

DEVELOPMENT OF THE DARKENING OF *TODARODES SAGITTATUS* BEAKS AND ITS RELATION TO GROWTH AND REPRODUCTION

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Beaks of 133 specimens of *Todarodes sagittatus* caught in the central East Atlantic were studied. Relationships between several measurements of the upper and lower beaks and dorsal mantle length (*DML*) and total mass were calculated. The darkening process or pigmentation of both beaks was investigated and a qualitative scale of eight degrees of pigmentation developed. Except for the hood of the lower beak, the growth of both beaks was allometrically negative in relation to *DML* in males, whereas the growth of several parts of both beaks of females was allometrically positive. The hood grew faster than all other parts of the male beak and faster than all parts of the lower beak of females. Regression coefficients calculated for the growth of the beaks revealed differences between the growth patterns of females and males ($p < 0.05$). The results relating to darkening and the maturing process suggest that they are related and that they take place over a very short period in the life of the squid.

The chitinous mandibles or beaks of cephalopods are characterized by a high resistance to erosion during the digestive process in predator stomachs. Because they are among the few hard structures of cephalopods, they are important taxonomically. This has led to the development of a specific classification method that permits identification of cephalopods from their beaks (Clarke 1962a, b, 1986). Therefore, beaks found on the sea bed or sampled from the stomach contents of cephalopod predators give valuable information on cephalopod distribution (Clarke 1962a, b, 1980, Pérez-Gándaras 1983). Also, the biomass of cephalopods consumed by a predator can be calculated for many species because species-specific relationships between the measurement of some part of the beak and the size and total mass of cephalopods are available.

Moreover, the development and the morphometry of the cephalopod body, particularly of the mouth structures, and of course the animal distribution are, in some way, related to diet. Ontogenetic shifts in the diet and habit of the ommastrephid squid *Illex coindetii* confirmed that the shifts were related to morphological variation in the mouth structures (Castro and Hernández-García 1995).

One of the most significant changes in growing beaks is the development of pigmentation (Mangold and Fioroni 1966). This is related to a strengthening of the beak that enables the cephalopod to prey on

larger and stronger animals (Castro and Hernández-García 1995). Therefore, knowledge of the development of beaks during cephalopod ontogeny is an important issue in cephalopod ecology.

This paper provides new information on the relationships between the growth of several parts and the pigmentation process of the beaks, and size and mass of *Todarodes sagittatus* collected from the central East Atlantic.

MATERIAL AND METHODS

In all, 133 beaks (112 females and 21 males) of *Todarodes sagittatus* were examined. They were derived from animals caught in the central East Atlantic along the west coast of Africa by commercial trawlers, near the Canary Islands by artisanal boats, and at the Gettysburg Bank, south-west of Portugal, by Engels trawl during a research cruise of F.R.V. *Poseidon*. Further details on the origin of the squid samples are presented by Piatkowski *et al.* (1998). The mandibles were extracted from the buccal mass after morphometric measurements of the defrosted squid. Beaks were kept in 70% ethanol.

Six measurements were taken of the upper (*UB*) and lower (*LB*) beaks, illustrated in Figure 1: rostral length (*RI*), hood length (*HI*), crest length (*CI*), wing

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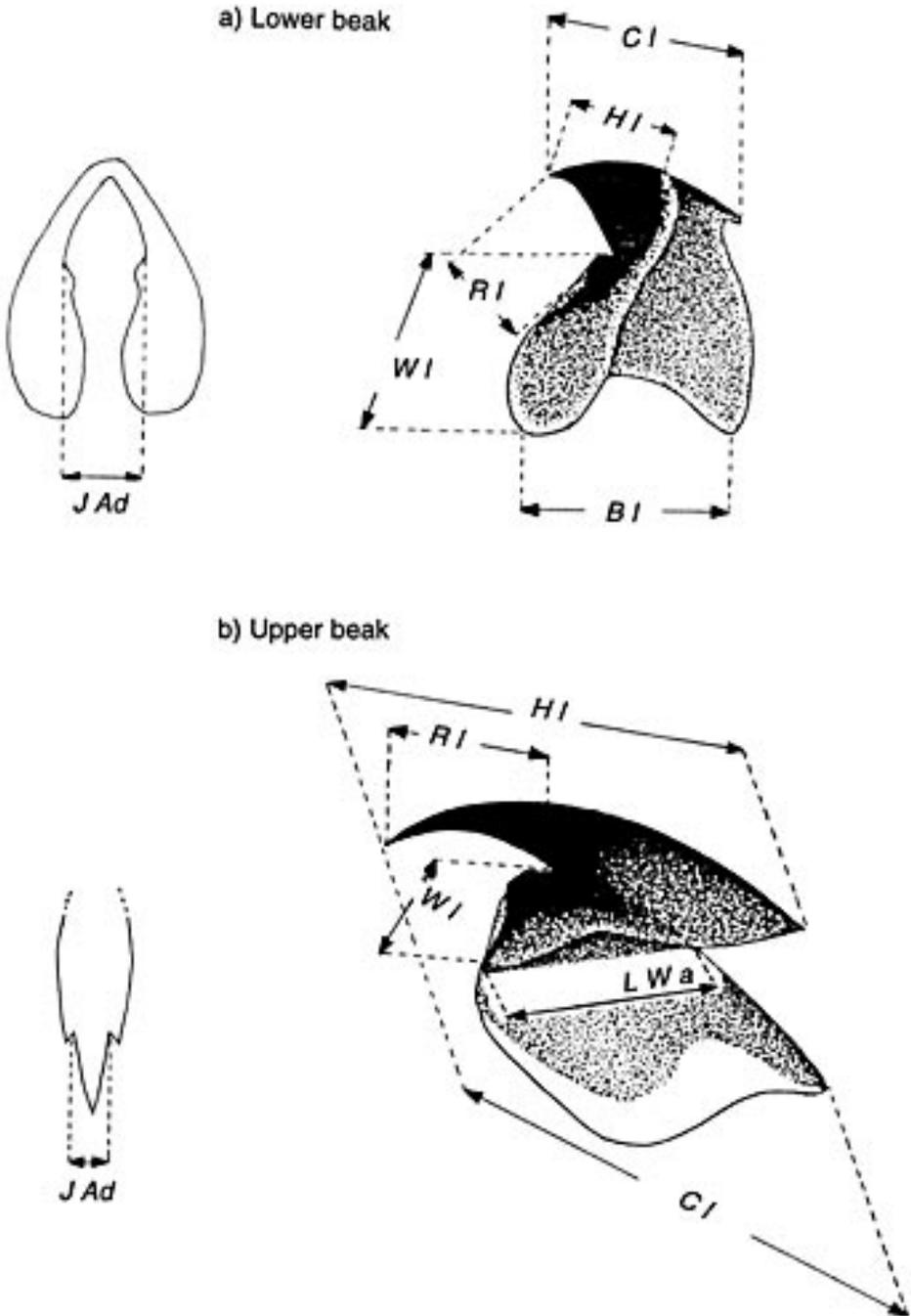


