistic behavior. Between-colonies, differences in diet were significant, probably due to differences in habitat and prey species diversity and composition. The low consumption of valuable fish prey by Great Cormorant nestlings (<10%, numbers and biomass) suggests minimal competition with human interests. *Received 2 May 2007, Accepted 26 November 2007.*

Key words.—Great Cormorant, nestling diet variability, commercial value of prey, Greece, *Phalacrocorax carbo sinensis.*

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The Great Cormorant (*Phalacrocorax carbo*) is a fish-eating, colonially nesting, semi-migratory waterbird that is found in both inland and coastal waters throughout large parts of the world (Cramp and Simmons 1977). The subspecies *P. c. sinensis* is found in continental Europe and Asia, and breeds in colonies mainly located in trees near fresh, brackish or salt water. During the first half of the Twentieth Century, its status was threatened, but the breeding population of the continental subspecies of the Great Cormorant in northwest Europe increased rapidly during the 1970s and 1980s, before levelling-off at *c.* 100,000 pairs in the mid-1990s, a more than 20-fold increase (Bregnballe 1996). Legal protection by the European Community and the increase in fish productivity due to eutrophication of aquatic habitats have been identified as the main reasons for the rapid growth of the Great Cormorant populations (Van Eerden *et al.* 1995; Russell *et al.* 1996). Increased cormorant numbers, along with its fish-eating habits, have led to conflicts with human interests over most of Europe (Russell *et al.* 1996; Cowx 2003). Upon this development, much research on the Great Cormorant's diet, energetics, and impact on fish populations has been conducted, especially during the last ten years (see Baccetti and Cherubini 1997; Cowx 2003; and Keller *et al.* 2003 for reviews), and management and control plans were formulated and applied (Kirby *et al.* 1996; Bildsøe *et al.* 1998; Keller and Lanz 2003).

The Greek breeding population of the Great Cormorant changed little from 550 pairs in 1971 to 660 pairs in 1990 (Handrinos and Akriotis 1997). Subsequently, and following the levelling-off of the northwest European population, it increased rapidly to *c.* 4,300 pairs in 1999-2001 and to *c.* 5,300 pairs in 2002-2006, showing an eight-fold increase since 1990 (Liordos 2004; S. Kazantzidis and T. Nazirides, pers. comm.). High food availability due to eutrophication of water bodies and low initial population density are considered the most probable causes of the high growth rate of the Great Cormorant population in Greece (Crivelli *et al.* 1997; Goutner *et al.* 1998).

The population increase has also led to conflicts with fishermen and fisheries industry in Greece and prompted an urgent need for dietary analyses, since diet composition data are very useful for: i) studying temporal and spatial variation in the diet of seabirds (Lorentsen *et al.* 2004), and ii) evaluating the economic importance of prey consumed and thus potential conflict with fisheries (Eschbaum *et al.* 2003). Only two other studies on Great Cormorant diet in Greece were found in the literature. Goutner *et al.* (1997) reported the diet of nestlings in the Axios Delta in 1993 and 1994. Liordos and Goutner (2007) compared the bird's diet in three wintering areas. Great Cormorant nestlings regurgitate their stomach contents when disturbed and collection of regurgitates is an easy and non-invasive method, providing abundant information on nestlings' diet (Linn and Campbell 1992). The aim of this paper was therefore to: 1) describe and compare the diet of the Great Cormorant between colonies and breeding seasons through the analysis of nestling regurgitates, and 2) evaluate the commercial value of the prey consumed and discuss potential conflict of Great Cormorants with human interests.

METHODS

Study Area

The study was conducted in the Axios Delta and at Lake Kerkini and Lake Mikri Prespa colonies (Fig. 1), all sites designated as Wetlands of International Importance under the Ramsar Convention. 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 breeding colony included four heron species and was located on an islet at a riverine forest of Tamarisks (*Tamarix hampaena*), Common Alders (*Alnus glutinosa*), and willows (*Salix* spp.) (Kazantzidis *et al.* 1997). The number of breeding pairs in the Axios Delta was 360, 400, 220 and 220 in 1999, 2000, 2001 and 2002 respectively (Liordos 2004).

Lake Kerkini (41°12'N, 23°9'E), a semi-artificial seasonally flooded lake, with a surface varying from 55 to 75 km^2, is located in northern Greece, near the Greek-Bulgarian border. Great Cormorants nested over water mainly on willow hybrids (*Salix alba* x *fragilis*) in a mixed colony situated at the northeast part of the lake including twelve waterbird species (Nazirides and Papageorgiou 1996). Colony size at Lake Kerkini was 2,200, 2,400, 2,500 and 3,500 pairs in 1999, 2000, 2001 and 2002 respectively (T. Nazirides, pers. comm.).

