

**DIET AND GROWTH OF GREAT CORMORANT (*PHALACROCORAX CARBO*) NESTLINGS IN A MEDITERRANEAN ESTUARINE ENVIRONMENT (AXIOS DELTA, GREECE)**

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**ABSTRACT**

The diet and growth of great cormorant (*Phalacrocorax carbo*) nestlings were studied in the Axios Delta, Greece in 1993 and 1994. The diet, based on analyses of regurgitations, consisted of fish from 12 families. In both years, the dominant prey were the goby *Gobius jazo* and mullets (Mugilidae). There were changes in number and wet-biomass prey composition during the study, probably due to the opportunistic foraging behavior of the birds. Most prey occurred in aquatic environments at all salinity levels, consisted mainly of benthic fish, and had no particular economic value. The growth of great cormorant nestlings was analyzed using a modification of the method proposed by Ricklefs and White (1975). Sets of estimated values for all variables studied (tarsus, bill, bill + head, and weight) plotted against age yielded sigmoidal curves. The increase in all growth variables over time was best described by the logistic equation. Body weight and tarsus increased at similar rates, and were faster than those for the bill and the bill + head measurements. The inflection point was reached by the tarsus, bill, bill + head, and weight at 10.0, 15.7, 13.5, and 18.6 days, respectively. The potential adaptive significance of this growth pattern is discussed.

**INTRODUCTION**

The great cormorant (*Phalacrocorax carbo*) breeds in large and increasing numbers in western and northwestern Europe (Cramp and Simmons, 1977; Suter, 1989), while its breeding population in the Mediterranean is smaller and localized. In the past, breeding has been recorded in Tunisia; nowadays small colonies are known in Spain, Italy, and the former Yugoslavia (Cramp and Simmons, 1977; Van Eerden and Munsterman, 1986). In Greece there are a few colonies, located in inland lakes, coastal wetlands, and

on offshore islands. In the Mediterranean, the great cormorant has been found to winter in Tunisia (Van Eerden and Munsterman, 1986), in the south of France and parts of Italy (Baccetti, 1986), and in Greece (Handrinos, 1993). The only dietary studies conducted in the area involve wintering birds and are based mainly on pellet analysis: Im and Hafner (1984) described the species' diet in southern France; Van Eerden and Munsterman (1986) provided some information for Tunisia; and Boldreghini et al. (1993) and Sara and Baccetti (1993) presented data from different parts of Italy. The growth and development of nestlings has received little attention, and we know of only one detailed study (Platteeuw et al., 1995).

In this study, we describe for the first time the diet and growth patterns of great cormorant nestlings in the Mediterranean. Motivated by fishermen's allegations that this species preys heavily upon fish populations of economic importance, we also investigated whether or not this was true in the Axios Delta area. The particular site was selected because it hosts the largest coastal colony of the great cormorant in Greece.

#### STUDY AREA AND METHODS

The Axios Delta (40°30'N, 22°53'E) is part of a wetland complex which covers 68.7 km<sup>2</sup> (Athanasiou, 1990) along the west coast of the Thermaikos Gulf, and includes the estuarine and deltaic areas of the rivers Axios, Aliakmon, Loudias, and Gallikos. This wetland complex has been recognized under the Ramsar Convention as internationally important for waterbirds. The Axios Delta comprises a variety of habitats, including salt- and freshwater marshes, ricefields, lagoons, open sea, vegetated coastal islets, sandy shores, forested river banks, and tamarisk bushland. The colony site was located on an island at the mouth of the Axios River. During the study period, approximately 160 pairs of cormorants nested there. Most nests were made on alder (*Alnus glutinosa*, 4–12 m high) and willow trees (*Salix* sp., 7–10 m high), but some were found on tamarisk bushes (*Tamarix* sp., 4–6 m high).

We visited the colony on 20 May, 30 May, 2 June, 6 June 1993, and 12 May, 23 May, and 3 June in 1994. For the diet study, we collected regurgitations dropped by older nestlings (most of them close to fledging) during our visits (from 1000 to 1300 hours). Regurgitations were collected in plastic bags and placed in a cooler until carried to the laboratory, where they were deep-frozen until analysis. This material was sorted after thawing and prey items were identified to the lowest possible taxon. We used the following methods to estimate prey biomass: For the most important fish taxa, we established relationships between body weight (WT) and linear dimensions [total (TL), standard (SL), and head (HL) length] which were of the type:

$$WT = a * (\text{linear dimension})^b$$

The equation for *Gobius jozo* (Table 1) was constructed from measurements taken from 30 intact regurgitated specimens collected in 1994. To estimate the equation for *Sardina pilchardus* (Table 1), we measured 37 sardines purchased in the market (their size range was the same as that of individuals found in regurgitations). The average weight of 57



Table 1

Parameters of length (mm) used to estimate fresh weight (g) of certain fish species from regressions

