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Abstract

Postnatal growth of nestling great cormorants *Phalacrocorax carbo sinensis* was studied at two northeastern Mediterranean wetlands, the Lakes Kerkini and Mikri Prespa, northern Greece. A method for constructing growth curves from only two visits to bird colonies was used. Logistic growth parameters re-calculated from the logarithmic equation fitted well to the actual growth data of initial-final measurements of body mass, bill length, bill + head length, and tarsus length. Growth rates (K) did not significantly differ between colonies for all variables: body mass (0.205 and 0.206 day^{-1} at Lakes Kerkini and Mikri Prespa respectively), bill length (0.131 and 0.147 day^{-1}), bill + head length (0.109 and 0.121 day^{-1}) and tarsus length (0.201 and 0.215 day^{-1}). Asymptotic values (A) did not significantly differ between colonies for body mass (2126.7 g and 2128.95 g) and bill length (70.57 and 68.83 mm) but did so for bill + head (147.89 and 151.51 mm) and tarsus length (75.42 and 71.31 mm). The inflection point (T) was similar for body mass (16.6 and 16.4 days) and tarsus length (7.9 and 7.1 days) but significantly different for bill (13 and 11.2 days) and bill + head length (12.2 and 11.1 days). Climatic conditions and food availability were not considered as factors greatly affecting the observed intercolony variation, and therefore other proximate and ultimate factors should be further examined. The proposed method is very helpful because growth curves can be constructed with the allocation of the smallest amount of time and effort, while at the same time keeping the disturbance of vulnerable breeding avian populations to the minimum level. Furthermore, and provided that other factors are controlled, this method could be used for the monitoring of the influence of spatial and temporal variation of ecological conditions on nestling growth.

Keywords: *Great cormorant, logistic growth, intercolony comparison, Greece*

Introduction

The great cormorant *Phalacrocorax carbo* is a top predator of aquatic ecosystems that feeds almost entirely on fish and is found in both inland and coastal waters throughout large parts of the world (Cramp & 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 20th century its status was threatened, but since the 1970s, its populations have rapidly increased throughout its European range (Debout et al. 1995; van Eerden & Gregersen 1995; Handrinos & Akriotis 1997; Røv et al. 2003; Volponi & Addis 2003; Liordos & Goutner 2008a), due mainly to legal protection by the European Community and

eutrophication of water bodies that led to increase in fish productivity (van Eerden et al. 1995).

The large populations combined with the fish-eating habits of this bird have caused considerable conflicts with fishermen and the fisheries industry in many countries (Kirby et al. 1996; van Dam & Asbirk 1997), which consequently resulted to a large number of studies on the bird's diet, energetics, and possible impact on fish populations and economic activities (see Baccetti & Cherubini 1997; Cowx 2003; and Keller et al. 2003 for reviews). In contrast, other aspects of the bird's biology and ecology, such as nestling growth and development received relatively little attention. We know of three studies on the growth of wild populations of continental great cormorants (Platteeau et al. 1995; Goutner et al.

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1997; Barati 2009) and another one of *P. c. sinensis* chicks kept in captivity (Shmueli et al. 2003).

Avian postnatal growth is a non-linear function of age (Ricklefs 1967, 1968, 1973). Each species has a characteristic and inherent growth pattern (Ricklefs 1967) and nestling growth provides valuable information on the behaviour and ecology of individuals and populations (Ricklefs 1968; Starck & Ricklefs 1998a). However, the study of growth is labour-intensive because it requires numerous data and many visits to the colony. To resolve this Ricklefs & White (1975) provided a method for constructing average growth curves from only two visits to bird colonies. In doing so, time and effort could be saved and the disturbance of birds could be minimised. The analysis of growth can then be achieved by fitting different types of equation to growth data (Ricklefs 1967). Three equations are most commonly used to describe avian growth and are known as the logistic, Gompertz and von Bertalanffy sigmoid curves (Ricklefs 1968). The comparison of average growth curves can reveal interspecific patterns of reproductive strategy and intraspecific variations in the feeding conditions of nestlings (Ricklefs 1967).