Lake Mikri Prespa (40°44'N, 21°4'E) in the far northwestern Greece, along with Lake Megali Prespa, is situated at an altitude of 853.5 m asl. Of its surface (47.35 km^2), 92% belong to Greece and the rest to Albania. Great Cormorants nested on Vidronissi island, on a stand of ancient juniper (*Juniperus foetidissima*) trees.

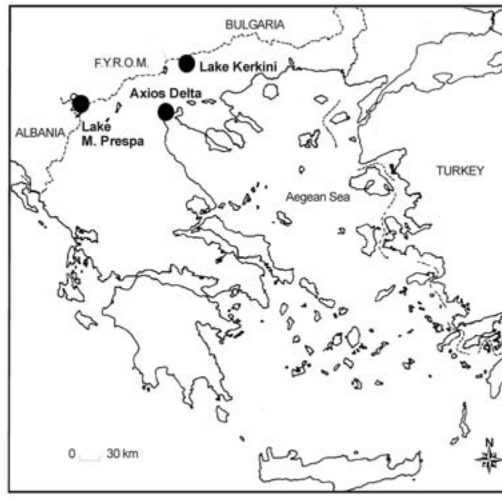

Figure 1. Map showing the location of the three study areas in Greece.

The Lake Mikri Prespa colony held 470, 170, 220 and 440 pairs in 1999, 2000, 2001 and 2002 respectively (Liordos 2004).

Diet Analysis

Nestling regurgitates were collected at the colonies from 1999 to 2002 between late April and the beginning of June in similar dates for each area. Three visits per season were conducted in each of the colonies, timed to coincide with early, middle and late nestling period, taking into account that Great Cormorant nestlings fledge at the age of about 8 weeks (Cramp and Simmons 1977). The visits will be henceforth referred to as "sample A", "sample B", and "sample C" for convenience. Collection dates were similar for all the areas and can be categorized as follows: 1) sample A, 29 April-4 May, more than 50% of the nestlings 1-2 weeks old, 2) sample B, 22-27 May, >50% of nestlings about 5 weeks old, and 3) sample C, 7-12 June, >50% of the nestlings about seven weeks old. Regurgitates were taken right after the morning feeding bout, from 10.00 to 12.00 h (GMT+2:00). Parent birds flee upon disturbance, and nestlings regurgitate collectively. This allowed the collection of nestling regurgitates only, but not discerning among individuals, since regurgitates were mixed on the ground due to high nest densities and plethora of regurgitated fish. All egested prey were collected, stored in ethanol, and taken to the lab for further analysis.

Fish prey were identified to the lowest possible taxon. Intact specimens were measured to the nearest one mm and weighed to the nearest 0.1 g. Length of partly digested prey was estimated in comparison with similarly-sized intact ones. Fish taxa found in the diet of the Great Cormorant are given in Table 1. Body mass of partly digested fish was calculated using regression equations given in Koutrakis and Sinis (1994), Petrakis and Stergiou (1995), Liordos and Goutner (2007), or constructed by the authors using intact fish found in regurgitates or bought from the local markets (Table 2).

Regurgitate contents were analyzed per sampling bout by relative abundance by both numbers and biomass (numbers and biomass of each prey type in the sample). Comparisons of diet composition in relation to season, year, and area were made with analysis of similarity (ANOSIM), a non-parametric multi-dimensional ordination method for detecting differences between groups of community samples (Clarke 1993), using the subroutine ANOSIM in the statistical software Primer V 5.1.2 (PRIMER-E Ltd., Plymouth, UK). Species diversity was also calculated for each sample using the Shannon-Weaver H´ diversity index (see Shannon and Weaver 1949, in Brower *et al.* 1997), and compared using Kruskal-Wallis and Mann-Whitney U tests (Zar 1999). Mean values are presented with ± one standard deviation (SD).

Fish prey taxa were classified according to their commercial value, following Goutner *et al.* (1997), Liordos and Goutner (2007) and local market research (Table 1). Proportions of the diet by numbers and biomass, according to commercial value, were then calculated to examine possible economic impact of the Great Cormorant.

Table 1. Common and scientific names of the fish species found in the diet of Great Cormorant nestlings in Greece during the 1999-2002 breeding seasons. Commercial value of prey is also given (1: high; 2: medium; 3: low). Common and scientific names are taken from FishBase online (www.fishbase.org).

