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GROWTH AND PIGMENTATION PROCESS OF THE BEAKS OF *TODAROPSIS EBLANAE* (CEPHALOPODA: OMMASTREPHIDAE)

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ABSTRACT

The mandibular growth, including the pigmentation process, was studied from 114 specimens of *Todaropsis eblanae* (Ball) caught in the central East Atlantic. Relationships between six measurements of both beaks, upper and lower, and dorsal mantle length (ML) and between the rostral length and the total mass (TM) were determined. Except for the distance between the jaw angles, both beaks showed positive allometric growth in relation to ML in both sexes. The hood and crest parts grew faster than others; the highest regression coefficients were obtained for these in both beaks. The upper and lower beaks of females were not different from those of males ($p > 0.05$). The darkening process or pigmentation of both beaks was analysed and a qualitative scale of eight degrees of pigmentation was developed. The results connected with the darkening and maturing processes suggest that these processes are related and take place over a very short period in the life of the squid; but, ontogenetic shifts in the diet seem also to be related with the development of the beaks during cephalopod ontogeny.

INTRODUCTION

The mouth of the cephalopods, surrounded by the base of the arms, is composed of a complex of hard structures, muscles and glandules. Among them, there are two large chitinous structures, the mandibles or beaks. They are characterised by a high resistance to erosion during the digestive process in the stomach of a predator (Clarke 1962a, 1986, Hernández-García 1995a). Moreover, because they are among the few hard structures in cephalopods and show differences, sometimes even at species level, they are important taxonomically. The latter has led to the development of a specific classification method, which allows us to identify cephalopods from their beaks found on the ocean floor or as part of the structures found in the stomach contents of their predators (Clarke 1962a, 1962b, 1986, Pérez-Gándaras 1983). Therefore, beaks can give us valuable information concerning cephalopod distribution (see Clarke 1980). Another feature of the beaks, at least in certain species such as *Moroteuthis ingens* (*Kondakovia longimana* Filippova, 1972, M. R. Clarke pers. comm. 2003) and *Octopus vulgaris*, is that they show markings related to regular growth cycles (Clarke 1965, Hernández-López *et al.* 2001).

The biomass of a cephalopod eaten by its predator can be calculated for many species, according to the relationships between the measurement of some parts of the beak and the total weight of the animal (Clarke 1962a, 1986, Pérez-Gándaras 1983). Therefore, a great deal of research includes basic studies of beak morphometry and the calculation of equations which relate certain beak measurements to size and weight. The equations obtained are specific for each area studied, which is of great importance in species with high geographical variability (see Note I).

The morphology and the development of the cephalopod body, and specifically the beaks (which facilitate the feeding on large prey), and animal distribution are, in some ways, related to diet (see Wootton 1992). Thus, ontogenetic shifts in the diet and habits of *Illex coindetii* were related to previous morphological variation in mouth structures

(Hernández-García 1995b, Castro & Hernández-García 1995). One of the most important changes in growing beaks is the development of pigmentation (Mangold & Fioroni 1966). This process is related to a strengthening of the beak, which enables the cephalopod to prey on larger and stronger animals (Castro & Hernández-García 1995). Thus, the study of the development of the beaks during cephalopod ontogeny should shed light on our understanding of cephalopod ecology.

This paper provides new information on the relationships between the growth of the most important parts and pigmentation process of the beaks and the squid size and mass, as well as on reproductive biology and feeding habits of *Todaropsis eblanae* (Ball) from the central East Atlantic. It is expected that this information will also help when identifying beaks from the stomach contents of predators.

MATERIAL AND METHODS

The material for this study was collected from the by-catches of bottom trawl fisheries in the central East Atlantic. A total of 713 frozen *Todaropsis eblanae* were sampled, which ranged from 43 to 215 mm dorsal mantle length (ML). For each specimen, ML, total squid body mass (TM), sex and maturity stage (see below) were noted. The reproductive and digestive systems were taken and preserved in 70% ethyl alcohol. From a selected subsample of 114 squids (59 females and 55 males), the mandibles were dissected out at the end of the squid sampling process. Thus, there was enough time for the buccal mass to be fully defrosted and the beaks could be easily removed without breakage. The beaks were later cleaned and preserved in 70% ethyl alcohol.

Nomenclature of beak parts followed that of Clarke (1962a, 1986). Six measurements were taken of the upper (UB) and lower (LB) beaks (Fig. 1): rostral length (Rl), hood length (Hl), crest length (Cl), wing length (Wl), distance between jaw angles (JAd) on both UB and LB; width of the lateral wall (LWa) in the UB, and length of the base line (Bl) in the LB. The measurements were made to the nearest 0.01 mm with digital callipers for large beaks and a micrometer installed in a stereoscopic microscope for small ones.

