

Age and growth of the short-finned squid *Illex coindetii* in Galician waters (NW Spain) based on statolith analysis

Angel F. González, Bernardino G. Castro, and Angel Guerra



González, A. F., Castro, B. G., and Guerra, A. 1996. Age and growth of the short-finned squid *Illex coindetii* in Galician waters (NW Spain) based on statolith analysis. – ICES Journal of Marine Science, 53: 802–810.

Age and growth of *Illex coindetii* in the fishery northwest of Spain were estimated from statolith growth increments. 341 statoliths were examined (170 males, 171 females) from individuals of 48–379 mm mantle length (ML). The maximum size of squids was 279 mm ML for males and 379 mm ML for females. Weight-at-length of mature males was greater than that of immature males and mature and immature females. Lifespan was estimated at 13 months for males and 15 months for females. Recruitment to the fishery occurred approximately at three months of age. Mantle length instantaneous relative growth rates were 0.72 mm d^{-1} for males and 0.84 mm d^{-1} for females. Weight growth rate was 2.22 g d^{-1} for males and 3.66 g d^{-1} for females. Maturity stages, however, influenced increase in weight in both sexes, such that weight-at-age was greater for mature than for immature individuals. The age at which individuals mature is variable, ranging from 140 to 271 d in males and between 183 and 285 in females. Growth rates in both sexes were dependent on the season of hatching. Squids hatched in winter attained larger sizes for the same age than squids in other seasons. These seasonal differences in growth were only evident after squids had reached 8 months of age. Reading daily increments in statoliths seems to be a reliable technique for studying the age and growth of *Illex coindetii*.

© 1996 International Council for the Exploration of the Sea

Key words: statoliths, growth, age, *Illex coindetii*.

Received 14 June 1995; accepted 16 January 1996.

Angel F. González, Bernardino G. Castro, and Angel Guerra: Instituto de Investigaciones Marinas (C.S.I.C.), Eduardo Cabello, 6, 36208 Vigo, Spain.

Introduction

Cephalopods are rapidly growing molluscs, the growth of which is influenced markedly by biotic and abiotic factors (Forsythe and Van Heukelem, 1987; Forsythe, 1993), giving rise to important differences between individual growth rates. Environmental conditions, particularly temperature, vary the growth rhythm between individuals of the same age. This influence is accentuated in regions where there are pronounced seasonal differences, to the extent that the time of year in which an individual is hatched will determine its growth (Natsukari *et al.*, 1988; Arkhipkin, 1990; Rodhouse and Hatfield, 1990a; Arkhipkin and Scherbich, 1991; Brunetti and Ivanovic, 1991; Hatfield, 1991; Forsythe, 1993).

Two of the most widely used methods for estimating growth in cephalopods are Modal Progression Analysis (MPA) and analysis of size-at-age data, based on growth increments in statoliths. In many cephalopod species,

such as *Illex coindetii* (González, 1994), due to its extended spawning season and possible migration, MPA is unable to discriminate among different microcohorts in a population, as Caddy (1991) postulated from a theoretical point of view. Therefore, the most reliable method for species of this type is examination of statoliths.

The first satisfactory attempts to determine age from statoliths were performed by Lipinski (1978) on *Illex illecebrosus* and Spratt (1979) on *Loligo opalescens*. These authors found periodic growth increments which they considered to occur daily, beside others which were more broadly spaced, which they considered to occur monthly. Since this first approximation, age of various cephalopod species has been studied based on growth increments in statoliths. In several species kept in captivity whose statoliths were marked with strontium (Hurley *et al.*, 1985) or with tetracycline (Dawe *et al.*, 1985; Jackson, 1990), the hypothesis that increment deposition is daily has been validated. On the basis of this hypothesis, several studies have been performed to

determine age in cephalopods (see Rodhouse and Hatfield, 1990a and Jackson, 1994 for a review).

Illex coindetii is an ommastrephid squid inhabiting the water column on the continental slope and shelf. Distribution of the species in the eastern Atlantic extends from the United Kingdom to the coast of Namibia (Roper *et al.*, 1969; Sánchez, 1981; Roper *et al.*, 1984; Guerra, 1992). Squid present in waters off Galicia (NW Spain) are larger than in other geographical areas (Sánchez *et al.*, in press).

As with other cephalopod species, for the reasons explained above, estimates of *Illex coindetii* growth based on MPA do not give valid results (González, 1994). However, in a closely related species (*Illex illecebrosus*), the value of statoliths to study growth has been shown and the hypothesis of daily increment formation (Dawe *et al.*, 1985; Hurley *et al.*, 1985) has been validated. It has therefore been assumed that *Illex coindetii* will also show daily increments in growth of statoliths. The aim of the present study was to provide information on the growth pattern of *Illex coindetii* in Galician waters. The use of statoliths for age and growth studies of this species was also evaluated. Differences in growth due to sex, maturity, and time of hatching were examined.