Common names	Scientific names	Commercial value
	Blenniidae	
Peacock Blenny	*Blennius pavo*	3
	Carangidae	
Mediterranean Horse-mackerel	*Trachurus mediterraneus*	3
Atlantic Horse-mackerel	*Trachurus trachurus*	3
	Centrarchidae	
Pumpkinseed	*Lepomis gibbosus*	3
	Clupeidae	
Twaite Shad	*Alosa fallax*	3
Pilchard	*Sardina pilchardus*	3
Round Sardinella	*Sardinella aurita*	3
	Cyprinidae	2
Bleak	*Alburnus alburnus*	3
Giebel	*Carassius auratus gibelio*	2
	Chalcalburnus belvica	3
	Chondrostoma prespense	2
Carp	*Cyprinus carpio*	1
Chub	*Leuciscus cephalus*	3
	Rutilus prespensis	2
Roach	*Rutilus rutilus*	2
Baltic Vimba	*Vimba vimba*	3
	Gobiidae	3
Black Goby	*Gobius jozo*	3
Grass Goby	*Zosterisessor ophiocephalus*	3
	Mugilidae	2
	Mullidae	
Striped Red Mullet	*Mullus surmuletus*	1
	Serranidae	
Painted Comber	*Serranus scriba*	3
	Soleidae	
Common Sole	*Solea solea*	1
	Sparidae	
Bogue	*Boops boops*	
Annular Gilthead	*Diplodus annularis*	3
Striped Seabream	*Lithognathus mormyrus*	1
Saddled Seabream	*Oblada melanura*	2
	Sphyraenidae	
Great Barracuda	*Sphyraena sphyreana*	2

Table 2. Parameters of the equations ($y = a{\cdot}x^b$) estimated by the authors for the calculation of fish body mass (M) from fish length (FL: fork length; SL: standard length; HL: head length).

Fish species	Dependent variable	Independent variable	a	b	N	Range (mm)	R^2
Bleak	M	FL	0.000015	28.419	39	57-115	0.912
	M	HL	0.0029	26.716	39	9-19	0.741
Pumpkinseed	M	SL	0.00001	31.801	18	59-108	0.985
Chalcalburnus belvica	M	SL	0.0000052	31.907	119	34-139	0.972
	M	HL	0.0004	31.939	119	9-39	0.962

RESULTS

The overall diet of Great Cormorant nestlings was composed of at least 26 fish species, belonging to twelve families (see Tables 1, 3, 4, 6, 7). Scientific names for fish species are given in Table 1.

Temporal Analysis of Diet

In the Axios Delta, diet composition (Tables 3 and 4) did not differ significantly between samples A, B, and C from 1999 to 2002 both by numbers (ANOSIM, P = 0.610) and biomass (ANOSIM, P = 0.751). Contribution of main prey species was fluctuating a little from early to late in the pre-fledging period. On the other hand, diet composition differed significantly between years both by numbers (ANOSIM, P = 0.005) and biomass (ANOSIM, P = 0.017). This was due to a change in diet between 1999, 2000 and 2001, 2002 (comparison of 1999-2000 with 2001-2002 samples: ANOSIM, P = 0.002; both numbers and biomass). Black Goby (*Gobius jozo*) was overall the most important in terms of both numbers and biomass, dominating in 1999 and 2000, while Mugilidae were important only by biomass in 1999, 2000 and 2002 (Tables 3 and 4, Fig. 2). Round Sardinella (*Sardinella aurita*) and Twaite Shad (*Alosa fallax*) had greater contribution in the 2001 and 2002 samples by numbers and especially by biomass, greatly replacing Black Goby (Tables 3 and 4, Fig. 2). The discrepancies between prey number and their contribution in biomass percentages were due to the relative size of fish prey (Table 5).

Significant differences were detected at Lake Kerkini between samples A and C from 1999 to 2002 both by numbers (ANOSIM, P = 0.029) and biomass (ANOSIM, P = 0.045). Samples A and B, B and C did not differ significantly (pairwise ANOSIM, P > 0.096; numbers and biomass). Bleak's (*Alburnus alburnus*) presence was very high early in the nestling period, but rapidly decreasing towards the late nestling period, replaced numerically by Roach (*Rutilus rutilus*) and both Roach and, mainly, Giebel (*Carassius auratus gibelio*) by biomass (Table 6). Between-year comparisons did not reveal significant differences (ANOSIM, P = 0.620, numbers; P = 0.420, biomass). Overall, Bleak was the most important prey by numbers and Giebel by biomass (Fig. 3). Roach was the most important prey only in 1999, whereas Giebel dominated by biomass in all years, except in 1999, because of its larger size compared to other important prey (Table 5).

Diet composition did not differ significantly between samples A, B, and C from 1999 to 2002 both by numbers (ANOSIM, P = 0.673) and biomass (ANOSIM, P = 0.240) at Lake Mikri Prespa, due to the predominance of *Chalcalburnus belvica* numerically and *Ch. belvica* and Giebel by biomass (Table 7). On the other hand, between-year comparisons revealed significant differences by numbers (ANOSIM, P = 0.013), but not by biomass (ANOSIM, P = 0.170). This is due to the increase of the Pumpkinseed (*Lepomis gibbosus*) in 2002 (Fig. 4), compared with the years 1999-2001 (comparison of 1999-2001 with 2002 samples: ANOSIM, P = 0.009, numbers; P = 0.182, biomass). Differences were not significant by biomass because of the increased presence of Giebel (Table 7, Fig. 4), being of larger size than other important prey (Table 5).