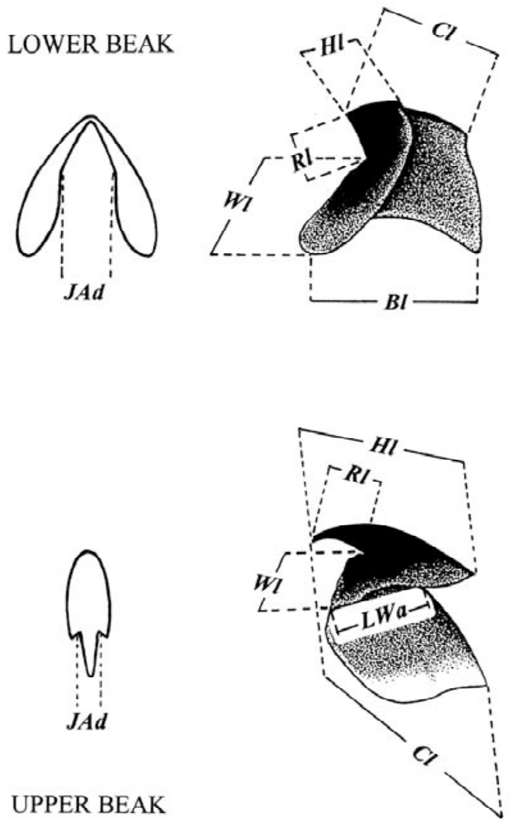

Fig. 1 Measurements taken of lower and upper beaks of *Todaropsis eblanae*: rostral length (Rl), hood length (Hl), crest length (Cl), wing length (Wl), the distance between the jaw angles (JAd), width of the lateral wall (LWa) (in upper beak only), length of the baseline (Bl) (in lower beak only). (Original drawings)

For females, only the measurements of Rl and JAd of both beaks were taken from all 59 beaks. The rest of the measurements were taken only from 38 beaks. For males, only the measurements of Rl and JAd of both beaks were taken from all 55 beaks. The rest of the measurements were taken from only 37 beaks. Each measurement was related to ML by linear regression, with previous decimal logarithmic transformation of the data series, using the minimum squares method to minimise the sum of the squares of the vertical distances between the points and the line (Ricker 1973). This process was also used to determine the relationship between the Rl of both mandibles and the total squid body mass (TM). The rostral length of the lower beak (Rl LB) has also been referred to as LRL in the figures.

With the objective to find possible differences between the mandibles of both sexes, the variance of the beak morphometry data was studied by applying

Table 1 Linear regression equations and statistics of beak characteristics of *Todaropsis eblanae* females. Rl = rostral length, Hl = hood length, Cl = crest length, Wl = wing length, JAd = distance between the jaw angles, LWa = width of the lateral wall in the upper beak (UB), Bl = length of the baseline in the lower beak (LB), ML = mantle length, TM = total mass, N = number of squids analysed

Regression equations	N	Regression coefficient	Standard error	r^2	F	p
$\mathrm{Ln}\ ML = 3.2174 + 1.055\ \mathrm{Ln}\ Rl$ UB	59	0.9769	0.0452	0.9543	1191.92	< 0.000001
$\mathrm{Ln}\ ML = 1.7382 + 1.164\ \mathrm{Ln}\ Hl$ UB	38	0.9940	0.0560	0.9880	2972.90	< 0.000001
$\mathrm{Ln}\ ML = 1.5017 + 1.145\ \mathrm{Ln}\ Cl$ UB	38	0.9907	0.0751	0.9815	1918.27	< 0.000001
$\mathrm{Ln}\ ML = 3.4527 + 1.002\ \mathrm{Ln}\ Wl$ UB	38	0.9776	0.0491	0.9557	777.96	< 0.000001
$\mathrm{Ln}\ ML = 3.5118 + 0.983\ \mathrm{Ln}\ JAd$ UB	59	0.9747	0.0387	0.9500	1084.77	< 0.000001
$\mathrm{Ln}\ ML = 2.3848 + 1.180\ \mathrm{Ln}\ LWa$ UB	38	0.9807	0.0800	0.9619	909.47	< 0.000001
$\mathrm{Ln}\ ML = 3.2563 + 1.095\ \mathrm{Ln}\ Rl$ LB	59	0.9829	0.0377	0.9662	1629.63	< 0.000001
$\mathrm{Ln}\ ML = 3.2531 + 1.086\ \mathrm{Ln}\ Hl$ LB	38	0.9867	0.0429	0.9736	1327.95	< 0.000001
$\mathrm{Ln}\ ML = 2.5145 + 1.093\ \mathrm{Ln}\ Cl$ LB	38	0.9794	0.0784	0.9593	848.63	< 0.000001
$\mathrm{Ln}\ ML = 2.5362 + 1.114\ \mathrm{Ln}\ Wl$ LB	38	0.9843	0.0677	0.9688	1119.35	< 0.000001
$\mathrm{Ln}\ ML = 3.3781 + 1.060\ \mathrm{Ln}\ JAd$ LB	59	0.9797	0.0380	0.9599	1366.93	< 0.000001
$\mathrm{Ln}\ ML = 2.2256 + 1.081\ \mathrm{Ln}\ Bl$ LB	38	0.9826	0.0808	0.9656	1010.81	< 0.000001
$\mathrm{Ln}\ TM = 0.3653 + 2.917\ \mathrm{Ln}\ Rl$ UB	59	0.9733	0.1346	0.9474	1027.68	< 0.000001
$\mathrm{Ln}\ TM = 0.4676 + 3.033\ \mathrm{Ln}\ Rl$ LB	59	0.9806	0.1115	0.9616	1429.78	< 0.000001

Table 2 Linear regression equations and statistics of beak characteristics of *Todaropsis eblanae* males. Rl = rostral length, Hl = hood length, Cl = crest length, Wl = wing length, JAd = distance between the jaw angles, LWa = width of the lateral wall in the upper beak (UB), Bl = length of the baseline in the lower beak (LB), ML = mantle length, TM = total mass, N = number of squids analysed