Materials and methods

A total of 341 *Illex coindetii* statoliths was examined from 170 males with mantle lengths (ML) of between 53 and 265 mm, and from 171 females of between 48 and 379 mm ML. The individuals were obtained from November 1991 to October 1992 as subsamples of 36 squid per month (18 males and 18 females) from a larger sample of 2652 males and 2432 females which were used to establish a mantle length–body weight relationship. Sampling was by otter trawling on the Galician shelf and slope between 100 and 350 m depth. Squid were taken on ice to the laboratory where they were frozen at -20°C until the statoliths were removed. ML in mm, total wet weight in g (BW), sex and maturity stage (immature or mature) were determined for each individual. Statoliths were extracted according to the method by Dawe and Natsukari (1991). Once removed, the maximum length of the statolith (SL) was recorded in mm (Clarke, 1978; Guerra and Sánchez, 1985). Statoliths were polished and mounted according to a modification of the method by Dawe and Natsukari (1991). Terminology describing different parts of statolith was as found in Lipinski *et al.* (1991). In all cases, the right-hand statolith was used having been ground on both sides.

An optical microscope ($\times 400$) and an image analysis system were used for counting the number of growth increments (NI) in statoliths. Each increment consisted of two components: an optically translucent ring and

a dark ring as in other cephalopods (Spratt, 1979; Kristensen, 1980; Rosenberg *et al.*, 1981; Dawe *et al.*, 1985; Morris and Aldrich, 1985; Natsukari *et al.*, 1988; Jackson, 1989; Villanueva, 1992). The image analyser made it possible to use an electronic cursor to mark each growth increment, to measure the length of the axis along which increments were counted and to determine the width of areas where increments were obliterated (white zones). Counts of rings were from the first check (hatching ring) to the margin of the dorsal dome (Dawe *et al.*, 1985; Villanueva, 1992).

Only those statoliths with a white zone smaller than 15% of the total length were considered. In all cases, only a single white zone was found in the distal zone of the dorsal dome. The total number of increments in the white zone was estimated by extrapolation (Natsukari *et al.*, 1988; Villanueva, 1992). The total number of increments was calculated by adding the number of increments counted to those estimated. Date of hatching was estimated by back-calculation from the time of capture, assuming that the increments were formed daily.

Estimated age was related to different variables: length of the statolith and length and weight of the animal, sex, and stage of maturity. Based on these relationships, the following growth rates were obtained by 30 day age class:

(a) Instantaneous relative growth rate, G (% BW or ML d^{-1})

$$G = \frac{\ln R_2 - \ln R_1}{t_2 - t_1} \times 100$$

Where R_2 is the BW or ML at age t_2 ; R_1 the weight or ML at age t_1 .

(b) Absolute growth rate, AGR (mm or g d^{-1})

$$\text{AGR} = \frac{R_2 - R_1}{t_2 - t_1}$$

Linear, power, exponential and logarithmic equations were fitted to the relationships between NI and values for SL, ML and BW of the animal were calculated. The same equations were also fitted to the ML and BW and between the ML and SL. In both cases only the best fit is shown. In the case of power equations, data were transformed into natural logarithms to achieve linearity. Student's 2-tailed t-test was used to determine the significance of the differences between slopes and intercepts of the calculated equations and for testing the allometry of growth (Zar, 1984)

To study the influence of seasonality on growth, individuals were grouped by sex according to season of hatching, based on their age. Only squid hatching in 1991 were considered. Four seasonal hatching groups were defined corresponding to individuals hatching during each season of the year. In each season of sampling, the mean ML of individuals from each hatching season

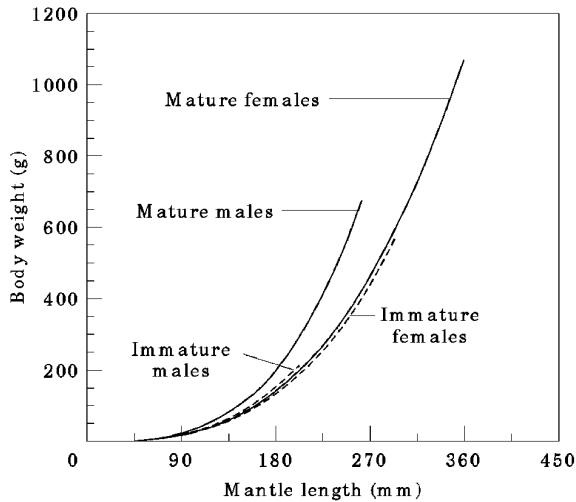


Figure 1. Relationships between mantle length (ML) and body weight (BW) for male and female *Illex coindetii* at each stage of maturity. Mature females: $BW=3.901 \times 10^{-5} ML^{2.910}$, $r^2=0.903$; mature males: $BW=1.496 \times 10^{-5} ML^{3.163}$, $r^2=0.902$; immature females: $BW=3.901 \times 10^{-5} ML^{2.0976}$, $r^2=0.941$; immature males: $BW=2.291 \times 10^{-5} ML^{3.022}$, $r^2=0.922$.

was calculated. The age assigned to each mean ML was the number of days from the start of the season of hatching to the middle of the season of capture.