The aims of the present study were thus to describe and compare the growth of great cormorant nestlings in two major lacustrine colonies in Greece, by fitting average curves to growth data from two successive visits.

Materials and methods

The study was conducted in two breeding colonies located in northern Greece (Figure 1), the Lakes Kerkini (41° 12′ N, 23° 9′ E) and Mikri Prespa (40° 44′ N, 21° 4′ E), both designated as Wetlands of International Importance under the Ramsar Convention. Lake Kerkini is a seasonally flooded semi-artificial lake with a surface varying from 55 to 75 km². Flooded and riverine forests of willow *Salix alba* x *fragilis* hybrids, common alder *Alnus glutinosa*, oriental plane *Platanus orientalis*, and tamarisk *Tamarix parviflora* occur at the northeast part of the lake, where great cormorants, 2400 pairs in 2000 (Liordos & Goutner 2008a) mainly nested on willows, over water, in association with 12 waterbird species (Nazirides & Papageorgiou 1996). Lake Mikri Prespa is part of the Prespa watershed,
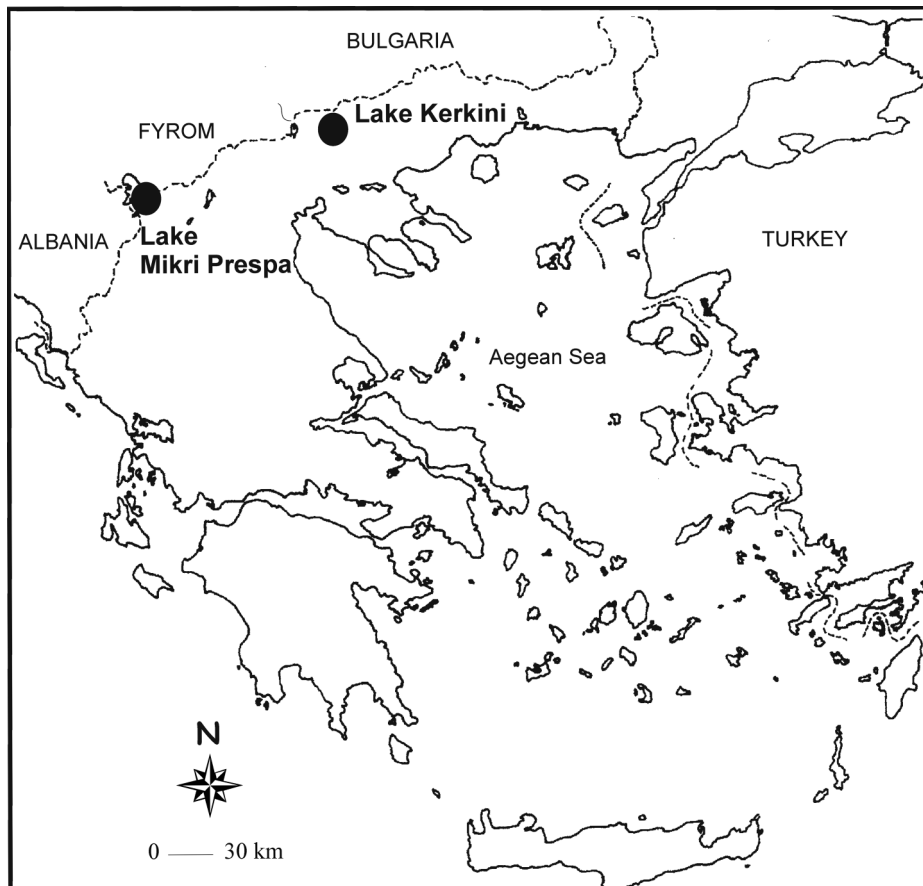

Figure 1. Map showing the study areas within the context of Greece.

along with Lake Megali Prespa and the surrounding forested mountain slopes. It is situated at an altitude of 853.5 m a.s.l. extending over 47.35 km^2 of which 43.5 km^2 belong to Greece. Great cormorants (220 pairs in 2001; Liordos & Goutner 2008a) nested on Vidronissi Island, the smaller of the two occurring in the lake, on a stand of ancient juniper *Juniperus foetidissima* trees.