Table 3. Percent relative abundance by numbers of prey in regurgitates of Great Cormorant nestlings in the Axios Delta, during the 1999-2002 breeding seasons. A, B, and C represent samples taken early, in the middle, and late in the nestling period respectively.

	1999			2000			2001			2002		
Fish taxa	A	B	C	A	B	C	A	B	C	A	B	C
Black Goby	64.7	78.4	76.6	59.7	70.1	79.3	30.0	23.0	20.4	27.3	24.3	19.8
Giebel	3.9	2.2	3.1	—	—	—	—	—	—	2.5	—	—
Mugilidae	7.8	5.2	4.7	3.0	2.6	5.4	—	—	—	12.4	2.7	5.7
Twaite Shad	9.8	5.2	1.6	10.4	5.2	3.3	13.3	—	11.8	19.0	10.0	14.2
Annular Gilthead	11.8	3.7	1.6	10.4	1.3	2.2	3.3	—	5.4	9.9	3.6	10.4
Roach	—	1.5	1.5	—	—	1.1	—	—	—	—	—	—
Bogue	—	2.3	1.6	—	—	—	—	—	—	—	7.2	—
Atlantic Horse-mackerel	—	—	—	—	3.9	—	—	—	—	4.1	—	5.7
Mediterranean Horse-mackerel	—	1.5	1.6	6.0	6.5	2.2	—	—	—	—	8.1	4.7
Round Sardinella	—	—	3.1	—	3.9	6.5	40.0	36.3	30.1	12.4	20.7	20.7
Striped Seabream	—	—	1.5	—	1.3	—	—	—	—	2.5	—	4.6
Painted Comber	—	—	3.1	—	—	—	—	—	—	—	—	3.8
Pilchard	—	—	—	9.0	1.3	—	—	—	—	4.1	—	—
Saddled Seabream	—	—	—	—	2.6	—	—	—	—	2.5	—	6.6
Great Barracuda	2.0	—	—	—	—	—	—	—	—	3.3	—	—
Peacock Blenny	—	—	—	—	1.3	—	5.0	19.8	10.8	—	6.3	—
Common Sole	—	—	—	1.5	—	—	6.7	5.5	8.6	—	4.5	3.8
Grass Goby	—	—	—	—	—	—	1.7	—	—	—	10.8	—
Striped Red Mullet	—	—	—	—	—	—	—	15.4	12.9	—	1.8	—
Total numbers (N)	153	134	128	134	154	92	120	91	93	121	111	106

Table 4. Percent relative abundance by biomass of prey in regurgitates of Great Cormorant nestlings in the Axios Delta, during the 1999-2002 breeding seasons. A, B, and C represent samples taken early, in the middle, and late in the nestling period respectively.

	1999			2000			2001			2002		
Fish taxa	A	B	C	A	B	C	A	B	C	A	B	C
Black Goby	34.6	42.4	50.9	28.0	31.5	38.8	15.6	8.2	6.6	7.7	8.8	7.0
Giebel	5.7	4.7	8.8	—	—	—	—	—	—	3.0	—	—
Mugilidae	39.1	30.0	17.7	12.3	13.5	26.4	—	—	—	38.5	10.6	13.7
Twaite Shad	13.3	11.6	3.6	21.1	14.1	10.2	24.2	—	16.8	15.7	15.8	15.7
Annular Gilthead	2.5	0.9	0.7	4.7	0.4	0.7	1.3	—	2.1	1.2	0.6	2.6
Roach	—	6.9	7.3	—	—	4.3	—	—	—	—	—	—
Bogue	—	0.4	0.3	—	—	—	—	—	—	—	1.1	—
Atlantic Horse-mackerel	—	—	—	—	8.2	—	—	—	—	6.0	—	8.3
Mediterranean Horse-mackerel	—	3.1	3.5	14.7	16.3	7.0	—	—	—	—	11.0	6.8
Round Sardinella	—	—	3.0	—	7.6	12.6	49.2	44.0	36.4	14.6	32.1	27.1
Striped Seabream	—	—	1.8	—	2.8	—	—	—	—	3.5	—	6.4
Painted Comber	—	—	2.4	—	—	—	—	—	—	—	—	1.7
Pilchard	—	—	—	18.7	2.0	—	—	—	—	3.6	—	—
Saddled Seabream	—	—	—	—	2.2	—	—	—	—	1.2	—	5.6
Great Barracuda	4.8	—	—	—	—	—	—	—	—	5.0	—	—
Peacock Blenny	—	—	—	—	1.4	—	2.3	6.6	5.1	—	—	—
Common Sole	—	—	—	0.5	—	—	6.8	5.6	7.9	—	6.6	5.1
Grass Goby	—	—	—	—	—	—	0.6	—	—	—	5.3	—
Striped Red Mullet	—	—	—	—	—	—	—	35.6	25.1	—	4.4	—
Total biomass (g)	4,990	3,695	3,446	4,474	5,074	2,828	5,936	4,225	5,066	6,678	4,370	5,123

Table 5. Standard length (mm) of intact items of the most important fish prey found in the diet of Great Cormorant nestlings in 1999-2002.