Fig. 1: Measurements taken of (a) lower and (b) upper beaks of *Todarodes sagittatus*. Rostral length (RI), hood length (HI), crest length (CI), wing length (WI), the distance between the jaw angles (JAd) and the amplitude of the lateral wall (LWa), length of the baseline (BI)

Table I: Linear regression equations and statistics of beak characteristics of *Todarodes sagittatus* females. *Rl* = rostral length, *Hl* = hood length, *Cl* = crest length, *Wl* = wing length, *JAd* = distance between the jaw angles, *LWa* = amplitude of the lateral wall in the upper beak, *Bl* = length of the baseline in the lower beak

Regression equations	Number of specimens investigated	Regression coefficient <i>r</i>	Standard error	<i>r</i> ²	<i>F</i>	<i>p</i>
$\ln DML = 3.8846 + 0.852 \ln RI UB$	112	0.954	0.0497	0.910	1 114.69	<0.000
$\ln DML = 2.3804 + 1.047 \ln HI UB$	76	0.979	0.0749	0.958	1 728.67	<0.000
$\ln DML = 2.1850 + 1.036 \ln CI UB$	76	0.977	0.0845	0.953	1 532.11	<0.000
$\ln DML = 3.8723 + 0.985 \ln WI UB$	76	0.968	0.0495	0.936	1 091.08	<0.000
$\ln DML = 4.1913 + 0.834 \ln JAd UB$	112	0.956	0.0399	0.913	1 159.93	<0.000
$\ln DML = 2.8926 + 1.100 \ln LWa UB$	76	0.970	0.0765	0.939	1 158.62	<0.000
$\ln DML = 3.9112 + 0.851 \ln RI LB$	112	0.955	0.0483	0.912	1 143.63	<0.000
$\ln DML = 3.5002 + 1.115 \ln HI LB$	76	0.976	0.0515	0.953	1 511.69	<0.000
$\ln DML = 3.0410 + 1.037 \ln CI LB$	76	0.964	0.0789	0.929	969.25	<0.000
$\ln DML = 3.0187 + 1.056 \ln WI LB$	76	0.968	0.0742	0.937	1 116.39	<0.000
$\ln DML = 4.1883 + 0.868 \ln JAd LB$	112	0.946	0.0444	0.895	938.96	<0.000
$\ln DML = 3.0140 + 0.961 \ln BI LB$	76	0.959	0.0849	0.920	855.15	<0.000
$\ln TM = 0.6765 + 2.713 \ln RI UB$	112	0.967	0.1330	0.935	1 583.42	<0.000
$\ln TM = 0.7650 + 2.711 \ln RI LB$	112	0.967	0.1300	0.935	1 603.76	<0.000

length (*Wl*), distance between jaw angles (*JAd*) on both upper and lower beaks, amplitude of the lateral wall (*LWa*) in the upper beak, and length of the baseline (*Bl*) in the lower beak. They were made to the nearest 0.01 mm with digital calipers for large beaks and with a micrometer installed in a stereoscopic microscope for small ones. For females, measurements of *Rl* and *JAd* of both beaks were taken from all 112 beaks, but the other measurements were taken only from 76 beaks. For males, all measurements were taken in all 21 beaks, both upper and lower. Each measurement was related to dorsal mantle length (*DML*) by linear regression, with previous logarithmic transformation. In the same manner, the relationship between the rostral length of both upper and lower mandibles and total squid body mass (*TM*) was determined. The rostral length of the lower beak (*RI LB*) has also been referred to as *LRL* in some figures. Nomenclature of beak parts followed that of Clarke (1986).

To find possible differences between the mandibles of females and males, the variance of the beak morphometry data was studied by applying analysis of covariance ($\alpha = 0.05$, Martín-Andrés and Luna del Castillo 1990). All regressions and statistics were performed using the software package CSS STATISTICA.