Regression equations	N	Regression coefficient	Standard error	r^2	F	p
$\mathrm{Ln}\ ML = 3.3582 + 0.948\ \mathrm{Ln}\ Rl$ UB	55	0.9376	0.0675	0.8791	385.57	< 0.000001
$\mathrm{Ln}\ ML = 1.8398 + 1.129\ \mathrm{Ln}\ Hl$ UB	37	0.9778	0.1018	0.9561	763.26	< 0.000001
$\mathrm{Ln}\ ML = 1.5350 + 1.133\ \mathrm{Ln}\ Cl$ UB	37	0.9793	0.1087	0.9591	821.02	< 0.000001
$\mathrm{Ln}\ ML = 3.4730 + 1.004\ \mathrm{Ln}\ Wl$ UB	37	0.9342	0.0772	0.8728	240.20	< 0.000001
$\mathrm{Ln}\ ML = 3.6790 + 0.844\ \mathrm{Ln}\ JAd$ UB	55	0.9373	0.0517	0.8786	383.87	< 0.000001
$\mathrm{Ln}\ ML = 2.4970 + 1.134\ \mathrm{Ln}\ LWa$ UB	37	0.9684	0.0939	0.9378	528.48	< 0.000001
$\mathrm{Ln}\ ML = 3.4350 + 0.953\ \mathrm{Ln}\ Rl$ LB	55	0.9597	0.0503	0.9210	618.34	< 0.000001
$\mathrm{Ln}\ ML = 3.3418 + 1.026\ \mathrm{Ln}\ Hl$ LB	37	0.9645	0.0614	0.9302	476.08	< 0.000001
$\mathrm{Ln}\ ML = 2.5530 + 1.071\ \mathrm{Ln}\ Cl$ LB	37	0.9681	0.0920	0.9372	522.69	< 0.000001
$\mathrm{Ln}\ ML = 2.5452 + 1.123\ \mathrm{Ln}\ Wl$ LB	37	0.9635	0.0990	0.9284	454.21	< 0.000001
$\mathrm{Ln}\ ML = 3.4639 + 0.979\ \mathrm{Ln}\ JAd$ LB	55	0.9578	0.0504	0.9174	589.24	< 0.000001
$\mathrm{Ln}\ ML = 2.3343 + 1.042\ \mathrm{Ln}\ Bl$ LB	37	0.9775	0.0845	0.9556	754.05	< 0.000001
$\mathrm{Ln}\ TM = 0.5494 + 2.802\ \mathrm{Ln}\ Rl$ UB	55	0.9510	0.1750	0.9045	502.34	< 0.000001
$\mathrm{Ln}\ TM = 0.8009 + 2.800\ \mathrm{Ln}\ Rl$ LB	55	0.9670	0.1331	0.9350	763.55	< 0.000001

the analysis of covariance (Martín & Luna del Castillo 1990). All regressions and statistics were performed using the software package CSS Statistica©. The fixed was 0.05.

Another task within the analysis of the beaks was the study of the development of pigmented zones in relation to increasing animal size. In order to establish a scale of pigmentation for the beaks, the beaks of 39 females and 38 males were studied, by comparing the extension of the pigmentation and the intensity of the colour.

A detailed description of the material (squids) and methods used for the studies on the reproductive biology, is included in a recent publication (Hernández-García 2002). The maturity stages of the sample specimens were recorded following Lipinski's

Table 3 Analysis of covariance of sex effect for squid of all sizes and for those < 165 mm dorsal mantle length (ML) on upper (UB) and lower (LB) beak measurements

Sample	Variables	Effect	Wilks' Lambda	df 1	df 2	*p*
both sexes	UB	1	0.9095	6	67	0.3656
both sexes	LB	1	0.8830	6	67	0.1984
both sexes, except females with ML > 164 mm	UB	1	0.8270	6	57	0.0825
both sexes, except females with ML > 164 mm	LB	1	0.8721	6	57	0.2330

Table 4 Description of characters defining the pigmentation degrees in *Todaropsis eblanae* (see Fig. 2)

Characters	Degree
UB: lateral walls without any pigmentation. LB: only the rostrum and the anterior part of the hood well coloured	0
UB: lateral walls without any pigmentation. LB: the pigmented area reaching the region of the shoulder; thus, the step is now well defined	1
UB: lateral walls without any pigmentation. LB: a small isolated spot in the central part of the wing is present	2
UB: lateral walls without any pigmentation. LB: the isolated spot much enlarged and extended almost along the whole wing, but without reaching the regions of the shoulder and the hood	3
UB: lateral wall with two small coloured areas or lobes (at the border with the wing and the hood). LB: no isolated spot, this area is now fused with the sparsely pigmented area of the hood by a thin coloured band	4
UB: lobes fused, pigmentation is smaller than 1/3 of the height of the lateral wall. LB: at the shoulder there is only one small band without pigmentation (cartilage is present yet) and the transparent strip of the tooth is also present, although very weakly	5
UB: no distinguishable lobes and pigmentation is about half of the height of the lateral wall. LB: wings pigmented with a soft coloration, only with an outlying strip (the growing area) relatively wide without colour; no transparent strip or very week one at the tooth; cartilage zone at the shoulder region has disappeared or is very much reduced, becoming a small transparent strip which defines the tooth	6
UB: pigmentation of the lateral wall is about 2/3 of its height; no strip at the shoulder region; general darkening of the beaks. LB: beak fully pigmented, only the growing margins without colour, colour dark-brown, nearly black at the hood and shoulder; end of the rostrum is usually eroded and the tooth can be reduced, becoming indistinct from a profile view	7

scale (1979). Beak size (LRL), squid size (ML), pigmentation degree and maturity stage were represented graphically in order to determine if there was a relation between these.