Results

Relationship between mantle length (ML) and body weight (BW)

The maximum sizes of squid were 279 mm ML for males and 379 mm ML for females. The relationships between ML and BW for immature males and females were similar (Fig. 1). However, mature males had a greater body weight at the same length than the rest of the animals and the regression coefficient was significantly higher than 3 ($p<0.001$). Mature females showed a negative allometry ($p<0.01$).

Relationship between statolith length (SL) and mantle length (ML)

The maximum length of statoliths varied between 0.53 and 1.53 mm in the case of males, from 0.47 to 1.66 mm in females. For males and females a linear equation best described the relationship between SL and ML ($SL=0.395+0.005 ML$, $r^2=0.77$ for males and $SL=0.556+0.003 ML$, $r^2=0.84$ for females).

Relationship between statolith length (SL) and number of growth increments (NI)

No significant differences were found between the slopes ($p>0.05$) or the intercepts ($p>0.01$) for males and

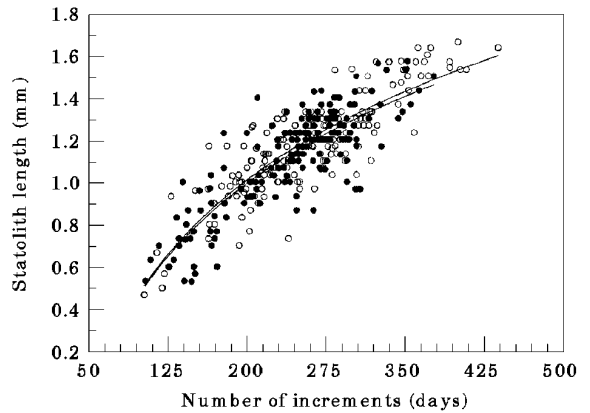


Figure 2. Relationships between number of increments (NI) and statolith length (SL) for male and female *Illex coindetii*. ●=Males: $SL=-2.90+1.690 NI$, $r^2=0.71$; ○=females: $SL=-2.95+1.719 NI$, $r^2=0.74$.

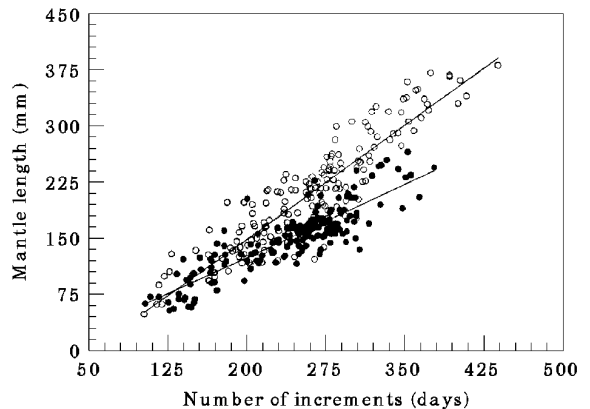


Figure 3. Relationships between number of increments and mantle length for male and female *Illex coindetii*. ●=Males: $ML=-5.86+0.65 NI$, $r^2=0.76$; ○=females: $ML=-53.63+1.01 NI$, $r^2=0.83$.

females (Fig. 2). This indicates that sex had no effect on the relationship between statolith length and the number of growth increments. Therefore, these relationships were estimated from the combined data from both sexes. The equation was: $SL=-2.92+1.701 \log NI$, $r^2=0.73$.

The number of increments varied between 104 and 393 in males and from 103 to 440 for females. Squids therefore recruited the fishery in approximately the third month of life. The life span for this species in Galician waters is approximately 13 months for males and 15 months for females.

Relationship between mantle length, body weight, and the number of growth increments

A linear equation fitted the data best for each sex (Fig. 3). The slopes for the regressions were significantly

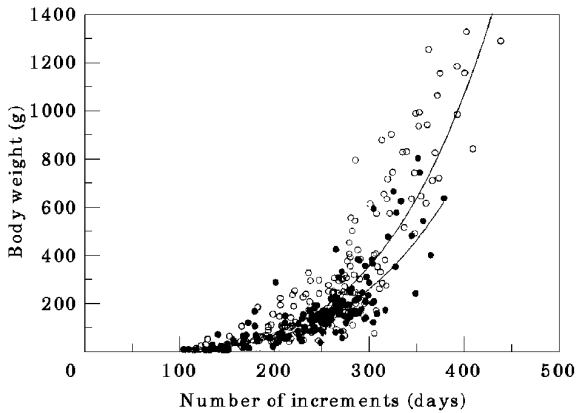


Figure 4. Relationships between number of increments and body weight for male and female *Illex coindetii*. ● = Males: $BW=1.38 \times 10^{-7} NI^{3.74}$; ○ = females: $BW=1.38 \times 10^{-7} NI^{3.80}$.

different between sexes ($p < 0.05$), indicating different growth rates for males and females (estimated as 0.72 mm d^{-1} and 0.84 mm d^{-1} for males and females, respectively).

The slopes of the relationships between body weight and number of growth increments did not differ significantly between sexes (Fig. 4; $p > 0.05$), but the intercepts did ($p < 0.001$). This indicates that, in individuals of the same age, females have a greater body weight than males.

In males, the greatest value for G in ML and BW was observed in 6-month-old individuals (Tables 1, 2), whereas the fastest rate of AGR in ML and BW was observed in 12-month-old specimens. In addition, the smallest G and AGR in ML and BW was found in 13-month-old squids.