Further analysis of the beaks of 80 females and 21 males was focused on the development of pigmented zones in relation to increasing animal size. Maturity stages of the sampled specimens were recorded following Lipiński's scale (Lipiński 1979).

RESULTS

Changes in shape with growth

The relationships of each mandible measurement to *DML* and of the rostral length of upper and lower beak to *TM* for female and male *Todarodes sagittatus* are shown in Tables I and II. The slopes of the linear regressions indicate the allometric nature of growth in the beaks of both sexes. The hood of each beak grew faster than all other parts of the beak in males and faster than any dimension of the lower beak of females, in relation to the size of the animal. Values of the respective regression coefficients were highest in females and in the upper range for males. In contrast, the regression between rostrum length and *DML* had the lowest coefficients for females and was in the lower range for males, probably partly the result of erosion effects on the rostrum tip. It should be noted that a great percentage of the beaks of the largest individuals (*DML* > 270 mm) possessed rostra with blunt tips.

Analysis of covariance confirmed that the upper and lower beaks of female and male *Todarodes sagittatus* are significantly different (Table III, $p < 0.05$). The same tests were carried out excluding those females with a *DML* > 250 mm, so avoiding the possible bias of different largest body size in the regression for the two sexes. Results from this analysis again revealed significant difference between the mandibles of the two sexes (Table III, $p < 0.05$).

Table II: Linear regression equations and statistics of beak characteristics of *Todarodes sagittatus* males. *Rl* = rostral length, *Hl* = hood length, *Cl* = crest length, *Wl* = wing length, *JAd* = distance between the jaw angles, *LWa* = amplitude of the lateral wall in the upper beak, *Bl* = length of the baseline in the lower beak

Regression equations	Number of specimens investigated	Regression coefficient <i>r</i>	Standard error	<i>r</i> ²	<i>F</i>	<i>p</i>
$\ln DML = 3.9284 + 0.845 \ln Rl UB$	21	0.949	0.1022	0.900	171.3	<0.000
$\ln DML = 2.6407 + 0.973 \ln Hl UB$	21	0.955	0.1867	0.911	196.0	<0.000
$\ln DML = 2.4168 + 0.970 \ln Cl UB$	21	0.967	0.1717	0.934	273.1	<0.000
$\ln DML = 4.1864 + 0.796 \ln Wl UB$	21	0.929	0.0992	0.862	119.9	<0.000
$\ln DML = 4.2916 + 0.781 \ln JAd UB$	21	0.960	0.0662	0.920	220.6	<0.000
$\ln DML = 3.2488 + 0.957 \ln LWa UB$	21	0.958	0.1388	0.916	209.7	<0.000
$\ln DML = 4.0635 + 0.778 \ln Rl LB$	21	0.944	0.0968	0.890	155.0	<0.000
$\ln DML = 3.7208 + 1.028 \ln Hl LB$	21	0.919	0.1518	0.844	103.0	<0.000
$\ln DML = 3.2117 + 0.980 \ln Cl LB$	21	0.960	0.1375	0.921	221.6	<0.000
$\ln DML = 3.4435 + 0.872 \ln Wl LB$	21	0.948	0.1397	0.898	169.1	<0.000
$\ln DML = 4.2972 + 0.783 \ln JAd LB$	21	0.926	0.0915	0.857	114.0	<0.000
$\ln DML = 3.1398 + 0.915 \ln Bl LB$	21	0.946	0.1662	0.895	162.4	<0.000
$\ln TM = 0.7561 + 2.714 \ln Rl UB$	21	0.959	0.2931	0.918	215.3	<0.018
$\ln TM = 1.1904 + 2.500 \ln Rl LB$	21	0.953	0.2811	0.909	189.9	<0.000

Changes in pigmentation with growth and maturation

To describe the development of pigmentation, a scale of eight degrees of pigmentation (0–7) was constructed (Table IV). The areas with highest variation in pigmentation with increasing size of the animal were the lateral walls and the shoulder in the upper beak, and the surface of the rostrum, the shoulder and the wing in the lower beak (Fig. 2).

Almost all the pigmentation of the lower beak wing takes place first, before it reaches the shoulder and the hood (Table IV, Degree 3, Fig. 2). In the upper beak, the pigmentation of the lateral walls forms three lobes, one postero-dorsally divided into two regions (first and second lobes). Later, during the darkening process, pigmentation is developed in a third lobe just under the wing (Degree 4, Fig. 2). The beaks of subadults are pigmented only at the rostrum, with a progression towards the posterior part of the hood. In

mature animals, the pigmentation covers the whole lateral wall of both mandibles and extends to the wings of the lower mandible; there is no pigmentation along the outer margins, which are the growth zones (Table IV, Degree 7, Fig. 2). The pigmentation becomes more intense throughout maturation, from dark brown to almost black in the most advanced stages.