The natural feeding was studied. The central part of the digestive system of a randomly selected subsample of *Todaropsis eblanae* (N = 195) was analysed. The subsample consisted of 97 females (ML = 48-195 mm) and 98 males (ML = 54-164 mm). To study the diet, the digestive content was placed on filter paper to remove the moisture and thereafter weighed. Prey items were identified to the lowest possible taxon. For each stomach examined, counts were made of the number of prey items per category (taxonomic group). An Index of the prey's numerical importance (IN) was calculated as % importance = (% number × % occurrence) 1/2 × 100 (Windell 1971, Vesin *et al.* 1981). In order to determine the existence of differences in diet during ontogenesis, squids were divided into two groups, juvenile-subadult and mature squids.

RESULTS

Changes in shape with growth

The regression equation for each of the beak measurements is given in Tables 1 and 2 for *Todaropsis eblanae* females and males respectively. The slopes of the linear regressions indicate the allometric (positive) nature of growth in the beaks of both sexes. UB in both sexes presented a very similar growth pattern, in that LWa grew faster than all other parts. On the contrary, Wl was the part growing faster in the LB of both sexes; the growth pattern was also very similar. Values of the respective regression coefficients were among the higher in all cases. The hood and crest were always among the parts growing faster, with high regression coefficients in both beaks. In contrast, the regression between Rl and ML had lower coefficients for females and males, probably due to the effect of the erosion of the tip to which they are subjected (most of the largest squids possessed rostra with blunt tips).

The upper and lower beaks of female and male *Todaropsis eblanae* are not significantly different (analysis of covariance, $p > 0.05$, Table 3). Due to the sexual dimorphism of this species, the same contrasts have been carried out excluding those females whose size was above 165 mm. Thus, homogenising size ranks has avoided the possible influence of the differential size in both sexes. The results obtained from this analysis confirmed that there are no significant differences between the mandibles of both sexes ($p > 0.05$, Table 3).

Changes in pigmentation with growth and maturation

The areas with highest variation of pigmentation with increasing size of the animal were the lateral walls and the shoulder area in the UB, as well as the surface of the rostrum and the shoulder and wings in the LB (Fig. 2). Therefore, to describe the development of pigmentation, a scale of eight degrees of pigmentation (0-7) for these areas was constructed (Fig. 2, Table 4).

The beaks of juveniles are pigmented only at the rostrum, with a progression toward the posterior part of the hood, which is softer the smaller the squid. In the LB, the pigmentation of the wings develops from its original centre toward the shoulder area, similar to *Illex coindetii*, but without reaching the pigmentation of almost all the wing, as in *Todarodes sagittatus* (degrees 2 and 3, Fig. 2). In contrast to, the UB, the pigmentation of the lateral walls forms two lobes (degree 4), although neither is as long as those in *Todarodes sagittatus*. In the LB of the smaller squid analysed (ML = 42-63 mm), the tooth of the shoulder was difficult to see (degree 0). In mature animals, the pigmentation covers the whole lateral wall of both mandibles and extends to the wings of the LB; there is no pigmentation along the outer margins, which are the growth zones (degree 7, Fig. 2). The pigmentation becomes more intense throughout maturation, from dark brown to almost black in the most advanced stages (this almost black colour is represented with the value 7.5 in the figures).

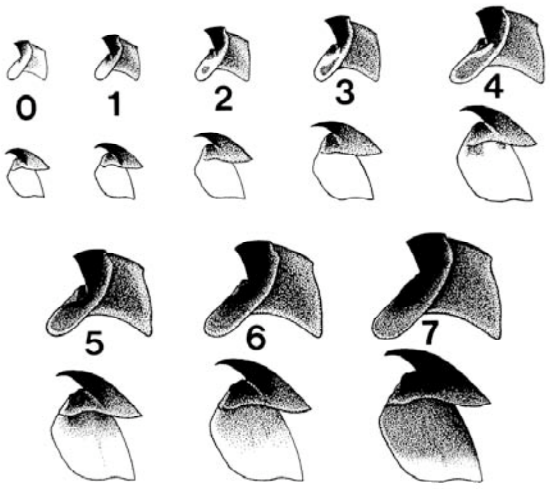

Fig. 2 Changes (darkening process) accompanying growth in beaks of *Todaropsis eblanae*. The numbers indicated are the pigmentation degrees (see Table 4). Drawings based on the beaks of females with LRL (mm): 2.16, 2.52, 3.83, 3.31, 4.09, 4.50, 5.60, 6.80. (Original drawings)