In females, the maximum value observed for G in ML and BW also corresponded to 6-month-old individuals. The maximum AGR in ML and BW corresponded with 12-month-old specimens. The lowest G in ML and BW

Table 1. Mantle length growth-rates for each age-class of male and female *Illex coindetii*.

(a) Males

Age class	n	X_{ML}	s.d.	Range		G	AGR
				Min	Max		
91–120	4	68	4.2	62	71	—	—
121–150	16	77	20.2	53	122	0.40	0.31
151–180	16	114	23.4	68	160	1.33	1.24
181–210	11	129	26.3	93	203	0.41	0.49
211–240	20	140	14.9	117	164	0.26	0.34
241–270	48	161	19.1	116	227	0.51	0.72
271–300	33	171	19.2	135	210	0.22	0.34
301–330	13	198	35.5	150	247	0.49	0.88
331–360	6	236	23.6	190	265	0.61	1.27
361–390	3	242	19.5	200	285	0.10	0.21

(b) Females

Age class	n	X_{ML}	s.d.	Range		G	AGR
				Min	Max		
91–120	4	64	14.2	48	87	—	—
121–150	4	108	12.2	99	129	1.73	1.47
151–180	9	115	21.6	93	134	0.23	0.23
181–210	23	148	26.9	106	198	0.84	1.07
211–240	27	174	31.0	118	235	0.56	0.88
241–270	22	198	30.3	125	230	0.46	0.80
271–300	39	223	33.7	138	281	0.39	0.82
301–330	19	263	38.5	177	325	0.94	1.34
331–360	11	309	25.4	273	358	0.54	1.58
361–390	7	337	18.6	310	370	0.83	0.94
391–420	5	352	15.2	329	369	0.18	0.50
421–450	1	380	—	—	—	—	—

n = Number of specimens; X_{ML} = mean mantle length (mm); s.d. = standard deviation; Min = minimum ML; Max = maximum ML; G = instantaneous relative growth rate (% ML d^{-1}); AGR = absolute growth rate (mm d^{-1}).

Table 2. Body weight growth rates for each age class of male and female *Illex coindetii*.

(a) Males

Age class	n	X_{BW}	s.d.	Range		G	AGR
				Min	Max		
91–120	4	6.9	0.3	6	7	—	—
121–150	16	15.6	16.0	5	70	2.70	0.28
151–180	16	60.1	42.2	8	166	4.49	1.48
181–210	11	71.7	69.6	41	283	1.95	0.38
211–240	20	99.4	37.5	42	151	1.09	0.92
241–270	48	157.9	60.2	36	424	1.54	1.95
271–300	33	196.6	71.4	53	382	0.73	1.28
301–330	13	342.2	177.5	118	661	1.85	4.85
331–360	6	568.5	183.5	238	797	1.69	7.54
361–390	3	575.0	96.5	518	633	0.03	0.23

(b) Females

Age class	n	X_{BW}	s.d.	Range		G	AGR
				Min	Max		
91–120	4	6.6	3.3	4	12	—	—
121–150	4	30.1	11.3	21	49	5.06	0.78
151–180	9	41.1	25.6	16	102	1.03	0.36
181–210	23	90.9	52.7	39	220	2.65	1.66
211–240	22	198.1	74.4	75	291	1.12	1.88
241–270	27	141.6	76.3	38	292	1.48	1.68
271–300	39	294.2	145.4	82	789	1.32	3.13
301–330	19	482.1	228.4	73	895	1.65	6.26
331–360	11	742.2	171.4	488	983	1.44	8.67
361–390	7	947.4	197.9	705	1250	0.81	6.83
391–420	5	1093.3	169.6	835	1323	—	—

n=Number of specimens; X_{BW} =mean body weight (g); s.d.=standard deviation; Min=minimum BW; Max=maximum BW; G=instantaneous relative growth rate (% BW d⁻¹); AGR=absolute growth rate (mm d⁻¹).

was observed in 14-month-old individuals, whereas the lowest AGR in ML and BW corresponded to 6-month-old individuals.

In males and females, fluctuations were found in both measures of growth rate between successive age classes.

Maturity stage and growth-rate in males and females

Significant differences were found between the slopes of the BW–NI relationship (Fig. 5; $p < 0.02$) which correlate BW with NI for different stages of maturity in males and females. Thus, growth rate might influence rate of maturation of either sex, and mature squid weigh more than immature ones of the same age.

The youngest mature male was aged 140 d, the youngest mature female 183 d, the oldest immature male, 271 d, and oldest immature female 285 d.

Growth and seasonal hatching groups

Back-calculation indicated that the squid hatched between January 1991 and July 1992. Comparison of

mean ML showed that, up to the age of 225 d, for males and females, there were no differences in growth-rates among seasonal hatching groups (Fig. 6). From 225 d onwards, growth-rates for both sexes were greatest for winter-hatched squid and were progressively smaller for later hatching seasons. The differences in ML between males and females became evident after age 225 d.