In females, Pigmentation Degree 2, the onset of wing pigmentation, was reached when *DML* was >215 mm, with a *Rl* size range of the lower beak between 5 and 6 mm (Figs 3, 4). The number of individuals with Pigmentation Degrees 2–4 was very small (Figs 3, 4), as was the number of animals in Maturity Stages III and IV (Fig. 3). The size at which female *T. sagittatus* start maturing seems to be a *DML* of 210–220 mm (Fig. 3). The results indicate that overall pigmentation is a continuous process, but that it develops faster when wing pigmentation is complete. On the other hand, data from the more common immature and mature squid suggest that maturation occurs within a short time-

Table III: Analysis of covariance of sex effect for squid of all sizes and for those <250 mm dorsal mantle length (*DML*) on upper (*UB*) and lower (*LB*) beak measurements

Sample	Variable	Effect	Wilks' Lambda	<i>df</i> 1	<i>df</i> 2	<i>p</i>
Both sexes	<i>UB</i>	1	0.83600	6	89	0.01227
Both sexes	<i>LB</i>	1	0.76288	6	89	0.00040
Both sexes, except females with <i>DML</i> >250 mm	<i>UB</i>	1	0.74630	6	59	0.00667
Both sexes, except females with <i>DML</i> >250 mm	<i>LB</i>	1	0.64117	6	59	0.00014

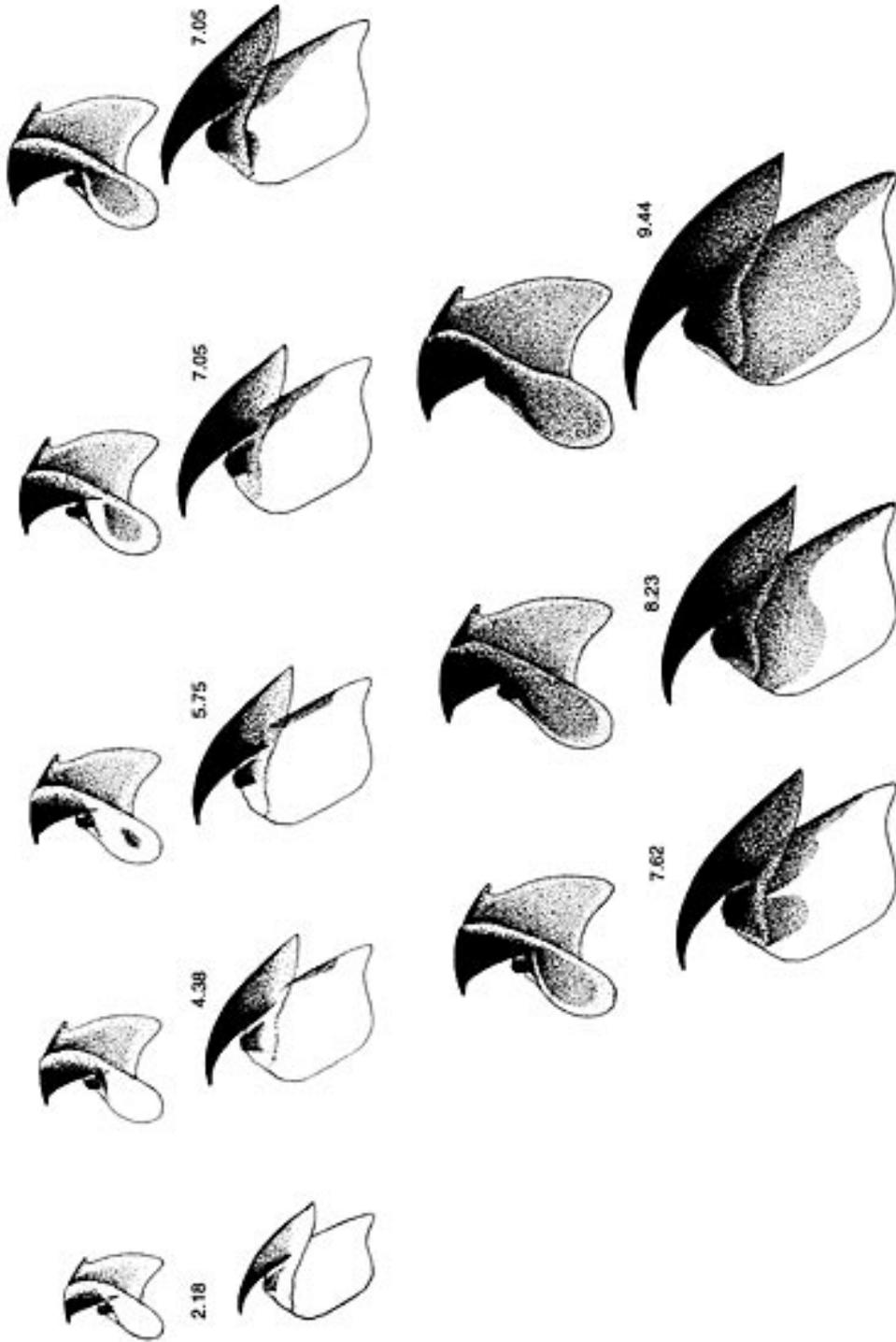


Fig. 2: Changes (darkening process) accompanying growth in beaks of *Todarodes sagittatus*. Fls in mm are given for each lower beak (sizes correspond to females)

Table IV: Description of characters defining the pigmentation degrees in *Todarodes sagittatus* (compare with Figure 2)