	Mean ± SD	Range	N
1. Axios Delta			
Black Goby	88.1 ± 9.4	68-110	57
Round Sardinella	159.3 ± 19.1	123-217	45
Twaite Shad	144.5 ± 17.8	111-199	36
Mugilidae	194.5 ± 25.6	148-230	19
2. Lake Kerkini			
Bleak	81.2 ± 12.7	61-110	137
Giebel	154.3 ± 33.7	55-230	38
Roach	76.0 ± 11.7	61-135	112
3. Lake Mikri Prespa			
Chalcalburnus belvica	101.4 ± 25.8	44-141	152
Giebel	161.7 ± 41.3	77-264	14
Pumpkinseed	70.4 ± 14.0	49-93	18

Between-habitat Diet Comparisons

Comparison of prey proportions between all studied areas revealed significant spatial variability (between-areas comparison: ANOSIM, P = 0.001; numbers and biomass). Mean Shannon-Weaver Diversity Index H´ in the Axios Delta was 1.481 ± 0.474 (SD) (N = 12, range 0.847-2.199), being significantly larger than at Lake Kerkini (H´ = 0.650 ± 0.330, N = 12, range 0.075-1.040) and Lake Mikri Prespa (H´ = 0.530 ± 0.295, N = 12, range 0.046-1.003), Kruskal-Wallis (K-W) test (χ^2_2 = 20.68, P < 0.001). In contrast, differences in specific diversity between the lakes were not significant (U_1 = 51.0, P = 0.225).

Commercial Importance of Prey

Fish of low commercial value dominated in nestling diet in the Axios Delta (86.8% numbers, 68.8% biomass) and at Lake Mikri Prespa (92.6% numbers, 52.9% biomass). Fish of low commercial value were also found in higher proportions by numbers (62.9%) at Lake Kerkini, but fish of medium commercial value dominated by biomass (73.7%), mainly due to the increased presence of Giebel. Striped Red Mullet (*Mullus surmuletus*), Common Sole (*Solea solea*), and Striped Seabream (*Lithognathus mormyrus*) were the only prey of high commercial value sporadically found in the Axios Delta samples and collectively contributed in low proportions in overall diet (5.1% numbers, 9.6% biomass). Carp (*Cyprinus carpio*) was the only prey of high commercial value that contributed in the Great Cormorant diet in lacustrine habitats. Carp was found in Lake Mikri Prespa regurgitates in 1999 and 2001 in negligible proportions (0.3% numbers, 1.5% biomass in overall diet). Commercially important fish were not found in Lake Kerkini diet samples.

DISCUSSION

Regurgitate analysis is considered an appropriate method for the qualitative analysis of avian diet with advantages; easy to collect large numbers of samples without harm to the birds, prey fed to the nestlings are generally in the early stages of digestion and give sufficient information on the species and sizes of fish eaten, and disadvantages; uncertainty of bird feeding completion at the time of collection, differential digestion of small and large consumed prey (Linn and Campbell 1992). However, it should not be used for the calculation of daily food intake rates because its disadvantages lead to underestimation of total prey biomass consumed (Linn and Campbell 1992; Harris and Wanless 1993). In addition to the above, daily food intake could not be calculated in this study since we could not collect individual nestlings' regurgitates.

Table 6. Percent relative abundance by (1) numbers and (2) biomass of prey in regurgitates of Great Cormorant nestlings at Lake Kerkini, during the 1999-2002 breeding seasons. A, B, and C represent samples taken early, in the middle, and late in the nestling period respectively.