The Ricklefs & White (1975) method was used to reduce disturbance at the colony. The Lake Kerkini colony was visited on 4 and 15 May 2000, while Lake Mikri Prespa on 28 April and 9 May 2001. Four body measurements of 39 nestlings from 18 broods (0.75% of total) and 30 nestlings from 11 broods (5% of total) were taken at the Lake Kerkini and Lake Mikri Prespa colonies respectively. In the first visit fresh body mass, bill length, bill + head length, and tarsus length of each nestling were measured. Body mass was measured using Pesola spring balances of 100, 500, 1000, 2500, and 5000 g to the nearest 1, 5, 10, 25, and 25 g respectively. Bill length (the upper mandible of the bill, from tip to first feathers), bill + head length together (from the tip of the bill to the back of the skull), and tarsus length (from middle of midtarsal joint to distal end of tarsometatarsus, with foot closed towards tail) were measured with digital calipers to the nearest 0.01 mm. All measurements were taken by the same person (Vasilios Liordos) to eliminate variation among investigators. All visits were made at the same time of day, from 09:00 to 12:00 am, to avoid diurnal variations in body mass. During the first visit at Lake Kerkini two "wet" nestlings were found, that could be assigned to 1-day-old status (i.e., day = 0, Cramp & Simmons 1977; Johnsgard 1993). The newly-hatched nestlings weighed 33 and 35 g respectively, and measured 9.6 and 11.6 mm bill length, 30.7 and 31.1 mm bill + head length, 12.4 and 12.4 mm tarsus length. After measurements, nestlings were individually marked with plastic colour rings placed on the tarsus, and returned to their nests. On the second visit, 11 days later, the measurements of the same nestlings were repeated. Body measurements of 11 adults collected from the Axios and Evros Deltas, northern Greece (Liordos & Goutner 2007, 2008b), were also used for comparison.

Data analysis followed Ricklefs & White (1975), using the S-PLUS® 6.2 statistical package (Insightful Corp.) for curve-fitting. The equation best describing the initial-final measurements plot was first estimated. Then, the values of each growth variable at ages incremented by the time interval between successive nest visits (11 days) were estimated, by using as starting values the average growth of the two "wet" nestlings from Lake Kerkini (34 g for body mass,

10.6 mm for bill length, 30.9 mm for bill + head length, and 12.4 mm for tarsus length). The starting values were calculated from only two nestlings and for one of the studied colonies, but were used for both colonies as they fell within their range of measurements. Re-calculated growth data points that fell within the original data range were only retained. Growth parameters were then derived iteratively by fitting logistic growth curves to the growth values re-calculated from the above equation (Ricklefs 1967, 1968, 1973) using the nls command in S-PLUS® 6.2 (Crawley 2002). Between-sites comparisons of growth parameters were made using two-tailed t tests (Motulsky & Christopoulos 2004). The t_{10-90} index, the time interval (in days) needed for growth from 10% to 90% of the equation's asymptotic value was also calculated according to Ricklefs (1967).

Results

The final to initial measurements plots were best described by the logarithmic equation, for all growth variables in both colonies:

$$M_2 = a + b \cdot \ln(M_1) \tag{1}$$

where M_1 and M_2 are the initial and final measurement respectively, a and b the logarithmic equation constants. The estimated values of the equation constants are given in Table I.