Species	<i>a</i>	<i>b</i>	SE( <i>b</i> )	<i>n</i>	range (mm)	<i>R</i> <sup>2</sup>
<i>Gobius jozo</i>						
TL	-2.847	1.958	0.258	30	95-165	0.673
HL	-2.149	2.306	0.236	30	24-36	0.774
<i>Sardina pilchardus</i>						
SL	-3.216	2.193	0.194	37	118-149	0.784
HL	-0.240	1.114	0.214	37	24-35	0.438
Mugilidae*						
SL	0.0000234	2.949	0.007	375	> 40	0.998

TL, total length (mm); HL, head length (mm); SL, standard length (mm); \* = data from Koutrakis and Sinis (1994, table 8); SE(*b*) = standard error of *b*; *n* = number of fish.

non-measurable *G. jozo* was assumed to be the same as that of the sample of measurable individuals (17 g, *n* = 220). All measurements were normally distributed so no transformations were made. For mullets (Mugilidae), due to difficulties in identification, we used the relationship between weight and SL for *Lisa ramada* (Table 1) given by Koutrakis and Sinis (1994, table 8), because this is the commonest mullet species in the wetlands of northern Greece and its dimensions are intermediate between those of the other co-existing species, *L. saliens* and *Chelon labrosus* (Koutrakis and Sinis, 1994). All specimens belonging to less common taxa were in good enough condition for their actual weight to be used, which generally appears to represent well the weight of the ingested food (Pilon et al., 1983). Information about habitat use was based on our observations in the study area.

The nestling growth study was conducted in 1994. Due to the height of the nests and the tendency of older chicks to fledge prematurely when disturbed, frequent nest visits were not possible. Therefore, we used measurements taken from individually marked (with colored plastic leg-bands) nestlings of unknown ages on two occasions to construct growth curves following the method proposed by Ricklefs and White (1975). Twenty-three young from eight broods were measured either on 12 and 23 May, or on 23 May and 3 June, between 1000 and 1300 hours (the interval between visits was 11 days in both cases). We measured the lengths of the tarsus (TARS), culmen (tip of bill to first feather, BILL) and bill and head together (B+H) to the closest 0.1 mm with vernier calipers, and body weight (WT) to the closest 5 g with spring scales. Dr. M.R. Van Eerden (Rijkswaterstraat Directie, The Netherlands), using weight gain data from young cormorants of known ages from The Netherlands (Platteeuw et al., 1995), estimated the age of the six youngest nestlings in our sample (within 0.1-day precision) from their weights. This allowed us to draw growth curves on a true, rather than a relative age scale. The fact that these age estimates were based on nestling weights

makes them, and the position of our growth curves relative to the X-axis, less reliable, but we believe that they are not highly inaccurate for reasons that will be discussed later.

In order to increase the precision of our estimates, we deviated from Ricklefs and White's (1975) methodology in several ways. First, for each growth variable, we estimated the line of best fit to the plot of final to initial measurements (curve A in their fig. 1) with a statistical package (SYSTAT Inc., 1992), instead of fitting the curve by hand. Second, in estimating the values of each growth variable at ages incremented by the time interval between successive nest visits (11 days), we used the equation of the above-mentioned line to calculate the ordinate of points on it for given x-values (or vice versa), instead of defining these points graphically (as in fig. 1 in Ricklefs and White, 1975). Next, for each growth variable, we estimated its values at 11-day intervals four times (instead of only once), starting from the values of actual measurements at four different early ages (5, 7, 10, and 11 days; Dr. Van Eerden's age estimates, see below). We did so because we could not be sure how well each of these measurements represented the average population value of the growth variable at the attributed age. Plotting all four sets of estimates against age should produce a more reliable growth curve (drawn on a true age scale) for the whole population than the plot of a single set of such estimates. Finally, we estimated the equations that best describe the growth curves of the different variables using the NonLin procedure of SYSTAT, which also computes asymptotic standard errors and 95% confidence intervals for each parameter involved in the model.

## RESULTS

### DIET

The diet of cormorant nestlings consisted exclusively of fish from 12 families, including at least 24 species (Table 2). *Gobius jozo*, the only gobiid species present in the samples, dominated the diet in numbers in both years, but only in 1993 by weight. Mulletts (Mugilidae), although considerably less numerous, followed *G. jozo* in weight in 1993 and dominated in 1994 due to their greater size: the mean total length of *G. jozo* was  $123 \pm 12$  mm ( $n = 30$ ), whereas the mean standard length of Mugilidae was  $167 \pm 32$  mm ( $n = 16$ ). Among other fish, *S. pilchardus* (Clupeidae) and *Lithognathus mormyrus* (Sparidae) were the most important, especially by weight. The remaining species appeared to be less important constituents of the diet.