Discussion

For squid recruiting to the fishery on the continental slope and shelf off Galicia, the relationship between ML and BW was isometric for immature specimens and allometric for mature ones: positive for males ($b > 3$) and negative for females ($b < 3$). The existence of positive allometry in mature males and negative allometry in females in the ML–BW relationship, therefore seems to be characteristic of this species (Sánchez *et al.*, in press). A possible adaptive explanation for this sexual dimorphism may be related to the sexual behaviour of this species during copulation, when males hold the female with their arms to deposit spermatophores inside the mantle cavity. Greater strength in the arms may mean

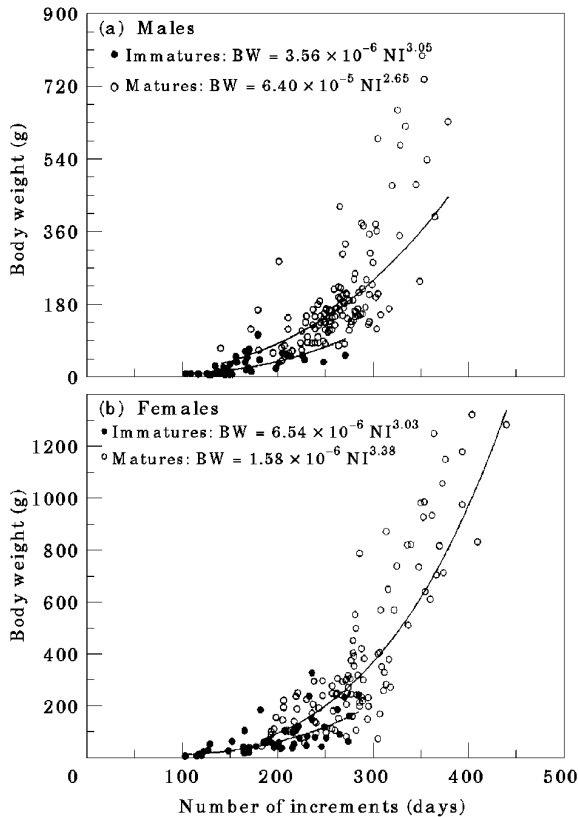


Figure 5. Relationships between number of increments and mantle length for male and female *Illex coindetii* at each maturity stage.

an advantage expressed in an increased effectiveness during copulation. In the case of mature females, negative allometry can be explained by the increase of reproductive tissues after maturation (Mangold *et al.*, 1969).

As in other geographical areas, female *Illex coindetii* attain larger sizes (ML) than do males in the Galician fishery (Sánchez *et al.*, in press). Especially large squids were captured (males >265 mm ML and females >340 mm ML), the largest found for this species. All these large animals were mature. However, in February 1993, a small proportion of immature females was caught with ML of over 300 mm, which indicates that the maximum ages of this species may be even greater than estimated in this study.

The life span calculated for *Illex coindetii* off the coast of Galicia (13 and 15 months for males and females, respectively) lies within the estimated range for other ommastrephid species in the Atlantic Ocean. Lipinski (1978) estimated the life span for *Illex illecebrosus* at 22 months; however, other authors suggest a life span of around 1 year for these species (Morris and Aldrich, 1985; Dawe and Beck, 1992). Rosenberg *et al.* (1981)

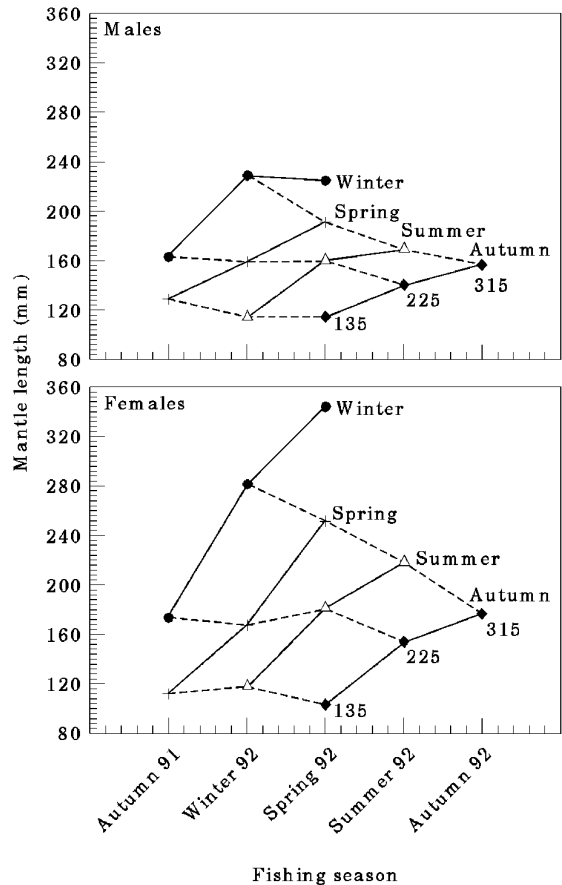


Figure 6. Growth in mantle length for male and female *Illex coindetii* in each seasonal hatching group. Continuous lines indicate hatching groups and broken lines show squids of the same age and different seasonal hatching groups. The numbers under these lines indicates age.

give 12 months for *Todarodes sagittatus*, Rodhouse and Hatfield (1990b) 12 months for *Illex argentinus*, and Villanueva (1992) 12 months for *Todarodes angolensis*.