Character	Degree
Upper beak: lateral walls without any pigmentation. Lower beak: only the rostrum and the anterior part of the hood coloured	0
Upper beak: lateral walls with a very small zone (sub-triangular) weakly pigmented at the posterior side of the lateral wall. Lower beak: only the rostrum and the anterior part of the hood coloured, pigmentation slightly darker than in the previous degree	1
Upper beak: pigmentation of the lateral wall begins to increase towards the anterior part, rectangular pattern of pigmentation zone. Lower beak: very small isolated spot at central part of the wing	2
Upper beak: pigmentation of the lateral wall has pattern of two lobes. Lower beak: an isolated spot with much enlarged colouring over almost total wing, but without reaching the regions of the shoulder and the hood	3
Upper beak: a new pigmented area at the anterior part (just under the wing region) of the lateral wall, the third lobe. Lower beak: no isolated spot; the area is fused with the sparsely pigmented area of the hood by a thin coloured band	4
Upper beak: Lobes 1 and 2 very close to Lobe 3, and clearly distinguishable. Lower beak: at the shoulder, only one small band without pigmentation (cartilage still present), and the transparent strip of the tooth is also present, although very weakly	5
Upper beak: lobes fused and pigmentation half of the height of the lateral wall. Lower beak: wings pigmented with a soft colouration, only with an outlying strip (the growing area) relatively wide but without colour; no transparent strip 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
Upper beak: pigmentation of the lateral wall is more than 2/3 of its height; no strip at the shoulder region; general darkening of the beaks. Lower beak: beak fully pigmented, only the growing margins without colour; colour dark brown, nearly black at the hood and shoulder; end of rostrum of <i>LB</i> is usually eroded and the tooth can be reduced, not appreciable in profile	7

period.

Although only a small sample of male *T. sagittatus* was available, results indicate similar development of pigmentation. The main difference is that pigmentation Degree 2 was reached at a smaller *DML* (200 mm) than in females (Fig. 5). At this degree of pigmentation, the *RI* of the lower beak ranged between 4.5 and 5 mm (Figs 5, 6). The number of individuals with Pigmentation Degrees 2–4 was very small (Figs 5, 6), as also was the number of animals in Maturity Stages III and IV (Fig. 5). The size at which the maturing process starts is between 150 and 200 mm *DML* (Fig. 5).

In conclusion, it seems that both processes (the development of beak pigmentation and maturation) are closely related, and that they take place synchronously within a very small window of time.

DISCUSSION

As for *Illex coindetii* (Hernández-García 1995), there were significant differences between the beaks of male and female *Todarodes sagittatus*, seeming to

coincide with the observations of Pérez-Gándaras (1983).

In both sexes, the hood of each beak grows faster than other dimensions of the beak, similar to observations for *Illex coindetii* (Castro and Hernández-García 1995, Hernández-García 1995). For *Todarodes angolensis*, Villanueva and Sánchez (1989) obtained a similar result, with the slope of the relationship *Hl UB* to *DML* being the largest. Sánchez (1981) also observed that the hood of the upper beak of *Illex coindetii* grew faster than the other parts. The hood is one of the most robust parts of the beak and covers a muscle, of which a prolongation wraps around the lateral walls behind the hood and whose fast growth will permit a rapid adaptation to ingest larger fragments of food while the animal grows. Therefore, a fast increment in size of those beak regions (hood and lateral walls) is not surprising. The hood is followed, in terms of growth increments, by other parts that possess important insertions of muscular mass (i.e. the lateral walls, the crest or the wings). Nevertheless, the growth of the beak rostrum is comparatively slower than the growth of those parts. Two reasons are advanced to account for this situation: first, the rostrum suffers erosion; second, it does not need to grow fast because it acts as a slicing