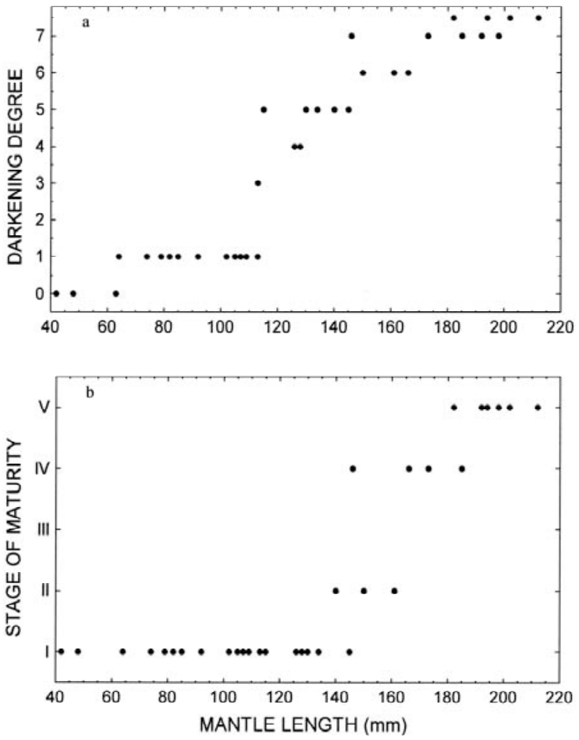

Fig. 3 Variation in (a) darkening degree (n = 39) and (b) stage of maturity (n = 39) with mantle length for female *Todaropsis eblanae*

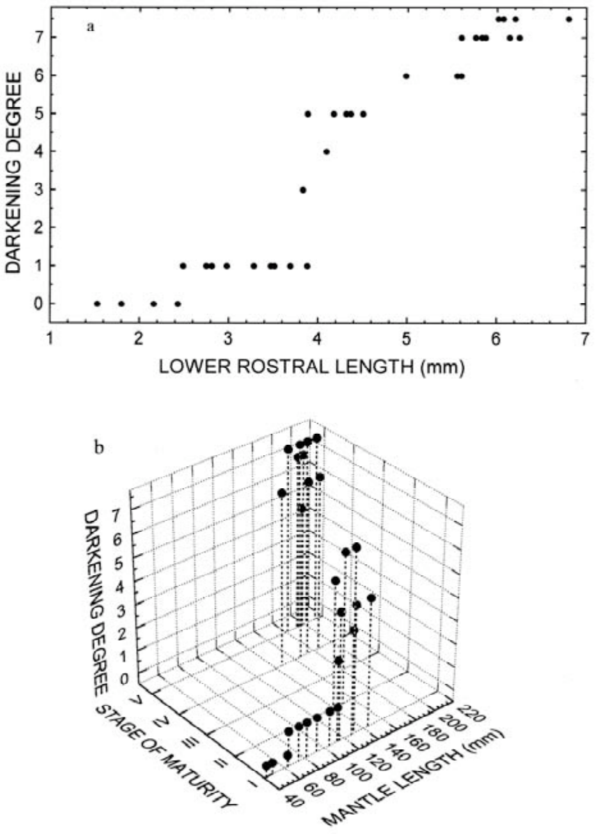

Fig. 4 Variation in darkening degree with (a) lower rostral length (LRL) (n = 39) and (b) mantle length and stage of maturity (n = 39) for female *Todaropsis eblanae*

In females, pigmentation degree 2, the onset of wing pigmentation, has been estimated to occur when the ML was over 100 mm, with a Rl size range of the lower beak between 3.5 and 4 mm (Figs 3 and 4). The number of specimens with degrees 2-4 was very small (Figs 3 and 4), as was the number of animals in maturity stages II and III (Fig. 3b). The size at which the maturing process starts has been estimated to be close to 120 mm ML (Fig. 5a). The smallest mature female found was 128 mm ML and the size at maturity was estimated at 168 mm (Hernández-García 2002). Degrees 6 and 7 corresponded to mature squid (Fig. 4b), with a Rl size of the LB no smaller than 4.5 mm, which occurred when the ML was over 140 mm (Figs 3 and 4). The results indicate that overall pigmentation is a continuous process, but wing pigmentation takes place in a very short period of time during this process.

On the other hand, data about the reproductive biology, most commonly immature and mature, but not maturing squid, suggest that maturation occurs within a short time-period (i.e. maturation process is fast) (Hernández-García 2002).

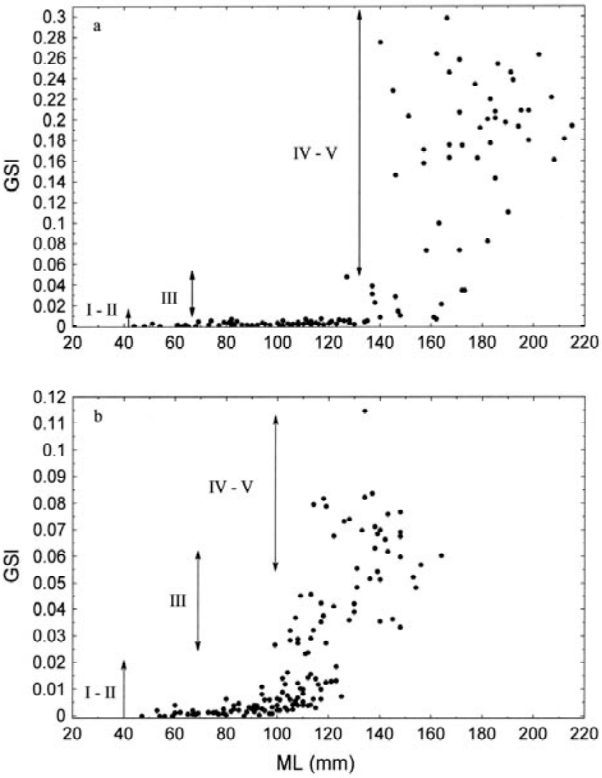

Fig. 5 Variation of the Gonadosomatic Index, GSI (GSI = mass of the reproductive system / (TM - weight of the stomach)) with the squid size in (a) females and (b) males of *Todaropsis eblanae*