The composition of the nestlings' diet changed over time during both study periods, in both numbers and wet biomass (Fig. 1). In both years, the abundance of *G. jozo* showed an increase early in the study period and then remained stable and high. This species' weight, however, increased continuously during the 1993 study period, but varied little in 1994. Mulletts did not vary much in either abundance or percent weight throughout most of each study period, but they disappeared completely from the nestlings' diet at the end of both periods. The importance of Sparidae was greater in 1994, and it increased towards the end of the study period. In 1993, it was greater in the

Table 2

Composition of the diet of great cormorant nestlings at the Axios Delta in 1993 and 1994

Diet composition	1993		1994		Salinity <sup>a</sup>	Habitat <sup>b</sup>	Economic value <sup>c</sup>
	Percentage	% wet weight	Percentage	% wet weight			
<b>Gobiidae</b>							
<i>Gobius jozo</i>	80.8	57.7	40.0	13.3	S, B,	V	3
Mugilidae <sup>d</sup>	4.4	19.8	13.6	36.2	S, B, F	E	2
<b>Clupeidae</b>							
<i>Sardina pilchardus</i>	2.7	4.0	17.0	8.7	S	E	3
<i>Sardinella aurita</i>	–	–	1.1	1.2	S	E	3
<b>Cyprinidae</b>							
<i>Cyprinus carpio</i>	0.3	3.5	–	–	F	V	2
<i>Carassius auratus</i>	0.3	0.9	–	–	F	V	2
<i>Carassius</i> sp.	–	–	1.1	0.5	F	V	2
<i>Leuciscus cephalus</i>	–	–	1.1	1.6	F	E, V	3
<i>Barbus</i> sp.	–	–	1.1	1.1	F	V	3
<i>Chondrostoma vardarensis</i>	0.3	1.0	–	–	F	E, V	3
<i>Vimba melanops</i>	0.7	1.1	–	–	F	V	3
<b>Carangidae</b>							
<i>Trachurus mediterraneus</i>	1.7	2.4	1.1	2.3	S	E, V	3
<i>Trachurus trachurus</i>	–	–	4.5	5.0	S	E, V	3
<b>Sparidae</b>							
<i>Diplodus annularis</i>	1.3	1.8	4.5	2.8	S, B	V	3
<i>Diplodus</i> sp.	0.3	1.3	–	–	S, B	V	3
<i>Sarpa sarpa</i>	–	–	1.1	4.0	S	V	3
<i>Oblada melanura</i>	–	–	2.3	3.5	S	E, V	2
<i>Lithognathus mormyrus</i>	–	–	3.4	10.5	S	V	1
<b>Soleidae</b>							
<i>Solea solea</i>	3.7	1.4	1.1	2.8	S, B	V	1
<i>Solea</i> sp.	1.3	3.1	–	–	S, B	V	1
<b>Scombridae</b>							
<i>Scomber scombrus</i>	–	–	2.3	3.7	S	E	2
<b>Labridae</b>							
<i>Coris julis</i>	0.3	1.1	–	–	S	V	3
<i>Symphodus doderleini</i>	1.3	0.7	–	–	S, B	V	3
<b>Centracanthidae</b>							
<i>Spicara</i> sp.	–	–	1.1	0.8	S	E, V	2
<b>Pomatomidae</b>							
<i>Pomatomus saltatrix</i>	–	–	1.1	1.2	S	E	1
<b>Atherinidae</b>							
<i>Atherina</i> sp.	0.3	0.1	–	–	S, B	E	3
Total	297	7,043	88	4,277 g			

<sup>a</sup>S: salt water; B: brackish water; F: fresh water; <sup>b</sup>E: column living, V: benthic; <sup>c</sup>1: great economic value, 2: some economic value, 3: no economic value; <sup>d</sup>*Lisa saliens* and *L. ramada*.