Growth data at successive 11-day intervals were then calculated using equation (1). Growth values for five age points (up to the approximate age of 44 days) fell within the original measurements for all growth variables and were used for the estimation of growth models. Logistic growth models were then fitted to the re-calculated growth patterns for all variables at both Lake Kerkini and Lake Mikri Prespa colonies (Table II, Figure 2):

$$GV = A / \left[1 + e^{-K \cdot (t-T)} \right] \tag{2}$$

where GV is the growth variable, A its asymptotic value, t the nestling's age in days, K the logistic growth rate constant in day^{-1}, which is proportional to the overall growth rate (Ricklefs 1968), and T the inflection point in days, which occurs when 50% of the total logistic growth has been accomplished.

The intercolony comparison of derived logistic growth parameters revealed variable patterns. Growth parameters (A, K, T) did not significantly differ between Lakes Kerkini and Mikri Prespa for body mass (Table II). The t_{10-90} index was also similar in both colonies. The asymptotic value (A) and

Table I. Parameter values of the logarithmic equation, $M_2 = a + b \cdot \ln(M_1)$, which best described the final (M_2)-initial (M_1) measurements plots, for each growth variable of nestling great cormorants, using measurements taken at the Lake Kerkini and Lake Mikri Prespa breeding colonies, at 11-day time intervals.

Growth variable	Lake Kerkini			Lake Mikri Prespa		
	a	b	R^2	a	b	R^2
1. Body mass (g)	−863.58	393.49	0.97	−836.66	390.12	0.97
2. Bill length (mm)	−19.06	21.21	0.94	−9.61	18.7	0.97
3. Bill + head length (mm)	−104.78	50.73	0.96	−89.33	48.19	0.95
4. Tarsus length (mm)	11.12	15.17	0.87	18.63	12.48	0.88

Table II. Values of the logistic equation parameters for body mass (1), bill length (2), bill + head length (3), and tarsus length (4) of nestling great cormorants, re-calculated from the logarithmic equation which fitted well to the actual growth data of initial-final measurements taken during the growth period at the Lake Kerkini and Lake Mikri Prespa breeding colonies. A is the asymptotic value of growth variables, K is the logistic growth constant (day^{-1}), and T is the age (days) at which the inflection point occurs. Parameters are given with their standard errors (SE) and compared with two-tailed t tests. Significant differences are given in italics. R^2 values of the regressions and the t_{10-90} time (days) required to complete logistic growth from 10 to 90% of the asymptote are also given.

Growth variable	Colony	A	SE	t_4	K	SE	t_4	T	SE	t_4	R^2	t_{10-90}
1. Body mass (g)	L. Kerkini	2126.70	26.37	0.060	0.205	0.011	0.064	16.6	0.327	0.431	0.98	21.4
	L. M. Prespa	2128.95	26.35		0.206	0.011		16.4	0.329		0.98	21.3
2. Bill length (mm)	L. Kerkini	70.57	0.47	1.966	0.131	0.003	2.101	13	0.201	*4.679***	0.98	33.6
	L. M. Prespa	68.83	0.75		0.147	0.007		11.2	0.328		0.98	29.9
3. Bill + head length (mm)	L. Kerkini	147.89	0.34	*4.078**	0.109	0.011	0.488	12.2	0.072	*5.929***	0.99	40.3
	L. M. Prespa	151.51	0.82		0.121	0.022		11.1	0.171		0,99	36.2
4. Tarsus length (mm)	L. Kerkini	75.42	1.24	*2.965**	0.201	0.016	0.721	7.9	0.376	1.761	0.96	21.8
	L. M. Prespa	71.31	0.62		0.215	0.011		7.1	0.255		0.97	20.4

*$p < 0.05$; **$p < 0.01$

growth rate (K) were also similar for bill length in both colonies, although the inflection point (T) occurred significantly later and the t_{10-90} time interval needed more time to be accomplished at Lake Kerkini than Lake Mikri Prespa. In contrast, asymptotic value (A) was significantly longer at Lake Mikri Prespa than Lake Kerkini for bill + head length, whereas the other parameters (K, T, t_{10-90}) followed the same trends as bill length. Opposing to bill + head's, asymptotic tarsus length (A) was significantly longer at Lake Kerkini than Lake Mikri Prespa, with other growth parameters (K, T, t_{10-90}) being similar in both colonies.