For males, results indicate a similar development of pigmentation. The number of squids with degrees 2-4 was small (Figs 6 and 7), as was the number of animals in maturity stages II and III (Fig. 6b). Degree 2 (onset of wing pigmentation) occurred when squid size was over 90 mm; at this degree, the Rl of the LB ranged between 3 and 3.6 mm (Figs 6 and 7). The size at which male *Todaropsis eblanae* start maturing seems to be close to 95-100 mm ML (Fig. 5b). The smallest mature male found was 109 mm ML and the size at maturity was estimated at 130 mm (Hernández-García 2002). Degree 6 corresponded to Rl values of the LB over 4.2 mm and to squid sizes over 135 mm (Figs 6 and 7). In conclusion, it seems that both processes (the development of beak pigmentation and the maturation) are closely related and that they take place synchronously within a very small window of time.

Food and feeding

A detailed contribution on this topic is currently in

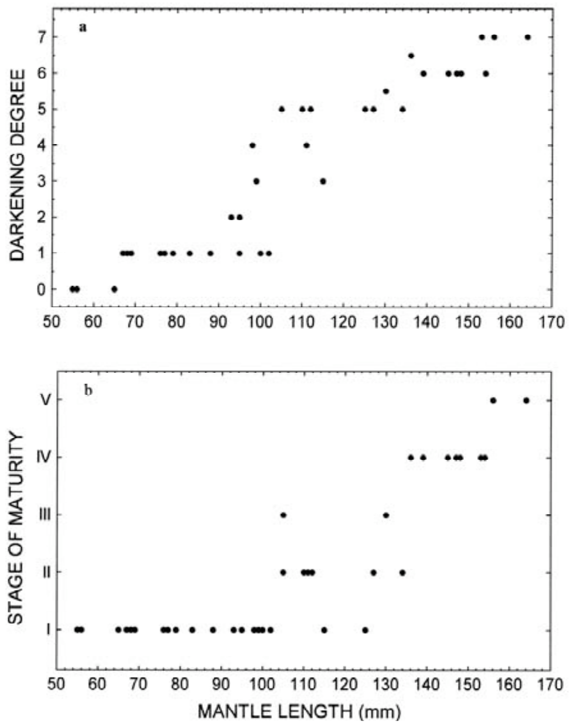

Fig. 6 Variation in (a) darkening degree (n = 38) and (b) stage of maturity (n = 38) with mantle length for male *Todaropsis eblanae*

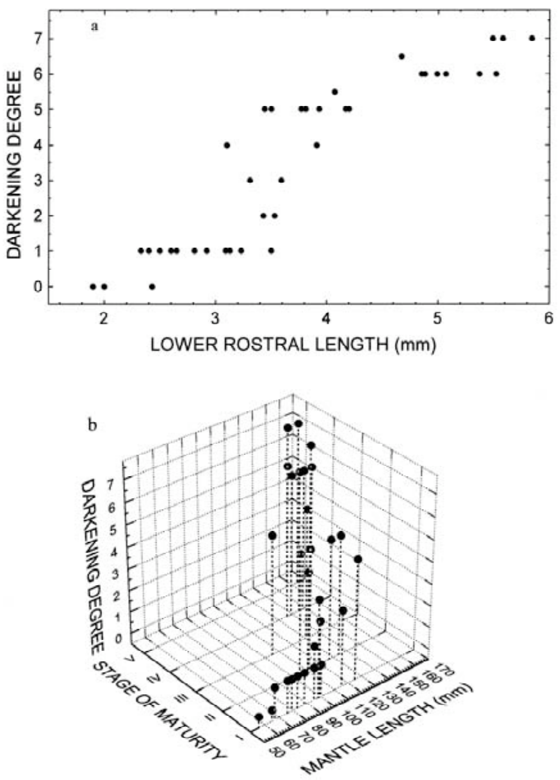

Fig. 7 Variation in darkening degree with (a) lower rostral length (LRL) (n = 38) and (b) mantle length and stage of maturity (n = 38) for male *Todaropsis eblanae*

preparation; only the values for the major groups are included here (Table 5). The digestive system of 118 squids (60.51% of the subsample analysed) contained food remains. The digestive content weights ranged between 0.01 and 15.08 g. The prey items identified belonged to Crustacea, Mollusca (Cephalopoda) and Osteichthyes. For female *Todaropsis eblanae*, the importance of fish in the diet increased with the squid size (Table 5) while crustacea in adults was less important and cephalopod did not change significantly. On the contrary, the diet of males was characterised by a slight increase of the crustacea importance with the squid size (ca. 7%; Table 5). The importance of fish and cephalopod was slightly reduced in maturing-mature squids.

DISCUSSION

For *Todaropsis eblanae*, and in contrast to the results obtained for *Todarodes sagittatus* and for *Illex coindetii* (Hernández-García 1995b, Hernández-García *et al.* 1998), no significant differences were found between the beaks of the males and females, which coincides with the observations of Pérez-Gándaras (1983). The separation between the "centroides" according to the sex was not significant in this species.