	1999			2000			2001			2002		
Fish taxa	A	B	C	A	B	C	A	B	C	A	B	C
1. Numbers (%)												
Bleak	78.7	71.8	16.0	98.6	86.7	47.1	69.8	55.1	49.3	98.5	39.6	50.0
Roach	17.5	26.3	84.0	—	—	43.9	11.4	7.9	46.2	—	53.2	25.0
Giebel	3.8	—	—	1.4	11.8	9.0	18.1	37.0	3.8	1.5	6.5	25.0
Chub	—	1.9	—	—	—	—	0.7	—	—	—	—	—
Pumpkinseed	—	—	—	—	1.5	—	—	—	0.7	—	—	—
Baltic Vimba	—	—	—	—	—	—	—	—	—	—	0.7	—
Total numbers (N)	160	156	293	140	279	255	149	165	288	268	139	80
2. Biomass (%)												
Bleak	63.9	53.4	18.4	84.3	17.0	23.0	25.2	7.4	20.2	76.0	14.3	8.1
Roach	22.1	29.8	81.6	—	—	32.6	11.1	5.0	59.8	—	50.2	9.5
Giebel	14.0	—	—	15.7	81.8	44.4	60.3	87.6	16.9	24.0	34.0	82.4
Chub	—	16.8	—	—	—	—	3.4	—	—	—	—	—
Pumpkinseed	—	—	—	—	1.2	—	—	—	3.1	—	—	—
Baltic Vimba	—	—	—	—	—	—	—	—	—	—	1.5	—
Total biomass (g)	822	876	1,140	650	3,870	1,898	1,879	3,322	1,533	1,233	1,810	2,182

Table 7. Percent relative abundance by (1) numbers and (2) biomass of prey in regurgitates of Great Cormorant nestlings at Lake Mikri Prespa, during the 1999-2002 breeding seasons. A, B, and C represent samples taken early, in the middle, and late in the nestling period respectively.

	1999			2000			2001			2002		
Fish taxa	A	B	C	A	B	C	A	B	C	A	B	C
1. Numbers (%)												
Chalcalburnus belvica	93.8	89.9	99.2	85.8	84.0	93.8	90.5	88.8	82.3	65.4	41.4	31.7
Giebel	4.1	5.0	—	5.7	4.2	3.1	9.5	10.3	4.3	12.8	8.6	10.1
Pumpkinseed	—	1.3	—	2.8	4.9	3.1	—	—	10.2	21.8	48.1	58.3
Rutilus prespensis	2.1	3.8	—	—	6.9	—	—	—	1.6	—	1.9	—
Chondrostoma prespense	—	—	—	4.3	—	—	—	0.9	—	—	—	—
Carp	—	—	0.8	—	—	—	—	—	1.6	—	—	—
Chub	—	—	—	1.4	—	—	—	—	—	—	—	—
Total numbers (N)	145	159	379	141	144	161	116	116	186	133	162	139
2. Biomass (%)												
Chalcalburnus belvica	63.5	45.4	89.2	30.8	58.0	68.5	37.2	34.2	68.0	33.7	14.7	13.0
Giebel	33.6	44.6	—	32.6	25.9	27.9	62.8	64.8	17.8	58.7	48.6	57.5
Pumpkinseed	—	1.1	—	1.7	9.4	3.6	—	—	5.1	7.6	34.0	29.5
Rutilus prespensis	2.9	8.9	—	–	6.7	—	—	—	2.9	—	2.7	—
Chondrostoma prespense	—	—	—	25.4	—	—	—	1.0	—	—	—	—
Carp	—	—	10.8	—	—	—	—	—	6.2	—	—	—
Chub	—	—	—	9.5	—	—	—	—	—	—	—	—
Total biomass (g)	3,688	3,422	4,527	3,565	1,413	2,344	3,736	4,675	3,070	5,085	5,067	1,413

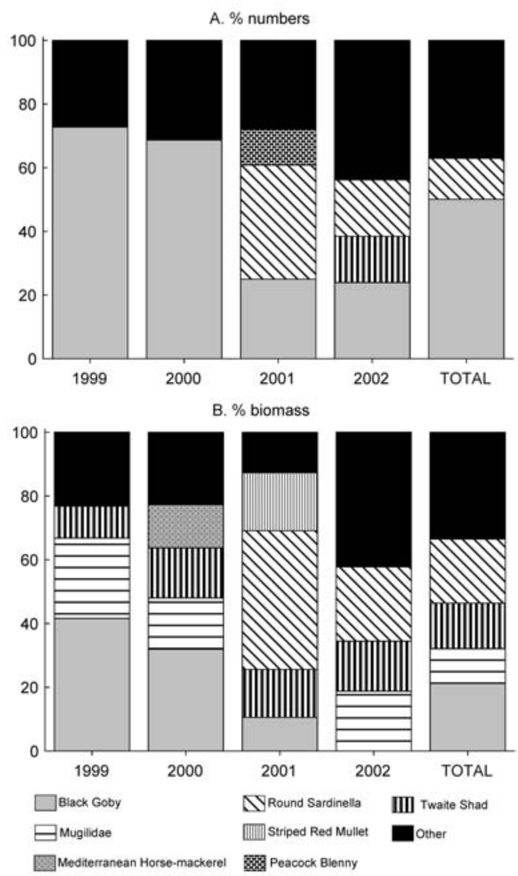

Figure 2. Annual variation in relative abundance by (A) numbers and (B) biomass of prey found in the diet of Great Cormorant nestlings in the Axios Delta, during the 1999-2002 breeding seasons. Prey types contributing less than 10% in diet, either by numbers or biomass, are shown collectively under the "Other" category.