The relationship between the ML and the NI in the Galician population is best represented by a linear equation. Observations by Lipinski (1978), Radtke (1983) and Morris and Aldrich (1985) for *Illex illecebrosus*, by Rodhouse and Hatfield (1990b) for *Illex argentinus*, and by Rosenberg *et al.* (1981) for *Todarodes sagittatus*, are also best represented by linear equations. Villanueva (1992), however, indicated that an exponential expression best described growth in *Todarodes angolensis*.

The relative growth rates in ML and BW tended to decrease with age, although exceptions were observed between the different age-classes (Table 1). The causes of variability in growth rates among age-classes (Table 1) may include both biotic (food, predators, spatial competition, etc.) and abiotic factors (temperature, light,

salinity, etc.), as indicated in the review by Forsythe and Van Heukelem (1987). A further explanation for these variations is the fact that the population was considered as a whole. Individuals from different microcohorts may have different growth rates. The differences in G and AGR would appear as fluctuations concealing the general decreasing pattern observed in the growth rates of the successive monthly age-classes. Some evidence of this effect was found when different seasonal hatching groups were analysed separately (Fig. 6). Similar results were found for *Illex argentinus* (Arkhipkin, 1990) and *Todarodes angolensis* (Villanueva, 1992); the greater the age of the individual, the smaller were the relative and absolute growth rates when each population was considered as a whole. Nevertheless, although instantaneous relative growth rate (G) tended to decrease with age, fluctuations in G between the successive age-classes were also found. Probably, these fluctuations were due to the high individual variability in growth rates.

Because counting growth increments is an extremely delicate, tedious, difficult and time-consuming task, attempts were made to estimate the age of *Illex coindetii* based on statolith length (SL). As found with *Illex illecebrosus* (Morris and Aldrich, 1985), *Illex argentinus* (Rodhouse and Hatfield, 1990b) and *Todarodes angolensis* (Villanueva, 1992; Lipinski *et al.*, 1993), it was observed that SL in *Illex coindetii* showed a significant dependence on age. The ML was also highly dependent on age and closely correlated with the SL, although this dependency showed inter-annual variations in other ommastrephids (Villanueva, 1992). The SL–NI relationship in *Illex coindetii* may therefore also vary annually. Thus, the use of the SL to estimate age would have to be verified over several years to check for any modification over a period of time. Moreover, the fit for ML–age is even better than that obtained for SL–age. This indicates that the use of SL as an estimator of NI (age) does not improve the results obtained using ML in *Illex coindetii*.

The relationship between BW and the NI was fitted by a power equation, which coincided with the only observations available for a closely related species, *Illex argentinus* (Rodhouse and Hatfield, 1990b).

G and AGR in BW of *Illex coindetii* were also estimated for each monthly age-class. Both rates of growth in BW were greater for females than for males, and both were faster than the rates found by Arkhipkin (1990) and Rodhouse and Hatfield (1990b) for *Illex argentinus*. Arkhipkin (1990) for *Illex argentinus* and Villanueva (1992) for *Todarodes angolensis* found fluctuations in these growth rates which were similar to those obtained in this paper for *Illex coindetii*. Increase in *Illex coindetii* BW was, however, greater than that calculated for the other two species.

A significant result was the influence of the stage of maturity on individual growth rate in such a way that, for each sex, at all times mature individuals weighed

more than immature individuals of the same age. Furthermore, males were larger than females. On this basis, it may be hypothesised that, from a minimum age, it is the capacity to grow, and not age, which influences the onset of maturation. This hypothesis may also explain the wide range of ages at which maturation seems to occur in males and females.

Taking into account the maximum ages of the immature individuals and life span of both sexes, the reproductive period of *Illex coindetii* (including maturation and spawning) may cover the final third of its life. These results agree with observations based on the percentage of mature individuals per ML class (González and Guerra, in press). Such a prolonged reproductive period supports the new concept that some species of cephalopods do not behave like populations that are semelparous *sensu stricto*, that is a short spawning period followed by death (see Mangold *et al.*, 1993 for review).

The differences in growth found from 8 months onward may have been due to the different availability of food from that age. This is what would happen if an abundant food resource was only available at a certain period of the year and with only one prey type of suitable size being available for the larger-sized individuals. *Illex coindetii* in Galician waters frequently prey on blue whiting (*Micromesistius poutassou*) (Rasero *et al.*, 1996). This fish does not appear to be available at sizes smaller than 14 cm in the habitat of *Illex coindetii*, because, as observed by Sánchez (1993), only large individuals of blue whiting (mostly between 20 and 26 cm) are available to larger-sized squid, mainly during autumn. The existing data on the sizes of blue whiting eaten by large *Illex coindetii* includes this range of sizes (Rasero *et al.*, 1996).

On the whole, the study of age and growth in *Illex coindetii* based on statoliths is a far more reliable technique than the analysis of modal progression would have been (González, 1994). This species has a rapid growth which seems to be highly dependent on environmental (season) and intrinsic (size, sex) factors.