In both sexes, the Wl grew faster than other parts of the lower beak; on the contrary, the Hl was the part of each beak growing the fastest in female *Todarodes sagittatus* (Hernández-García *et al.* 1998) and the Cl and Hl in female and male *Illex coindetii* respectively (Hernández-García 1995b). For *Todarodes angolensis*, the same result has been obtained for the UB (Villanueva & Sánchez 1989). Sánchez (1981) also observed that the hood of the UB grew faster than the other parts for *Illex coindetii* from the Mediterranean Sea. In both cases, the wing or the hood, the values of the regression coefficients were always among the highest. These parts, together with the crest, cover the main muscles or act as a support area for them; as a result, fast growth will permit a rapid adaptation to ingest larger fragments of food while the animal grows. Thus, a rapid increase in the size of those beak parts should not be surprising. For all three species, *Todaropsis eblanae*, *Illex coindetii* and *Todarodes sagittatus*, the wings in the LB, the lateral walls or the crest are among the fastest growing parts. Nevertheless,

Table 5 Index of Numerical Importance (IN) of the food categories identified from gut contents of *Todaropsis eblanae* from the central East Atlantic (mantle length, ML, in mm)

	Index of numerical importance IN (%)			
Prey	Female		Male	
	ML < 126	ML > 125	ML < 106	ML > 105
Osteichthyes	52.03	61.42	58.44	56.47
Cephalopoda	6.77	6.62	17.34	12.10
Crustacea	41.19	31.95	24.21	31.41

the growth of each beak rostrum is comparatively slower than the growth of those parts. The last can be understood when considering firstly that the rostrum suffers erosion, and secondly, that fast growth is not needed as they act as a slicing element. On the contrary, the maximum size of the prey fragments (to be ingested) will depend directly on the dimension of the hood, the crest and the width of the lateral walls (between which the oesophagus starts); therefore, on the parts which are growing faster.

Pigmentation of the beaks in *Todaropsis*, in general, follows the same pattern presented by species like *Illex coindetii* or *Todarodes sagittatus* (e.g. an isolated spot is the first step of wing pigmentation in the LB) (Hernández-García 1995b, Hernández-García *et al.* 1998). However, the shape (of the "drawing" generated by the pigmented areas) does not coincide exactly with the shapes observed in beaks of those species.

In females, the Rl of the LB, where the pigmentation of the wings start (at approximately 3.5-4 mm), has a value close to that found in samples of this species off the U. K. and South African coasts (3-4.5 mm; Clarke 1986). This coincides with the similarities in squid maximal size along its geographical range (paper in preparation).

The results obtained for *Todaropsis eblanae*, as for the other two ommastrephid species, *Illex coindetii* and *Todarodes sagittatus*, show a close relationship between darkening of the beak and the maturity of the squid. The existence of such relationships in cephalopods, without comparing different beak measurements and detailed analysis of the pigmentation process, was suggested earlier (Clarke 1962a, Mangold & Fioroni 1966, Clarke & Kristensen 1980). The most important fact is that the process of development of the pigmentation on the wings seems to coincide with sexual maturation (squids in "advanced" II, III and probably "earlier" IV). The absence or presence of a low number of cases of the darkening degrees 2, 3 and 4 coincides with a low number of maturing squids in all three species. This low number can perhaps best be explained by the very short period of the darkening process and, thus, the rapid process of maturing (low number of squids in maturing phase). The absence of bias is accepted as the same results were obtained for *Illex coindetii* when a much larger sample was available (200 upper and lower beaks and about 1300 squids used in the analysis of reproductive aspects (Hernández-García 1995b, Hernández-García 2002)). Only a few specimens of maturity stages II and III were found (Hernández-García 2002). In most of the cases, they corresponded to beaks with degrees 2 to "early" 5 (from onset of pigmentation of the wings to nearly fully coloured wings, according to the scale used here for *Todaropsis eblanae*).

Before reaching full sexual maturity, the squids undergo morphological changes, including beak morphology, which allow them to exploit a wide variety of prey. The darkening process means an increase of beak strength as well. This has a strong influence on the choice of diet, which subsequently will directly influence the squids behaviour, as observed in *Illex coindetii* (Hernández-García 1995b, Castro and Hernández-García 1995). Changes in mouth structures, including the increase of beak hardness with body growth, allows the squid to prey on larger animals with more complex hard structures (e. g. fish). The results obtained relative to morphological changes of the mandibles and to the diet of *Todaropsis eblanae* during its life cycle, suggest a similar feeding ecology to the other two species in the central East Atlantic (Nigmatullin 1972, Hernández-García 1995b, Castro and Hernández-García 1995, Piatkowski *et al.* 1998). Although the results are not as clear as for *Illex coindetii*, adult female *Todaropsis eblanae* prey more on fish than do juveniles. Thus, the latest observation and other results coincide with those obtained for this species in other areas (Rasero *et al.* 1996, Lordan *et al.* 1998). The lack of clearer differences in the diet during the life cycle could be due to (1) the low number of digestive contents analysed and (2) the fact that only two range sizes were defined. Moreover, the beaks of *Todaropsis eblanae* are larger when compared with beaks from the other two species, especially with those from *Illex coindetii* and this could also have some influence on the results.