Goutner et al. (1997) studied the growth of great cormorant nestlings in 1994 in the Axios Delta, northern Greece, also using the same method and time interval between visits (11 days), their findings being therefore directly comparable with the present study. Pairwise comparisons showed that asymptotic values (A) were not statistically different between the Axios and the two lacustrine colonies for body mass and bill length (2105 g and 68.8 mm respectively for the Axios Delta nestlings; $t_4 < 2.322$, $p > 0.081$), whereas the Axios Delta nestlings had shorter bill + length and tarsus (141.5 and 67.7 mm respectively) than either the Kerkini or Mikri Prespa ones ($t_4 > 3.923$, $p < 0.017$). On the other hand, growth rates (K 0.203, 0.132, 0.126, 0.222 day^{-1} for body mass, bill, bill + head, tarsus respectively in the Axios Delta) were not significantly different in the Axios Delta than either of the other colonies for all the growth variables ($t_4 < 1.861$, $p > 0.136$). In contrast, the inflection point (T 18.6, 15.7, 13.8, 10.0 days for body mass, bill, bill + head, tarsus respectively in the Axios Delta) occurred significantly later in the Axios Delta than either of the other colonies for all the growth variables ($t_4 > 4.594$, $p < 0.010$).

The mean body mass of 11 adult birds was 2529 ± 311 g (min. 1940 g, max. 3000 g), mean bill length 70.64 ± 3.28 mm (66.00−74.72 mm), mean bill + head length 152.43 ± 2.74 mm (149.00-155.00 mm), and mean tarsus length 71.66 ± 1.85 mm (68.69-74.48 mm). Adult body mass was about 460 g higher than asymptotic nestling body mass. Adult values of the bill, bill + head and tarsus were similar to asymptotic values of nestling growth.

Discussion

Great cormorants exhibit sexual dimorphism in size, with males generally being larger and heavier than females (Koffijberg & van Eerden 1995; Liordos &
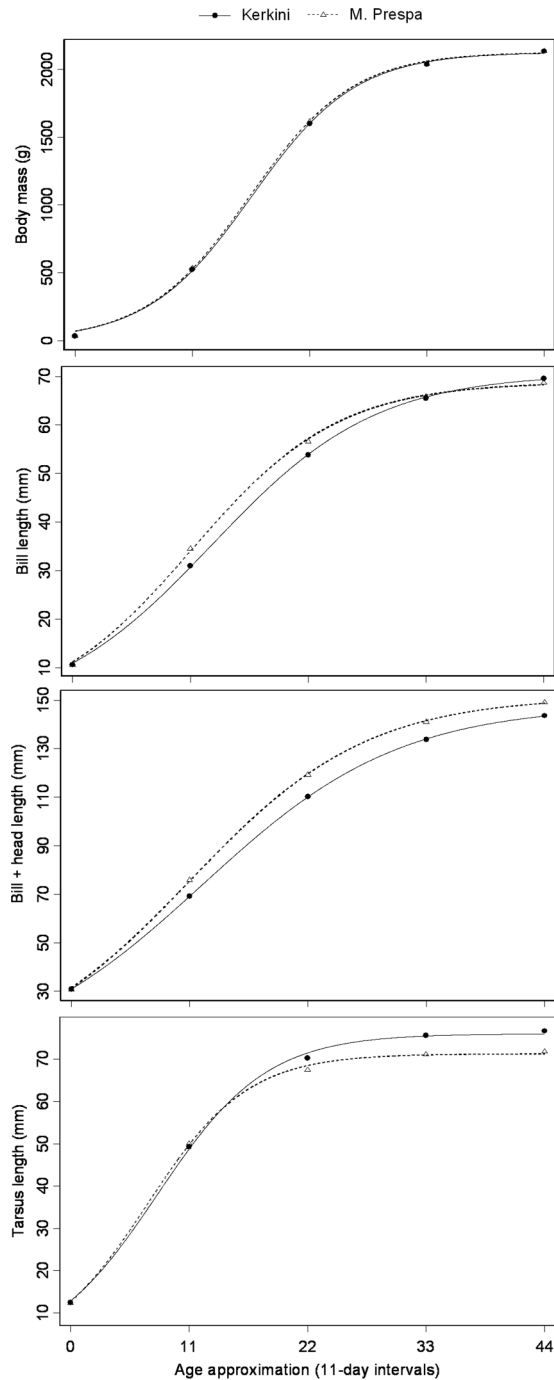
Figure 2. Postnatal growth of four body components of great cormorant nestlings from Lake Kerkini and Lake Mikri Prespa. Composite logistic growth curves were fitted to 5-point data sets, re-calculated from the logarithmic equation, which fitted well to the actual growth data of initial-final measurements of 39 and 30 nestlings from Lakes Kerkini and Mikri Prespa respectively. Approximate age at 11-day intervals is given, by using the average values of two newly-hatched nestlings found at Lake Kerkini as starting points. Data points that fell within the range of actual measurements were only used.