Acknowledgements

We thank all members of the Group of Ecophysiology of Cephalopods (Instituto de Investigaciones Marinas, Vigo, CSIC) for their helpful criticism and suggestions of the manuscript. This work was funded by the Commission of the European Communities within the framework of the EU research programme in the fisheries sector (AIR, contract no. AIR1-CT92-0573).

References

- Arkhipkin, A. I. 1990. Edad y crecimiento del calamar (*Illex argentinus*). Frente Marítimo, 6(A): 25–35.

- Arkhipkin, A. I. and Scherbich, Z. N. 1991. Crecimiento y estructura intraespecífica del calamar, *Illex argentinus* (Castellanos, 1960) (Ommastrephidae) en invierno y primavera en el Atlántico sudoccidental. *Scientia Marina*, 55(4): 619–627.
- Brunetti, N. E. and Ivanovic, M. L. 1991. Morfología y morfometría de los estatolitos del calamar (*Illex argentinus*). *Frente Marítimo*, 9(A): 53–61.
- Caddy, J. F. 1991. Daily rings on squid statoliths: an opportunity to test standard population models? *In* Squid age determination using statoliths. Proceedings of the International Workshop held in the Istituto di Tecnologia della Pesca e del Pescato, Special publication, pp. 53–56. Ed. by P. Jereb, S. Ragonese, and S. V. Boletzky.
- Clarke, M. R. 1978. The cephalopod statolith – an introduction to its form. *Journal of the Marine Biological Association of the UK*, 58: 701–712.
- Dawe, E. G. and Beck, P. C. 1992. Population structure, growth and sexual maturation of short-finned squid at Newfoundland, Canada, based on statolith analysis. *ICES C.M.* 1992/K: 33.
- Dawe, E. G., O'Dor, R. K., Odense, P. H., and Hurley, G. V. 1985. Validation and application of an ageing technique for short-finned squid (*Illex illecebrosus*). *Journal of NW Atlantic Fishery Science*, 6: 107–116.
- Dawe, E. G. and Natsukari, Y. 1991. Light microscopy. *In* Squid age determination using statoliths. Proceedings of the International Workshop held in the Istituto di Tecnologia della Pesca e del Pescato, Special publication, pp. 83–95. Ed. by P. Jereb, S. Ragonese, and S. V. Boletzky.
- Forsythe, J. W. 1993. A working hypothesis of how seasonal temperature change may impact the field growth of young cephalopods. *In* The Recent Advances in Cephalopod Fisheries Biology, pp. 133–143. Ed. by T. Okutani, R. K. O'Dor, and T. Kubodera. Tokai University Press, Tokyo.
- Forsythe, J. W. and Van Heukelem, W. F. 1987. Growth. *In* Cephalopod Life Cycles. Vol. 2, pp. 135–156. Ed. by P. R. Boyle. Academic Press, London.
- González, A. F. 1994. Bioecología de *Illex coindetii* Vérany, 1839 (Cephalopoda, Ommastrephidae) de las aguas de Galicia. Ph.D. Thesis. Facultad de Biología, Universidad de Vigo: 237 pp.
- González, A. F. and Guerra, A. (in press). Reproductive strategies of the short-finned squid *Illex coindetii* (Cephalopoda, Ommastrephidae) of the Northeastern Atlantic waters. *Sarsia*.
- Guerra, A. 1992. Mollusca, Cephalopoda. *In* Fauna Ibérica, Vol. 1. Ed. by M. A. Ramos *et al.*, Museo Nacional de Ciencias Naturales. CSIC, Madrid, 327 pp.
- Guerra, A. and Sánchez, P. 1985. Crecimiento relativo del estatolito de *Sepia officinalis* (Cephalopoda, Sepioidea) de la ría de Vigo. *Investigación Pesquera*, 49(4): 545–557.
- Hatfield, E. M. C. 1991. Post-recruit growth of the Patagonian squid *Loligo gahi* (d'Orbigny). *Bulletin of Marine Science*, 49(1–2): 349–361.
- Hurley, G. V., O'Dense, P., O'Dor, R. K., and Dawe, E. G. 1985. Strontium labelling for verifying daily growth increments in the statolith of short-finned squid (*Illex illecebrosus*). *Canadian Journal of Fisheries and Aquatic Sciences*, 42(2): 280–283.
- Jackson, G. D. 1990. The use of tetracycline staining techniques to determine statolith growth ring periodicity in the tropical loliginid squid *Loliolus noctiluca* and *Loligo chinensis*. *Veliger*, 33(4): 389–393.
- Jackson, G. D. 1994. Application and future potential of statolith increment analysis in squid and sepiolids. *Canadian Journal of Fisheries and Aquatic Sciences*, 51: 2612–2625.
- Kristensen, T. K. 1980. Periodical growth rings in cephalopod statoliths. *Dana*, 1: 39–51.
- Lipinski, M. R. 1978. The age of squid *Illex illecebrosus* (LeSueur, 1821) from their statoliths. *ICNAF Research Documents*, 78/II/15.