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REFERENCES

Castro JJ, Hernández-García V (1995) Ontogenetic changes in mouth structures, foraging behaviour and habitat use of *Scomber japonicus* and *Illex coindetii*. Scientia Marina 59(3-4): 347-355

Clarke MR (1962a) The identification of cephalopod “beaks” and the relationship between beak size and total body weight. Bull Br Mus (Nat Hist) Zool 8: 419-480

Clarke MR (1962b) Significance of cephalopods beaks. Nature 193: 560-561

Clarke MR (1965) "Growth rings" in the beaks of the squid *Moroteuthis ingens* (Oegopsida: Onychoteuthidae). Malacologia 3(2): 287-307

Clarke MR (1980) Cephalopoda in the diet of sperm whales of the southern hemisphere and their bearing on sperm whale biology. Discovery Rep 37: 1-324

Clarke MR (ed.) (1986) A handbook for the identification of cephalopod beaks. Clarendon Press. Oxford

Clarke MR, Kristensen TK (1980) Cephalopod beaks from the stomachs of two northern bottlenose whales (*Hyperoodon ampullatus*). J mar Biol Ass U K 60 (1): 151-156

Hernández-García V (1995a) The diet of the swordfish *Xiphias gladius* Linnaeus, 1758, in the central East Atlantic with an emphasis on the role of cephalopods. Fish Bull NOAA 93(2): 403-411

Hernández-García V (1995b) Contribución al conocimiento bioecológico de la familia Ommastrephidae Steenstrup, 1857 en el Atlántico Centro-Oriental. Ph.D. Thesis, Universidad de Las Palmas de Gran Canaria, Las Palmas de GC

Hernández-García V (2002) Reproductive biology of *Illex coindetii* and *Todaropsis eblanae* (Cephalopoda, Ommastrephidae) off Northwest Africa (4° -35° N). Bull Mar Sci 71: 347-366

Hernández-García V, Piatkowski U, Clarke MR (1998) Development of the darkening of the *Todarodes sagittatus* beaks and its relation to growth and reproduction. South Afr Jour of Mar Sci 20: 363-37

Hernández-López JL, Castro-Hernández JJ, Hernández-García V (2001) Age determined from the daily deposition of concentric rings on common octopus (*Octopus vulgaris*) beaks. Fish Bull NOAA 99: 679-684

Lipinski MR (1979) Universal maturity scale for the commercially important squids. The results of maturity classification of the *Illex illecebrosus* population for the years 1973-77. ICNAF, Res Doc 79/2/38, Serial 5364, 40 pp

Lordan C, Burnell GM, Cross TF (1998) The diet and ecological importance of *Illex coindetii* and *Todaropsis eblanae* (Cephalopoda: Ommastrephidae) in Irish waters. South Afr Jour of Mar Sci 20: 153-163

Mangold K, Fioroni P (1966) Morphologie et biométrie des mandibules de quelques céphalopodes Mediterranéens. Vie Milieu, sér A, 17: 1139-1196

Martín-Andrés A, Luna del Castillo J de D (1990) Bioestadística para las ciencias de la salud. Ediciones Norma (3ª edi.), Madrid

Nigmatullin ChM (1972) Feeding of ommastrephids from North-West Africa shore. Trudy AtlantNIRO 42: 152-155

Pérez-Gándaras G (1983) Estudio de los cefalópodos ibéricos: sistemática y binomia mediante el estudio morfométrico comparado de sus mandíbulas. Ph.D. Thesis, Universidad Complutense de Madrid, Madrid

Piatkowski U, Hernández-García V, Clarke MR (1998) On the biology of the European flying squid *Todarodes sagittatus* (Lamarck 1798) (Cephalopoda, Ommastrephidae) in the central eastern Atlantic. South Afr Jour of Mar Sci 20: 375-383

Rasero M, González AF, Castro BG, Guerra, A (1996) Predatory relationships of two sympatric squid, *Todaropsis eblanae* and *Illex coindetii* (Cephalopoda: Ommastrephidae) in Galician waters. J mar biol Ass U K 76: 73-87

Ricker, WE (1973) Linear regressions in fishery research. J Fish Res Board Can 30: 409-434

Sánchez P (1981) Características bioecológicas de *Illex coindetii* (Vérany 1837) en el mar Catalán. Ph. D. Thesis. Universidad de Barcelona, Barcelona

Vesin JP, Leggett WC, Able KW (1981) Feeding ecology of capelin (*Mallotus villosus*) in the estuary and western Gulf of St. Lawrence and its multispecies implications. Can J Fish Aquat Sci 38(3): 257-267

Villanueva R, Sánchez P (1989) Some data on the biology of the squid *Todarodes angolensis* (Cephalopoda: Ommastrephidae) in Namibian waters. Sel Pap ICSEAF int Comm SE Atl Fish 1: 17-22

Windell JT (1971) Food analysis and rate of digestion. In: WE Ricker (Ed.) Methods for assessment of fish production in fresh waters. IBP Handbook No. 3, 2nd ed. Blackwell Scientific Publications, Oxford and Edinburgh, pp 215-226

Wootton RJ (1992) Fish ecology. Blackie and Son Ltd, Glasgow

NOTE I:

Some researchers working on cephalopods include in their works basic studies of beak morphometry and the calculation of equations which relate certain beak measurements to size and weight. However, only recently an attempt to co-ordinate the available information on this subject has been made. Drs L. Allock and M.R. Clarke have been working on a database of beak measurements and related information, an initiative product of the workshop held during the CIAC meeting in Aberdeen (July, 2000).

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