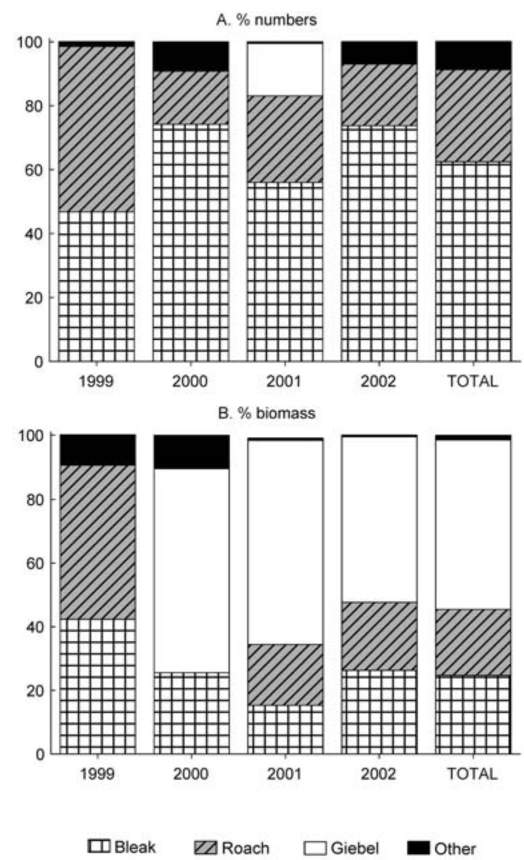

Figure 3. Annual variation in relative abundance by (A) numbers and (B) biomass of prey found in the diet of Great Cormorant nestlings at Lake Kerkini, during the 1999-2002 breeding seasons. Prey types contributing less than 10% in diet, either by number or biomass, are shown collectively under the "Other" category.

Great Cormorant diet during the breeding season included a considerable number of prey types, but only a few of them usually composed the bulk of diet either by numbers or biomass. The same trend was reported by Goutner *et al.* (1997) and Liordos and Goutner (2007). The preponderance of few fish species in the diet of the Great Cormorant is not uncommon, but has also been observed in other countries (e.g., Italy, Boldreghini *et al.* 1997; France, Lekuona 2002; Poland, Martyniak *et al.* 2003; Norway, Lorentsen *et al.* 2004) and is rather due to the opportunistic foraging behavior of the Great Cormorant (Johnsgard 1993). This leads to the prevalence of the prey types which are mostly available and abundant in a particular area and season (Grémillet and Wilson 1999; Grémillet *et al.* 2001).

The diet of Great Cormorant nestlings in the Axios Delta was similar to that found by Goutner *et al.* (1997) in 1993 and 1994, with Black Goby and Mugilidae being the most important prey. Black Goby by numbers and Mugilidae by biomass were also the most important prey of wintering birds in 2001 (Liordos and Goutner 2007). These results suggest little variation between breeding and wintering seasons and age of birds in the Axios Delta. Annual variation at Lake Mikri Prespa was mainly due to the presence of the exotic Pumpkinseed, whose populations have gradually increased after its introduc-

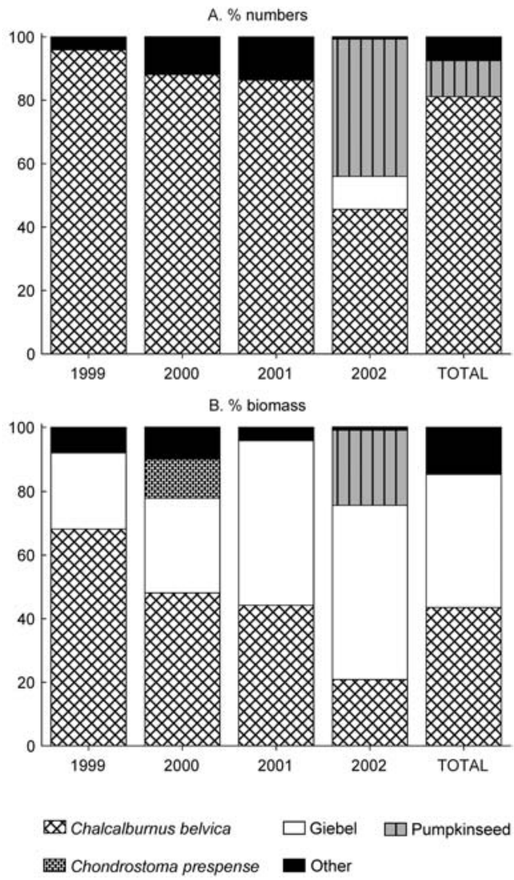

Figure 4. Annual variation in relative abundance by (A) numbers and (B) biomass of prey found in the diet of Great Cormorant nestlings at Lake Mikri Prespa, during the 1999-2002 breeding seasons. Prey types contributing less than 10% in diet, either by numbers or biomass, are shown collectively under the "Other" category.