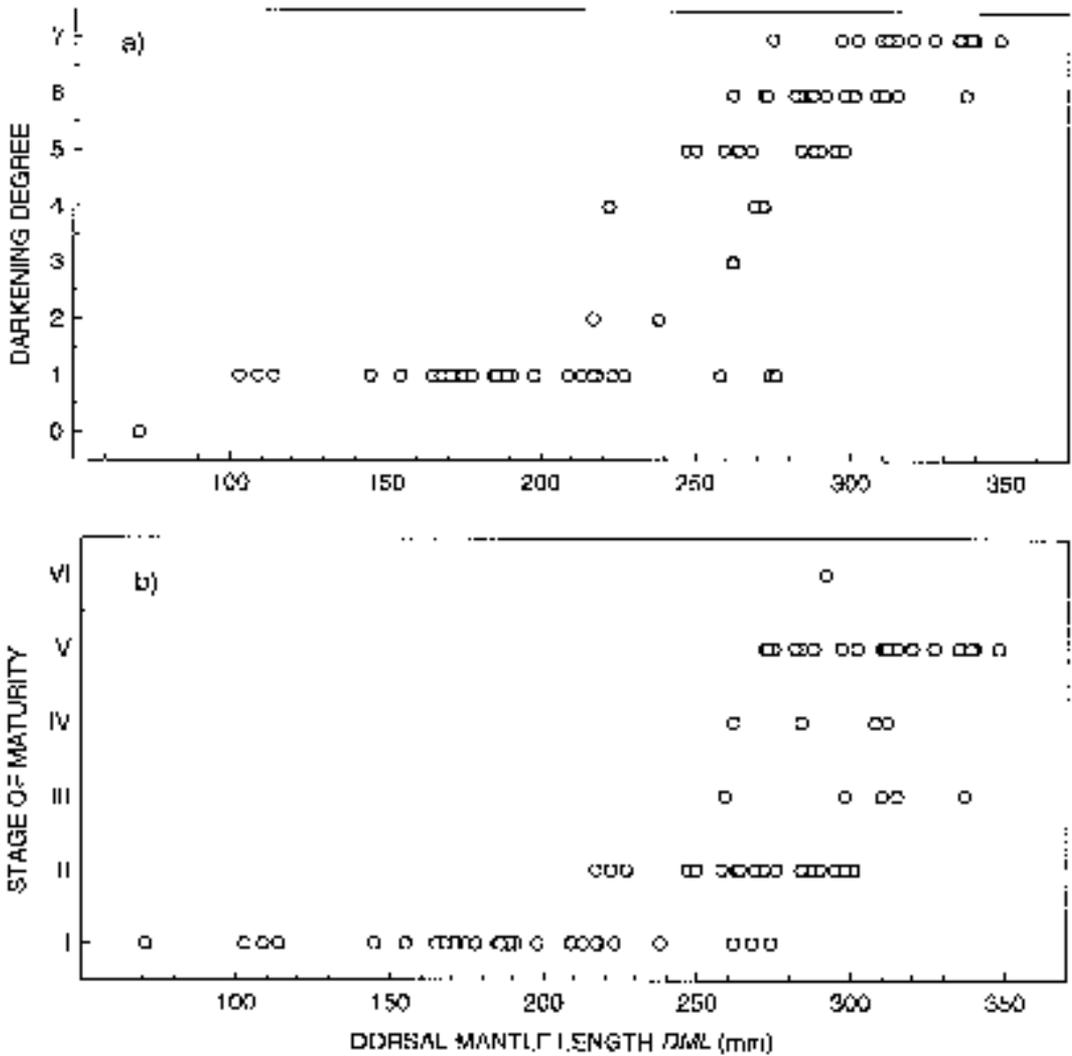


Fig. 3: Variation in (a) darkening degree ($n = 80$) and (b) stage of maturity ($n = 80$) with mantle length for female *Todarodes sagittatus*

element. Therefore, the size of the prey and the resulting fragments will depend more on the dimensions of the hood and the crest and the amplitude of the lateral walls (between which the oesophagus starts) than on the size of the rostrum.

In general, pigmentation of the beaks follows the same pattern (see Fig. 2) as that of such other omastrephids as *Illex coindetii* and *Todaropsis eblanae* (Hernández-García 1995). However, the “drawing” gen-

erated by the pigmented areas has a different shape. In females, the *Rl* of the lower beak, where the pigmentation of the wings starts (at approximately 5–6 mm), is smaller than that found for *Todarodes* in waters off Iceland (5–9 mm, Clarke 1986). This difference can be related to the larger size attained by *Todarodes sagittatus* in its northern range, e.g. off Norway and around the Shetland Islands (Wiborg and Beck 1984, Joy 1990). In fact, statistically significant differences