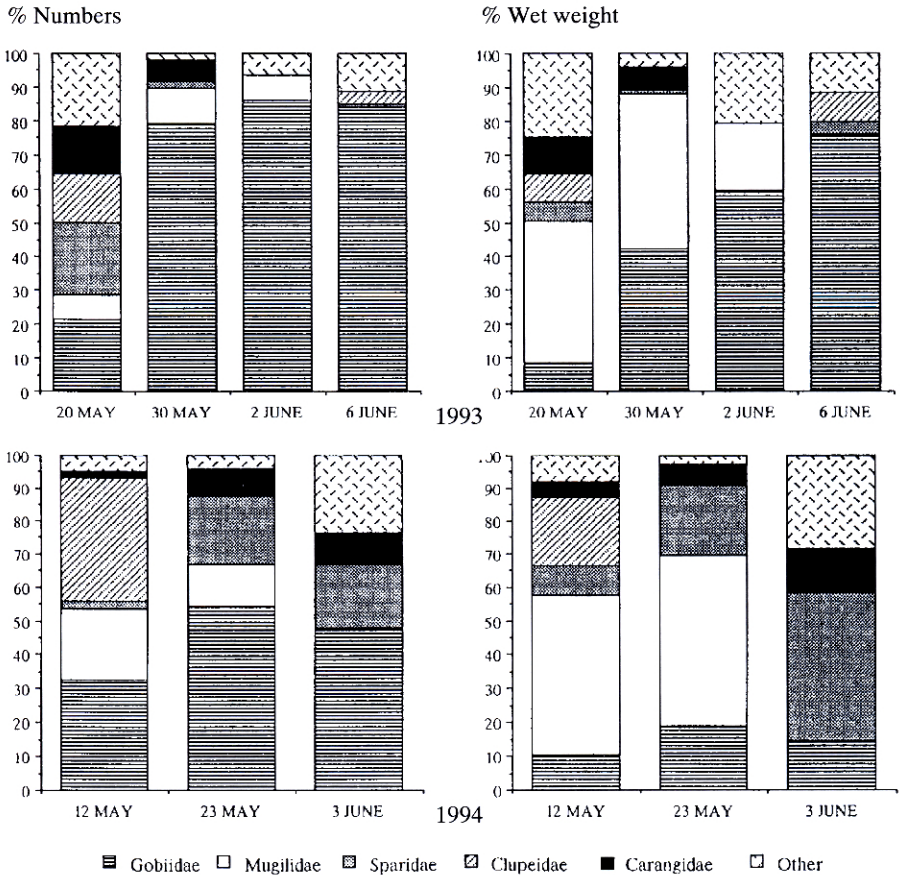


Fig. 1. Changes in the diet of great cormorant nestlings at the Axios Delta in 1993 and 1994.

beginning of the period, but it was insignificant overall. Clupeidae were more common in 1994, but they disappeared completely before the end of May. In 1993, they occurred in varying amounts, which were greater at the beginning and at the end of the study period. Carangidae showed little variability in 1994 (especially in weight), but in 1993 they declined with time and disappeared in early June. The importance of other fish fluctuated in 1993, being greatest in the beginning of the period, while in 1994, they reached a maximum at the end of the study period. The combined abundance and percent weight of the two most common taxa (Gobiidae and Mugilidae) were, overall, lower in 1994, allowing the other groups to reach higher percentages.

Most fish found in our samples, including the most common prey taxa, *G. jozo* and mullets, can be encountered in almost all salinity environments (Table 2, Fig. 2a). Fish limited to freshwater or fresh- and brackish-water areas made up a minor percentage of the cormorant nestling diet in both years. The proportion of saltwater fish was consider-

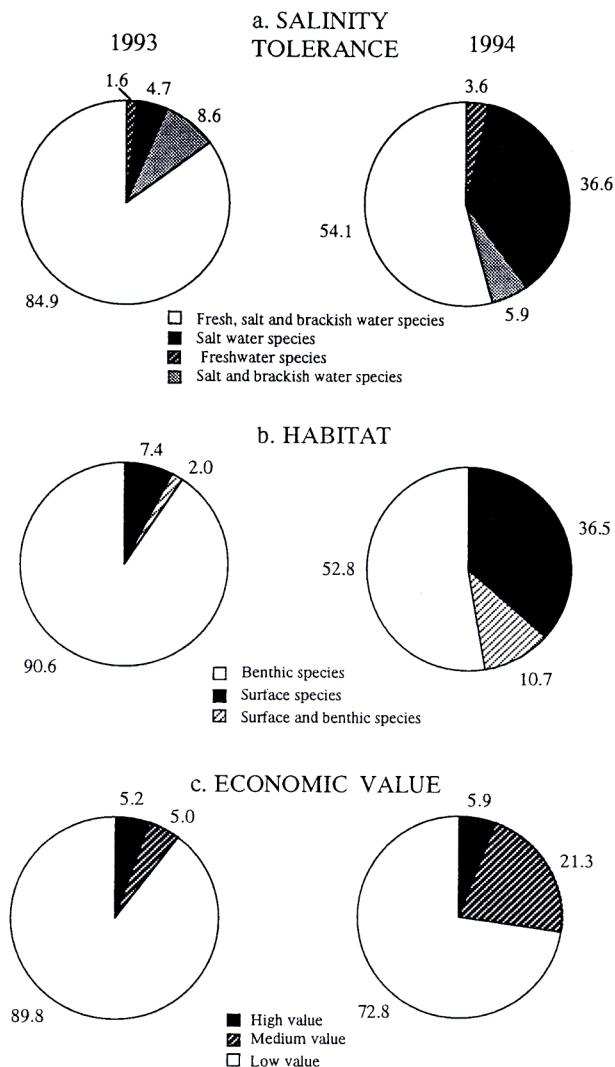


Fig. 2. Proportions of the prey numbers of great cormorant nestlings at the Axios Delta during 1993 and 1994, separated according to (a) salinity tolerance, (b) habitat use and (c) economic value.

able only in 1994, due mainly to the lower levels of *G. jozo* and mullets in that year. More than 90% and 50% of all prey fish were benthic in 1993 and 1994, respectively (Fig. 2b). In 1994 we found a significant proportion of pelagic species in the nestlings' regurgitations, mainly because *G. jozo*, which is a benthic species, was less common that year. Most fish in the cormorants' diet (70–90%) were of no economic importance (Fig. 2c). In both years, only 5–6% of prey fish were economically valuable. These

belonged to *Solea* spp., *Lithognathus mormyrus*, and *Pomatomus saltatrix* (Table 2), the first of which enjoys the highest price in the region. Among a total of 16 *Solea* specimens collected in the two years, only one was of almost marketable size (150 g). Four averaged 54 g and the remaining 11 were very small (8.5 g average).