tion in the lake (Crivelli *et al.* 1997), probably accounting for the increased contribution in the Great Cormorant's diet in 2002. Generally, various findings suggest that seasonal and annual changes can be attributed to changes in prey availability and abundance (Grémillet and Wilson 1999; Grémillet *et al.* 2001) and the bird's opportunistic behavior (Johnsgard 1993). Great Cormorants are thought to target prey patches of very high density (Grémillet *et al.* 2001) and the link between foraging performance and prey abundance is considered to be stronger than in any other species of diving bird (Grémillet and Wilson 1999).

The presence of freshwater fish (Giebel, Roach) in Axios Delta nestlings' diet suggests that Great Cormorants do not feed exclusively along the coast, but also fly to nearby freshwater bodies (Lake Koronia, Lake Volvi) to forage. Great Cormorant prey diversity in the Axios Delta from nestling regurgitates (19 prey types in this study, 24 in Goutner *et al.* 1997) is among the highest ever reported in the Mediterranean area (compared with Boldreghini *et al.* 1993; Sara and Baccetti 1993; Boldreghini *et al.* 1997; Pizzaro *et al.* 1997; Privileggi 2003). This happens because Great Cormorants forage in saline, brackish and freshwater habitats, taking advantage of the high diversity of the Axios Delta (Zalidis and Mantzavelas 1994) as well as nearby water bodies. In contrast, few fish species were found in the samples from Lakes Kerkini (6) and Mikri Prespa (7). This is probably due to the fact that Great Cormorants forage only in freshwater habitats. High spatial variation in diet composition is emphasized by the fact that Giebel was the only species, of 26 recorded in diet, found in samples from all the areas studied. In addition, Giebel was found in more samples and contributed in higher proportions at the lakes than in the Axios Delta.

Our results suggested that fish of low commercial value mainly participated in the Great Cormorant's diet. Goutner *et al.* (1997) reported low contribution of commercially important fish in Great Cormorant nestlings' diet. Liordos and Goutner (2007) also found low proportions of valuable prey in the diet of wintering Great Cormorants. Proportions were higher at Messolonghi Lagoon, where fishponds of commercially important species exist within the foraging areas of the Great Cormorant. Many other European studies (Scotland, Rae 1969; Switzerland, Suter 1991; Germany, Keller 1995; Netherlands, Veldkamp 1995; Poland, Mellin and Krupa 1997; France, Carpentier *et al.* 2003) also indicated high contribution of non-commercial fish in the diet, suggesting small economic damage. On the other hand, serious economic impact may occur in small areas of high fish concentrations such as intensive aquacultures, wintering ditches, small lakes, and reservoirs (Moerbeek *et al.* 1987; Cornelisse and Cristensen 1993; Kirby *et al.* 1996; Leopold *et al.* 1998; Wright 2003). Concerns have been raised whether local fisheries will be sustainable in the presence of large numbers of fish-eating predators, as at Lake Kerkini, since European studies suggest they may suffer some, or even serious, economic damage. Overall at the areas studied, competition of the Great Cormorant with fisheries and fishermen seems minimal because of the small overlap between the bird's diet and valuable fish species. The decrease in Carp's population, the only valuable fish at Lake Kerkini, was mainly attributed to the destruction of its spawning grounds (shallow marshes) through water level increase by closing the lake dam that took place for the first time in April 1992 (Crivelli *et al.* 1995). The low population of Carp in the lake is considered the main reason of its absence from nestling regurgitates. Moreover and despite Great Cormorant depredation, the total fish biomass was found stable at Lake Kerkini (T. Nazirides, pers. comm.) and slightly increased at Lake Mikri Prespa (Crivelli *et al.* 1997) during the 1990s, due mainly to increased eutrophication of the lakes and the introduction of exotic species such as the highly adaptable Pumpkinseed (Crivelli *et al.* 1997). Nevertheless, before final conclusions are drawn, future studies should concentrate on the assessment of locality-specific impact size through the estimation of fish stock levels and total prey biomass removal (Davies *et al.* 2003).

This study presented the diet of the Great Cormorant in the three major Greek colonies through the analysis of nestling regurgitates. Results revealed spatial and temporal variation in diet and confirmed the bird's opportunistic foraging behavior. Moreover, the analysis of qualitative diet data showed very low consumption of valuable fish species, thus suggesting small economic impact on fisheries. Overall, the results presented in this study provide important information on the ecology and for the management of a fish-eating avian predator, creating a basis for the monitoring of its diet with which future studies can be compared.

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