Goutner 2008b), so sex has a large effect on nestling growth patterns (Shmueli et al. 2003). However, the sex of the nestlings studied in this paper was not known. Other proximate and ultimate factors that could affect nestling growth include food supply, weather, hatching order, parental quality, hatching date and brood size, nest predation, subspeciation and hybridisation. Given these potential sources of bias, the method proposed by Ricklefs & White (1975) was applied on growth data of nestling great cormorants. The study of avian growth is labour-intensive and time-consuming because many nestlings must be measured several times during the growing season. This involves many visits to the colony that can stress both nestlings and parents and, if combined with other factors (bad weather, nest predation), can cause nest abandonment and breeding failure (Zach & Mayoh 1986). Great cormorants nest high in trees (4-6 m) in both colonies and nestlings tend to leave the nest when scared, risking falling off the tree and dying. In addition, they nest in a mixed colony with 12 waterbird species at Lake Kerkini, including the also sensitive pygmy cormorant *Phalacrocorax pygmeus* and Eurasian spoonbill *Platalea leucorodia*, which are at a similar risk. To avoid these shortcomings, the method of Ricklefs & White (1975), which requires only two visits to the breeding colony was used to describe the patterns of postnatal growth of the great cormorant. Adding to this, another significant advantage of this method is that the constructed composite growth curves can be used as biological indicators of the environment by revealing spatio-temporal variation in ecological conditions that influence nestling growth (Ricklefs & White 1975). The conditions that animals face during their growth period can affect survival and later reproductive success (Lindström 1999) and therefore the comparison of avian growth models is useful for revealing intraspecific variation in the inherent growth pattern (Ricklefs 1973).

Ricklefs & White (1975) used measurements from 25 nestlings to describe their method. In this study their methodology was followed by taking measurements of 39 and 30 nestlings from Lakes Kerkini and Mikri Prespa respectively. The measurements were taken when nestlings of different age/developmental stages were available in the colonies so that a large part of the growth period could be studied. In fact, subsequent analysis allowed for the description of approximately the 44 first days of nestling age, the greatest part of the fledging period (c. 50 days, Cramp & Simmons 1977). In addition, the average growth values of two newly-hatched chicks, which fell within the range of measurements of both