### GROWTH

The line of best fit to the plot of final (MEAS2) to initial (MEAS1) measurements was estimated to be defined by the logarithmic equation  $MEAS2 = a + b \cdot \ln(MEAS1)$  for all variables, with different parameter values in each case. The initial measurements taken from the six smallest chicks in our sample and Dr. Van Eerden's estimates of their ages in days (based on weights) are shown in Table 3. Since no age estimate deviates more than 0.2 days from an integer value, for all growth variables, we used our actual measurements as representatives of the population's mean values at the closest integer-day ages (5, 7, 10, and 11 days; measurements from nestlings of the same age were averaged). Then, for each growth variable, we used these measurements as independent starting points for estimating the variable's values at ages incremented by the 11-day interval between nest visits (using the equation describing the MEAS2-MEAS1 relationship in the calculations). Hatchling (day 0) measurements were estimated by moving one 11-day "step" down from the values for day 11.

The four sets of estimates are plotted against age for each growth variable in Fig. 3A–D. In most cases, the points fit quite well clearly defined sigmoidal curves. This indicates that, generally, the measurements shown in Table 3 adequately represent the mean population values at their attributed ages. If these initial values are inaccurate, each set of estimates would produce a curve with a different relative position on the  $x$ -axis, and the fit to the average curve would be poor. This can be seen to some extent in tarsus length (Fig. 3A), where the scatter of points around the average curve is wider than in the other growth variables. If we had used, for example, only the set of values estimated from the measurement of the chick aged 11 days (open circles), we would have gotten a curve of a similar shape and the same asymptote, but shifted slightly to the

Table 3  
Initial measurements and age estimates for the six youngest great cormorant nestlings

Chick no.	TARS	BILL	B + H	WT	AGE
1	19.3	13.6	37.3	95	4.8
2	23.8	16.6	42.5	145	6.8
3	24.0	17.9	42.4	150	7.0
4	32.1	19.9	54.4	285	10.1
5	32.9	21.3	55.2	290	10.2
6	33.9	23.6	55.4	330	10.9

TARS, tarsus (mm); BILL, culmen (mm); B + H, bill and head (mm); WT, body weight (g); AGE (days), estimated by Dr. M.R. Van Eerden.



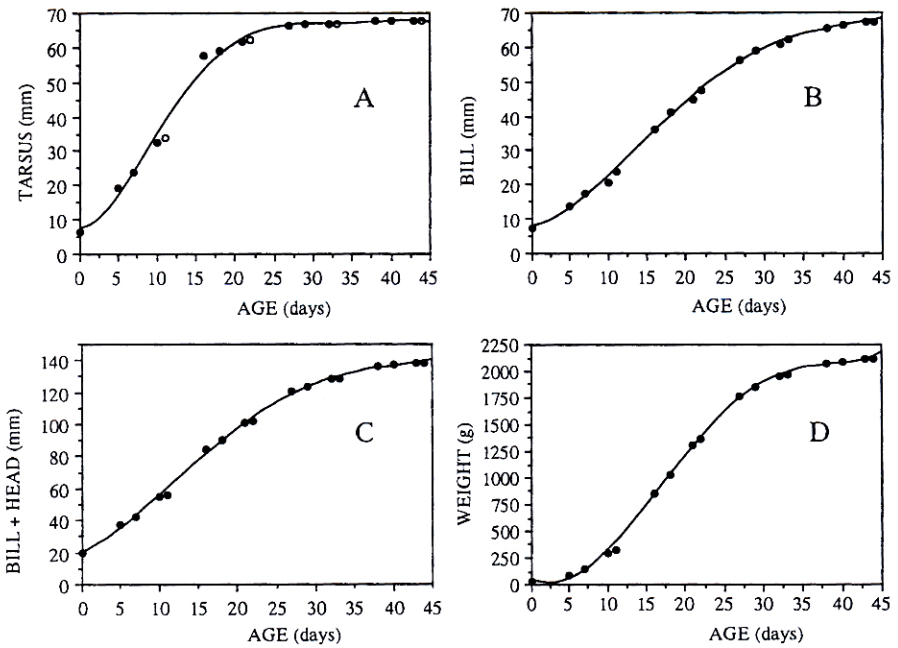


Fig. 3. Growth curves for great cormorant nestlings at the Axios Delta in 1994. Variables: A) tarsus; B) culmen (BILL); C) bill + head ; D) body weight (WEIGHT). Open circles in A are estimates derived from the tarsus measurement from 11-day old chick 6 (see text for further explanation).

right of the one shown. The position of the average curve shown (relative to the true chronological age scale of the  $x$ -axis) should be more reliable because it averages out possible errors across four different sets of estimated values.