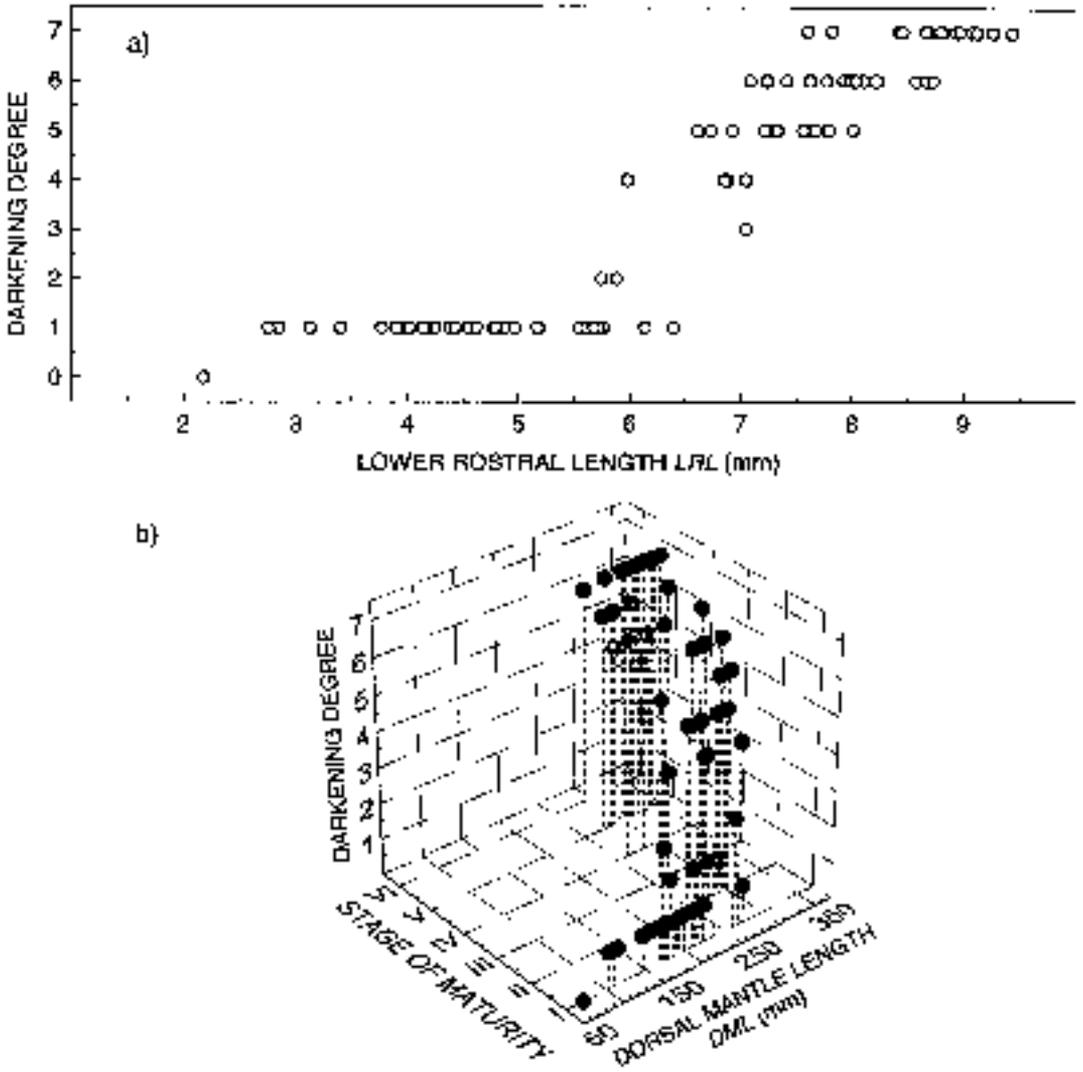


Fig. 4: Variation in darkening degree with (a) lower rostral length *LRL* ($n = 80$) and (b) mantle length and stage of maturity ($n = 80$) for female *Todarodes sagittatus*

in the morphometric characters of *T. sagittatus*, including beak measurements, have been shown to exist between geographic areas in the North-East Atlantic, i.e. Norway, Scotland and Portugal (Borges 1995).

The current data confirm a close relationship between darkening of the beak and the maturity of the animal. This has already been suggested earlier (Clarke 1962a, 1986, Mangold and Fiorini 1966), but without

as detailed an analysis of the development of the pigmentation or contrasting with different beak measurements. The process of development of the pigmentation on the wings seems to coincide with sexual maturation (Stages 2, 3 and probably 4).

Only a few cases with darkening degrees of 2–4 were found in the few maturing squids in the present sample. This low number can perhaps best be explained by the very short duration of the darkening process

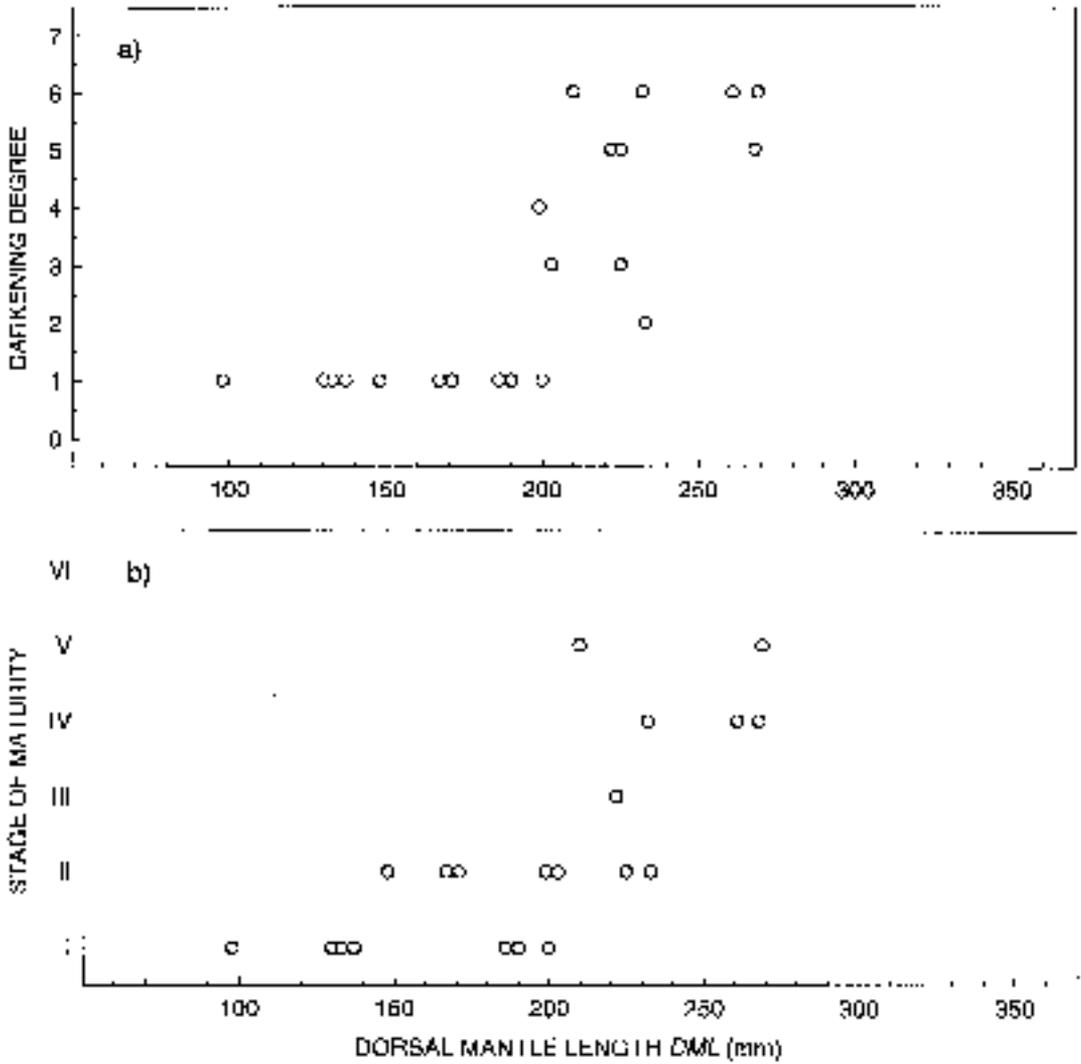


Fig. 5: Variation in (a) darkening degree ($n = 21$) and (b) stage of maturity ($n = 21$) with mantle length for male *Todarodes sagittatus*

and, thus, the rapid process of maturing. For *Illex coindetii*, only a few specimens of Maturity Stages 2 and 3 were found to be subject to beak pigmentation in a rather larger sample (Hernández-García 1995). Those represented beak darkening Degrees 2, 3 or 4, relating to the onset of full pigmentation of the wings.