colonies, were taken as starting points for the calculation of the 11-day intervals, thus allowing for the comparison between the subsequently re-calculated growth patterns, while at the same time representing a reasonable approximation of nestling age. The logistic growth model fitted well with the growth pattern re-calculated from the logarithmic equation (R^2 between 0.96 and 0.99). The growth parameter estimates can be useful indicators of the growth patterns, if the logarithmic function has a good fit for the initial-final measurements relationship. Indeed, the logarithmic equation fitted well to the actual growth data of initial-final measurements, with R^2 ranging from 0.87 (tarsus length) to 0.97 (body mass). The comparison of the calculated nestling growth models between the studied Kerkini and Mikri Prespa and also the Axios (Goutner et al. 1997) colonies, revealed several differences and similarities, with the most important being: a) logistic growth rates did not significantly differ between all three colonies for all growth variables; b) asymptotic length was significantly different for bill + head and tarsus between all three colonies; and c) the inflection point occurred significantly later in the Axios than at both the Kerkini and Mikri Prespa colonies for all the growth variables.

During their period of growth, nestlings may encounter unfavourable environmental conditions that cause phenotypic changes from the normal ontogenetic development given by their genotype. Such phenotypic changes, arising from variation in food availability or other environmental conditions, are known as developmental plasticity (Schew & Ricklefs 1998; Moe et al. 2004). In a comparative study of altricial birds, Saether (1994) showed that nestling growth significantly correlated with the provisioning rate of the parents (after adjusting for body size). Food availability seems to be the most important environmental factor for postnatal growth (Martin 1987) and also most other environmental causes of growth variation seem somehow related to food supply (Gebhardt-Henrich & Richner 1998). On the other hand, Moe et al. (2004) showed that overall structural growth was very well conserved even during food restriction in nestling European shags *Phalacrocorax aristotelis* and they argued that this could have been shaped by sibling competition. Structural size is therefore expected to vary less between years and areas (with varying food availability) than body mass. The high increase of fish prey abundance and availability in the great cormorant's fishing grounds has been identified as the major factor responsible for the bird's high rate of population increase in Greece during the last 20 years (Liordos & Goutner 2008a). Therefore, food

supply could not be considered as a restricting factor of growth in the studied colonies, especially of structural variables such as bill + head and tarsus length. Adverse weather conditions have been found to affect the foraging success of the parents in the European shag, thus exposing nestlings to variable food provisioning during early development (Velando et al. 1999). Adverse weather also increases the need for brooding at the expense of foraging (Beintema & Visser 1989). During the course of this study, and also when studying the reproductive performance of great cormorants at the Kerkini, Mikri Prespa and Axios colonies in 2001 and 2002, neither extreme weather events nor differences in climatic conditions between the colonies were reported (pers. obs.; NOA 2011).

When the possibility that the observed differences in growth were caused by differences in environmental conditions can be excluded, other factors such as hatching order, brood size, sex-specific growth, subspeciation and hybridisation should be examined. Léger & McNeil (1987) reported that nestling double-crested cormorants *Phalacrocorax auritus* were fed the same amount of food and their growth rates and final weights did not seem to vary as a function of hatching order or brood size. Kalmbach & Becker (2005) found that the growth rates of nestling neotropic cormorants *Phalacrocorax brasilianus* did not vary with hatching position, irrespective of brood size, except in four-chick broods where last-hatched chicks grew slower and showed a higher pre-fledging mortality. The effects of these factors on nestling growth are exacerbated during periods of low food availability, when parents cannot provide enough food for all chicks (Gebhardt-Henrich & Richner 1998), which did not seem to be the case in the studied colonies. Velando et al. (2000) found that the wing, tarsus and body mass asymptotes were larger in male European shags, but females had a higher growth rate. Asymptotic head length was also larger in males, contrasting to the similar asymptotes in bill length between the sexes. As referred to earlier, male great cormorants are also generally larger and heavier than females (Liordos & Goutner 2008b) and the observed differences in the asymptotic bill + head and tarsus lengths between the colonies could be partly explained by possible differences in the sex ratio of each sample. Subspecific differentiation also occurs, with the continental *P. c. sinensis* being smaller than the Atlantic coast *P. c. carbo* (Newson et al. 2004). The two subspecies of the great cormorant have been found to coexist and hybridise in England (Kirby et al. 1995; Goostrey et al. 1997; Winney et al. 2001). The smaller *P. c. sinensis* is regularly occurring in Greece,

however the incidence of *P. c. carbo* and their potential hybridisation have not been established. All in all, avian growth is a complex phenomenon determined by many factors and by their interactions and present findings do not allow for drawing additional conclusions on how they affected the growth of nestling great cormorants. Further investigations are therefore required to resolve these issues, through research integrating the study of physiological, ecological and genetic aspects of growth.