- Lipinski, M. R., Dawe, E. G., and Natsukari, Y. 1991. Practical procedures of squid aging using statoliths. A laboratory manual. Introduction. *In* Squid age determination using statoliths. Proceedings of the International Workshop held in the Istituto di Tecnologia della Pesca e del Pescato, Special publication, pp. 77–81. Ed. by P. Jereb, S. Ragonese, and S. V. Boletzky.
- Lipinski, M. R., Compagno, R. M. A., and Underhill, L. G. 1993. Comparison of the statoliths of *Todaropsis eblanae* and *Todarodes angolensis* (Cephalopoda: Ommastrephidae). *In* The Recent Advances in Cephalopod Fisheries Biology, pp. 263–273. Ed. by T. Okutani, R. K. O'Dor, and T. Kubodera. Tokai University Press, Tokyo.
- Mangold, K., Lu, C. C., and Aldrich, F. A. 1969. A reconsideration of forms of squid of the genus *Illex* (Illicinae, Ommastrephidae). II Sexual dimorphism. *Canadian Journal of Zoology*, 47: 1153–1156.
- Mangold, K., Young, R. E., and Nixon, M. 1993. Growth versus maturation in cephalopods. *In* The Recent Advances in Cephalopod Fisheries Biology, pp. 697–704. Ed. by T. Okutani, R. K. O'Dor, and T. Kubodera. Tokai University Press, Tokyo.
- Morris, C. C. and Aldrich, F. A. 1985. Statolith length and increment number for age determination of *Illex illecebrosus* (LeSueur, 1821) (Cephalopoda: Ommastrephidae). *NAFO Scientific Council Studies*, 9: 101–106.
- Natsukari, Y., Nakanose, T., and Oda, K. 1988. Age and growth of Loliginid squid *Photololigo edulis* (Hoyle, 1885). *Journal of Experimental Marine Biology and Ecology*, 116: 177–190.
- Radtke, R. L. 1983. Chemical and structural characteristics of statoliths from the short-finned squid *Illex illecebrosus*. *Marine Biology*, 76: 47–54.
- Ragonese, S. and Jereb, P. 1992. Length-weight relationship of *Illex coindetii* Vérany, 1839 (Mollusca: Cephalopoda) in the Sicilian Channel. *Oebalia*, 18: 17–24.
- Rasero, M., González, A. F., Castro, B. G., and Guerra, A. (1996). Predatory relationships of two sympatric squid, *Todaropsis eblanae* and *Illex coindetii* (Cephalopoda: Ommastrephidae) in Galician waters. *Journal of the Marine Biological Association of the UK*, 76: 73–87.
- Rodhouse, P. G. and Hatfield, E. M. C. 1990a. Age determination in squid using statolith growth increments. *Fisheries Research*, 8: 323–334.
- Rodhouse, P. G. and Hatfield, E. M. C. 1990b. Dynamics of growth and maturation in the cephalopod *Illex argentinus* de Castellanos, 1960 (Teuthoidea, Ommastrephidae). *Philosophical Transactions of the Royal Society of London B*, 329 (1254): 229–241.
- Roper, C. F. E., Lu, C. C., and Mangold, K. 1969. A new species of *Illex* from the Western Atlantic and distributional aspects of other *Illex* species (Cephalopoda: Oegopsida). *Proceedings of Biological Society of Washington*, 82: 295–322.
- Roper, C. F. E., Sweeney, M. J., and Nauen, C. E. 1984. *FAO Species Catalogue. Cephalopods of the World*. *FAO Fisheries Synopsis*, 3(125): 277 pp.
- Rosenberg, A. A., Wiborg, F. K., and Bech, I. M. 1981. Growth of *Todarodes sagittatus* (Lamarck) (Cephalopoda, Ommastrephidae) from the Northeast Atlantic, based on counts of statolith growth rings. *Sarsia*, 66: 53–57.
- Sánchez, P. 1981. Características bioecológicas de *Illex coindetii* (Vérany, 1839) en el Mar Catalán. Ph.D. Thesis. Universidad de Barcelona: 219 pp.

- Sánchez, P., González, A. F., Jereb, P., Laptikhovsky, V. V., Mangold, K., Nigmatullin, CH. M., and Ragonese, S. (in press). In A Review of Recruitment Dynamics in the squid genus *Illex*. FAO Fisheries Technical Papers. Ed. by E. Dawe, R. K. O'Dor, and P. G. Rodhouse.
- Sánchez, F. 1993. Las comunidades de peces del la plataforma del Cantábrico. Publicación especial del I.E.O., 13: 137 pp.
- Spratt, J. D. 1979. Age and growth of the market squid *Todarodes sagittatus* (Lamarck) in the Barents Sea. ICES C.M.1979/K:3.
- Villanueva, R. 1992. Interannual growth differences in the oceanic squid *Todarodes angolensis* Adam in the Northern Benguela upwelling system, based on statolith growth increment analysis. *Journal of Experimental Marine Biology and Ecology*, 159: 157–177.
- Zar, J. H. 1984. *Biostatistical analysis*. Prentice Hall, Inc. Simon and Schuster Company. Englewood Cliffs, New Jersey, USA. 718 pp.