After considering the logistic, Gompertz, and von Bertalanffy equations (Ricklefs, 1967, 1968, 1979), we found that the increase in all growth variables over time is described best by the logistic equation:

$$\text{VAR} = A / \{1 + \text{EXP}[-K*(\text{AGE} - T)]\}$$

where VAR is the growth variable in question,  $A$  its asymptotic value,  $K$  the logistic growth constant, AGE the nestling's age in days and  $T$  the time (in days) at which the inflection point of the curve occurs. The estimates of parameters  $A$ ,  $K$ , and  $T$  for each growth variable and their standard errors are given in Table 4. The high  $R^2$  values (even for tarsus, which shows the widest scatter of points) confirm the very good fit of all sets of points seen in Fig. 3A–D. Body weight and tarsus length increased at similar rates (indicated by  $K$  values of 0.203 and 0.222, respectively), which are faster than those of the bill and B + H (with  $K$  values of 0.132 and 0.125). Tarsus length was the first variable

Table 4

Estimated values of logistic equation parameters with their standard errors (SE) and  $R^2$  values of the model for each growth variable

Variables	A	SE	K	SE	T	SE	$R^2$
TARS	67.7	0.68	0.222	0.014	10.0	0.26	0.991
BILL	68.8	0.60	0.132	0.004	15.7	0.23	0.998
B + H	141.5	1.19	0.126	0.004	13.8	0.23	0.998
WT	2105.0	17.75	0.203	0.007	18.6	0.19	0.998

Symbols and units of growth variables as in Table 3. Logistic growth parameters: A, asymptote; K, growth rate coefficient; T, age (in days) at which inflection point occurs.

to approach its asymptotic value (by the end of the 4th week, Fig. 3A; all other variables did so around day 45, Fig. 3B–D). The inflection point of maximum growth, which occurs when 50% of the total logistic growth has been accomplished, was first reached by the tarsus, next by B + H, then by the bill, and finally by body weight (at 10.0, 13.5, 15.7, and 18.6 days, respectively); the 95% confidence intervals of these estimates did not overlap. We would expect weight to reach the inflection point earlier than bill and B + H, since it has a higher K value. The reason why we see the opposite trend is that weight gain is very slow in the beginning (until day 5). The differences in growth parameters between the bill and B + H are probably due to the fact that the skull has a different growth pattern from the bill and that it significantly influences the composite B + H length.

## DISCUSSION

### DIET

Although gobiids and mullets usually constituted more than 50% (and up to 90%) of the cormorant nestling diet, the full spectrum of the fish taxa taken (at least 24 species from 12 families) is the broadest ever recorded in the Mediterranean (Im and Hafner, 1984; Bolderghini et al., 1993; Sara and Baccetti, 1993). The difference between our results and those from other researchers may be partially attributed to the different origin of their material, i.e., pellets regurgitated by older birds in the winter. Nevertheless, it also reflects the species richness of the estuarine ecosystem of the Axios River, which comprises diverse aquatic habitats (Kazantzidis and Goutner, 1996). Other studies have also shown that a few fish species dominate the otherwise broad diet of cormorants (Pilon et al., 1983; Barrett et al., 1990; Suter, 1991a; Schratte and Trauttmansdorff, 1993). Gobiids have also been found to be eaten by cormorants elsewhere (Lack, 1945), but the dominance of this group, together with mullets, in our study seems to be due to the high local availability of these taxa. Cormorants, and Phalacrocoracidae in general, are opportunistic foragers, and their diet varies with availability of prey (Pilon et al., 1983; Blaber and Wassenberg, 1989; Ludwig et al., 1989). Therefore, although there are

no data from our study area on the population dynamics of the fish eaten by cormorants, the observed variation in diet between and within the study periods may be attributed to the birds' opportunistic feeding behavior. This is supported by the fact that their most common prey taxa can be encountered in aquatic environments of all levels of salinity, which means that they should be readily available. Additionally, among all fish species found in regurgitations, only *Sardina pilchardus* and *Sardinella aurita* consistently form large schools. Of these two, only the former was occasionally (early 1994 period) important for cormorants, which shows that these birds do not prey systematically on predictable fish congregations, but rather take whatever prey is available. Benthic species made up most of the nestlings' food, and this agrees with previous studies that reported on the cormorants' preference to forage near the bottom (Lack, 1945; Pilon et al., 1983; Barrett et al., 1990).