In a study of nestling great cormorants in the Barents Sea, Belopol'skii (1957 in Ricklefs 1973) calculated a Gompertz growth rate of 0.078 day^{-1} for body mass. This corresponds to a logistic growth rate of 0.115 day^{-1} (Starck & Ricklefs 1998b), lower than the Greek populations' values. Higher energetic demands for thermoregulation not met by food provisioning rates in the cold arctic Barents Sea, compared to the temperate Mediterranean colonies, may explain the differences in nestling growth.

Structural size variables displayed different growth patterns. Tarsus grew faster and completed growth earlier than bill at both Lakes Kerkini and Mikri Prespa (this study), and in the Axios Delta (Goutner et al. 1997) for the great cormorant and in New England for the double-crested cormorant (Dunn 1975). Great cormorant nestlings beg for food by waving their bill and throat, then inserting their head into their parent's mouth to eat (Cramp & Simmons 1977; Olver & Kuyper 1978; Johnsgard 1993). Nestlings therefore may not benefit from an early bill growth, but a fast growing tarsus may confer competitive advantage in the struggle to reach parental mouth before siblings. The lower growth rates of bill + head than bill, also observed in all the areas, may be probably due to the fact that the skull is growing slower than the bill, thus affecting the composite bill + head growth (Ricklefs 1973; Ricklefs et al. 1998).

Asymptotic lengths of the bill, bill + head and tarsus were similar to the average adult lengths. On the other hand, asymptotic body mass of nestlings was only 84% of adult body mass. The same trend has been observed for other members of the family Phalacrocoracidae, such as the double-crested cormorant (Dunn 1975; Léger & McNeil 1987) and the European shag (Østnes et al. 2001). This contrasts other altricial and semialtricial birds, which normally achieve higher body mass than adults before fledging (Ricklefs 1973).

Growth rates of Greek great cormorant nestlings are similar to those of the double-crested cormorant and higher than those of the European shag. Growth rates of body mass have been found 0.191 day^{-1} (Léger & McNeil 1987), 0.196 day^{-1}

(Palmers 1962 in Ricklefs 1968, 1973), 0.208 day^{-1} (Dunn 1975), 0.235 day^{-1} (Cleary 1977) for the double-crested cormorant, and 0.172 day^{-1} (Østnes et al. 2001), 0.147–0.190 day^{-1} (Starck & Ricklefs 1998b) for the European shag. Members of the family Phalacrocoracidae usually have higher growth rates when compared to other altricial seabirds of comparable size. Members of the family Fregatidae (A = 854–1455 g) have logistic growth rates from 0.039–0.051 day^{-1}, and of the family Sulidae (A = 800–4080 g) from 0.052–0.138 day^{-1} (Starck & Ricklefs 1998b).

This study presented the postnatal growth of the great cormorant in two Greek colonies. The method proposed by Ricklefs & White (1975) for constructing average growth curves from only two visits was used. This method has considerable advantages such as: it can be applied fast and with little effort, the disturbance to birds is kept at a minimum, and spatial and temporal comparisons of growth patterns can be made. Results revealed similarities in nestling growth rates between the colonies for all the growth variables, as well as significant variations, especially in the asymptotic values of structural variables such as bill + head and tarsus length. The need for further examination of the effects of proximate and ultimate factors on nestling growth has also been highlighted. In doing so, this method could be useful for the monitoring of the influence of spatial and temporal variation of ecological conditions on nestling growth.

Acknowledgements

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