In conjunction with the darkening process, beak strength also increases which, consequently, has further impact on the choice of diet and the behaviour of the

animal, as observed for *Illex coindetii* by Castro and Hernández-García (1995) and Hernández-García (1995). Increase of beak hardness with body growth allows squid to prey on larger animals with more complex hard structures. Morphological changes in the beak characteristics and in the diet of *T. sagittatus* during its life cycle (Breiby and Jobling 1985, Piatkowski et al. 1998) suggest a similar behaviour and feeding ecology to that of *Illex coindetii* in the

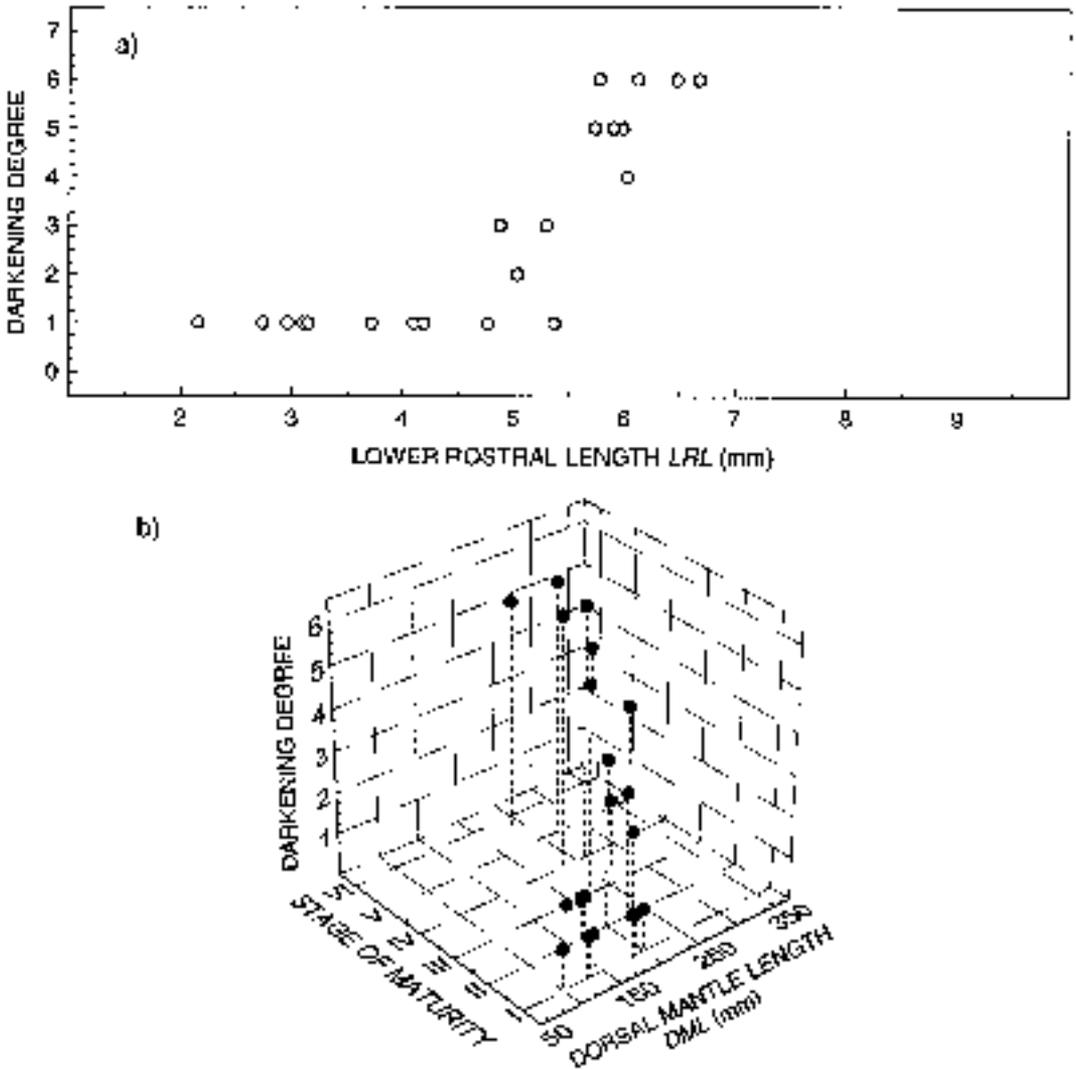


Fig. 6: Variation in darkening degree with (a) lower rostral length *LRL* ($n = 21$) and (b) mantle length and stage of maturity ($n = 21$) for male *Todarodes sagittatus*

central Eastern Atlantic (Castro and Hernández-García 1995, Hernández-García 1995). Adult *T. sagittatus* prey more on fish and other squid than do juveniles/subadults, and they tend to feed more on bottom fauna, indicated by the occurrence of demersal fish (e.g. *Microchirus boscanion*) in the stomach contents. Before reaching full sexual maturity, *T. sagittatus* undergoes various morphological changes (including

beak morphology). Such changes cause adaptations which allow them to make significant vertical day-night migrations, and probably also a later spawning migration, as reported for *Illex illecebrosus* by O'Dor (1987). Therefore, all changes allow them to find a wide variety of prey and to feed on a larger biomass spectrum.

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