Many studies (summarized in Barrett et al., 1990) have shown that, although commercial fish species often contribute to the cormorant's diet, their consumption has no effect on fisheries. However, higher predation occurs in fish farms (Moerbeek et al., 1987; Suter, 1991b) and some rivers (Kennedy and Greer, 1988; Schratte and Trauttmansdorff, 1993). In certain Mediterranean countries, such as France, Tunisia, and Italy, cormorants consume economically important species in considerable proportions (Im and Hafner, 1984; Van Eerden and Munsterman, 1986; Sara and Baccetti, 1993). In our study area, our findings suggest that, at least during the main period of their growth, young cormorants are mainly fed species that are either unimportant (gobiids) or of secondary importance (mulletts) to fishermen. Moreover, since our samples were regurgitated mostly by large nestlings close to fledging, larger and more valuable (commercially) fish should not be under-represented in them. Thus, the economic effect of this cormorant population's reproduction on the local fishing community seems to be insignificant. Nevertheless, the Axios colony site was invaded by local residents in early May 1995, and most young birds were shot dead in their nests. This event indicates that objective results of scientific research did not affect deeply rooted prejudices of fishermen against large piscivorous birds.

### GROWTH

According to Ricklefs and White (1975), their method can produce accurate average growth curves drawn on a relative age scale. The shape of a growth curve constructed in this way depends on the relationship between final (MEAS2) and initial (MEAS1) nestling measurements, and it is expected to be the same for every randomly selected starting point on the MEAS2-MEAS1 curve (curve A in their fig. 1). This method yields best results when the number of nestlings measured is large and their age and size range at the time of the initial measurement is broad. Nevertheless, even when these conditions are not strictly met, results can still be used for comparisons between populations. Our sample of 23 nestlings should be adequate since Ricklefs and White (1975) used measurements from 25 young terns in their original paper. Although we do not have a lot of data from young and small nestlings (the six smallest ones were estimated to be between 5 and 11 days old), the age range of the chicks measured is very broad (from 5



days until close to fledging). Therefore, we believe that the shape of our growth curves, and the estimates of their asymptotes ( $A$ ) and growth rate coefficients ( $K$ ) are not in great error.

There is greater uncertainty about the position of our growth curves on the true chronological age scale of the  $x$ -axis, because our nestling age estimates were derived from body weights and used a relationship between weight and true age developed for a cormorant population in The Netherlands (Platteeuw et al., 1995). Ricklefs and White (1975) do not suggest the use of body weight for such purposes because of its sensitivity to feeding conditions and its high variability. If the pattern of weight gain and/or overall body size differs significantly between the Netherlands population and ours, our age estimates will be biased. Such errors affect the relative position of the growth curves on the  $x$ -axis and can influence estimates of the time at inflection point ( $T$ ) and the growth variables' values at hatching (day 0), but they do not weaken the reliability of the estimated asymptotes ( $A$ ) and growth coefficients ( $K$ ). Moreover, we believe that such errors were not great in our case for the following reasons: all age estimates are within 0.2 days from an integer value (Table 3); we constructed growth curves using four different sets of values (derived from the measurements taken from the nestlings of estimated ages) to average out possible errors associated with each set of values; for all growth variables (not only body weight), all sets of points cluster very tightly around the average growth curve (Fig. 3A–D); therefore, if there is an error in the age estimates, all nestlings' ages must be over- or underestimated by the same integer number of days; this is unlikely, given that age was estimated for six different chicks ranging from 5 to 11 days old.

Our least reliable estimates are those for hatchlings because they lie outside the range of our actual measurements. The one for weight (28 g), however, is at the lower limit of the range (28–30 g) given by Cramp and Simmons (1977) for European birds, but lower than that reported by Olver and Kuyper (1978) from South Africa (38 g). We were not able to find any information about hatchling linear measurements for comparisons. Our estimated asymptotic weight (2105 g) is found within the range (1938–2511 g) reported by Cramp and Simmons (1977) and very close to the value (2042 g) estimated from the Netherlands population studied by Platteeuw et al. (1995). Our asymptotic tarsus length (67.7 mm) is essentially the same as the average for adults of both sexes (67.75 mm) given by Cramp and Simmons (1977).

The logistic growth constant we estimated for body weight (0.203) is very similar to the one Dunn (1975) found for the double-crested cormorant (*Phalacrocorax auritus*) in New England (0.208), and which she considered as exceptionally high for the bird's size (*P. carbo* is even larger; Harrison, 1985). Platteeuw et al. (1995) report that *P. carbo* chicks in the Netherlands gain on the average 74.86 g/day (SE = 1.99) during the linear part of their growth curve (between days 5 and 30). During the same age interval, the slope of the linear regression of weight on age is 79.95 g/day (SE = 3.05) in our sample. Linear weight gain rate is 6.5% higher in our population, but the two values are not significantly different. The logistic  $K$  value (transformed from the reported Gompertz  $K_G$  using equation 5 in Ricklefs (1973) calculated for *P. carbo* from Belopol'skii's

(1957, in Ricklefs, 1973) data from the Barents Sea is much lower (0.115). This may be partially due to greater provisioning rates relative to nestling demands in our population: possibly higher food availability in a highly productive estuary, reduced costs for thermoregulation in the warmer Mediterranean environment, and a lower asymptotic weight (2105 g compared to about 2500 g in Belopol'skii's study); the range of clutch sizes reported (in Ricklefs, 1973) for that population (3–5 eggs) does not seem to differ from that in our study. We had no indications of chick malnourishment or starvation during our study (except for some possible cases of brood reduction, see below), and we believe that in our population nestling growth is not food-limited.

The growth curves we constructed (Fig. 3A–D) indicate that during the first week of life the lengths of the tarsus, the bill, and B + H increase faster than weight (which should reflect overall body size): weight enters the phase of rapid, linear growth after the 5th day, while the other variables do so close after hatching. This suggests that the development of the tarsus, the bill, and the head is more advanced than that of other body parts, and that their relative sizes must increase early in life. The same growth pattern can be seen in *P. auritus* (Dunn, 1975), while in that species the length of the ulna (a measurement we did not take) initially grows slowly, like weight.

O'Connor (1977), studying three species of altricial passerines in England, similarly found that the tarsus and the bill grow faster than other body parts and increase in relative size early in the nestling period, while wing length does so later. He interpreted these results as evidence for "adaptive variation within the development pattern", with resources being "allocated at any time to the growth of the components with the highest functional priority". The young birds studied by O'Connor use their legs and bill from the first day of life for orienting, stretching, and gaping towards parents in order to receive a meal. So, according to the author, more resources are allocated to the growth of these parts early in life, rather to the development of wings, which become functional only at fledging.

Our results also indicate that the tarsus grows faster and reaches its asymptotic length earlier than the bill, a phenomenon also seen in *P. auritus* (Dunn, 1975). Werschkul (1979) proposed that the adaptive significance of rapid hindlimb development and early locomotion in the little blue heron (*Egretta caerulea*) may be related to enhanced predator avoidance ability, which in turn releases the parents from having to guard the brood and allows them to invest more time in foraging for their young, increased competitive ability in an environment of intense sibling rivalry, and the potential to move away from the nest, if the latter is damaged, or while seeking protection from the elements.

Due to the inaccessibility of nest sites to terrestrial predators and the absence of large raptorial birds from our study area, cormorant nestlings were essentially immune from predation. A similar paucity of chick predation has been found for the shag (*Phalacrocorax aristotelis*) in Norway (Amundsen and Stokland, 1988). This, however, does not preclude the possibility that predation has been a selective factor in the evolution of certain morphological or developmental traits in the past (Caldwell, 1986). Bosque and Bosque's (1995) results support the hypothesis that predation represents a

selective pressure favoring rapid overall nestling growth, at least in small-sized altricial birds. Moreover, they indicate that species recently introduced to predator-free environments (and having experienced a relaxation of this selective pressure only for a relatively short period of time) do not exhibit any reduction in their nestling growth rates.

We have occasionally observed the disappearance, between visits to the nest, of smaller (and presumably later-hatched) nestlings, which may have died because of their inferior competitive status in the brood. Hatching asynchrony and brood reduction due to the starvation or eviction from the nest of smaller siblings have been reported for *P. carbo* (Cramp and Simmons, 1977; Olver and Kuyper, 1978). Platteeuw et al. (1995) have also found that younger great cormorant chicks grow significantly slower than their older siblings, with the greatest difference being between 2nd and 3rd chicks in broods of three. In the shag, large competitive asymmetries among broodmates reduced the feeding opportunities of smaller nestlings and caused a higher starvation mortality rate among them (Amundsen and Stokland, 1988). As in the altricial passerines studied by O'Connor (1977), early tarsus growth should be advantageous for cormorant chicks competing for parental feedings because they have to stretch their bodies in order to get a meal by inserting their head in the parent's bill to access partially regurgitated food in the gular pouch (Cramp and Simmons, 1977; Olver and Kuyper, 1978; our observations). Unlike O'Connor's passerines, however, in which nestlings attract parental feedings by gaping, cormorant chicks, given their feeding mode, may not benefit from an early-grown bill.

The potential advantages that faster-growing legs or bills may confer to nestlings remain to be tested by more detailed studies. It is also possible that unequal growth rates of different body parts are manifestations of developmental constraints rather than adaptations. Similarly, both ultimate and proximate explanations have been proposed for the interspecific variability in the overall growth rate of nestlings (measured by weight gain). The observation of lower and more variable growth rates among avian species that raise a single nestling led Werschkul and Jackson (1979) to conclude that sibling competition has been a "dominant force" in the evolutionary maximization of growth rates in species that rear multi-chick broods. In reply to them, however, Ricklefs (1982) has argued that the lower growth rates of the single-chick species may simply result from nutritional limitations or from the more precocial development of their young (due to the inverse relationship between the functional maturity and the growth potential of a developing structure; Ricklefs, 1979).

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