Dynamics of Growth and Maturation in the Cephalopod Illex argentinus de Castellanos, 1960 (Teuthoidea: Ommastrephidae)

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Marine Life Sciences Division, British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, U.K.

SUMMARY

Post-recruit *Illex argentinus* were collected from the fishery on the Patagonian Shelf between 1986 and 1988. Age was determined by analysis of daily growth increments in ground sections of the statolith, female fecundity was determined, specimens were dissected, weighed and assigned a maturity stage. The relation between mantle length and age is best approximated by a linear model. Both sexes live approximately one year. Females grow faster and attain a larger size than males, but males mature younger. Hatching occurs during the austral winter, peaking in June–July. There is a consistent trend of increasing growth rate with later date of hatching. Statolith growth is negatively allometric with body growth and there is greater divergence between statolith and body growth in females. In post-recruit *Illex* growth in mass of somatic tissues, apart from the digestive gland, approximates isometry with growth of the whole body. Growth of the digestive gland and the reproductive organs is positively allometric with growth in whole body mass. There is poor correlation between the mass of female reproductive organs and whole body mass, which is due to differences in size at maturity. Mating rarely occurs on the feeding grounds. Fecundity of fully mature females in the sample falls in the range 113 835–246 098 eggs per individual. This possibly underestimates average fecundity because mature squid on the feeding grounds may be precocious and smaller than average at full maturity. A model combining absolute and relative growth, predicts average male and female growth and growth of the major somatic and reproductive organs. This poorly predicts average female maturity indices with age because of variability in mass of the female reproductive organs. A model that treats maturity stages separately gives close agreement with measured mass of the reproductive organs and maturity indices of a mature female at age one year. Females invest approximately 20 % of total body mass in gonad and accessory reproductive organs at full maturity.

1. INTRODUCTION

The Argentine shortfin squid, *Illex argentinus* de Castellanos, 1960, is distributed in the western South Atlantic (figure 1) from approximately 30 °S to 54 °S over the Patagonian Shelf, shelf break, and around the Falkland Islands at depths of 80–800 m (de Castellanos & Menni 1969; Roper *et al.* 1984). Since about 1970 a fishery has developed for the species, exploiting what appears to be a single stock (Sato & Hatanaka 1983; Csirke 1987).

The life cycle of *Illex argentinus* is poorly understood. Most of the population spawns in the winter and a smaller part, probably only about 1 %, spawns in the summer (Hatanaka *et al.* 1985; Koronkiewicz 1986; Hatanaka 1988). Juveniles of the winter spawners appear over the northern part of the Patagonian Shelf in the austral spring, spread southwards and offshore, and then move over the Shelf during the summer. In autumn they move eastwards towards the edge of the shelf and northwards, towards the spawning area which is presumed to be in the Brazil Current. This flows southwards off the east coast of South America. The minor group of summer spawners are thought to lay their eggs in the shallow coastal waters of the Shelf, but the spawning grounds have not been identified.

Growth of *Illex argentinus* has been estimated from means, or modal lengths, of size–frequency distributions derived from sequential samples from the fishery, and both linear and von Bertalanffy models have been fitted to the data (Hatanaka 1986; Koronkiewicz 1986). These studies have revealed that the lifespan is approximately one year with females growing faster, and attaining a larger size, than males.

There are several problems associated with determining cephalopod growth from size frequency distributions. They include identifying age classes where there is more than one spawning group in the population (Rodhouse *et al.* 1988), Lee's phenomenon, whereby faster growing individuals have a higher mortality rate than slower growers (Ricker 1975), and the confounding effects of immigration and emigration (Hurley & Beck 1979; Dawe *et al.* 1985). It is therefore important that, where possible, methods of ageing
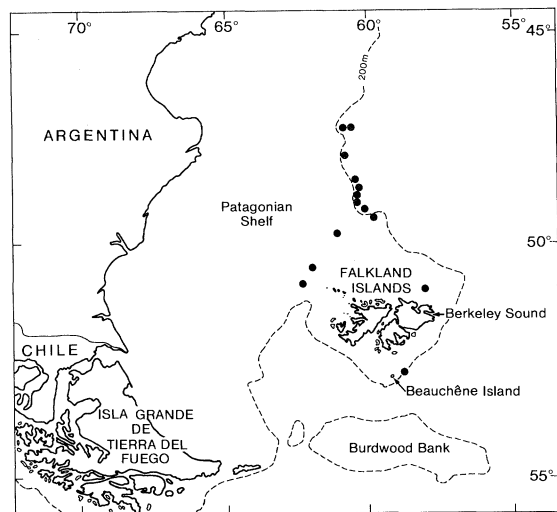
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Figure 1. Map of the Patagonian Shelf region showing positions where *Illex argentinus* samples were taken.

individuals be employed in studies of cephalopod growth to derive reliable size-at-age data.

This study examines absolute and relative growth of *Illex argentinus*, in relation to sexual maturation, from the time of recruitment into the commercial fishery on the Patagonian Shelf until the time when the squid depart from the fishing grounds to spawn. Size-at-age data have been derived by analysis of growth increments in the statolith (Rodhouse & Hatfield 1990). Relative growth is examined to determine the differential allocation of resources, during sexual maturation, primarily between the soma and the gonad but also between the major somatic organs.

The daily nature of growth increments in the statolith of the closely related squid, *Illex illecebrosus*, from the North Atlantic has been verified by Dawe *et al.* (1985) and Hurley *et al.* (1985). Growth data derived from increments in the statolith have been published for several other squid species by Hurley & Beck (1979), Rosenberg *et al.* (1980), Martins (1982), Kristensen (1983), Radtke (1983), Wiborg *et al.* (1984), Wiborg & Beck (1984), Morris & Aldrich (1985), Natsukari *et al.* (1988) and Jackson (1989).

2. MATERIALS AND METHODS

Samples of *Illex argentinus* were taken from the commercial jig fishery on the Patagonian Shelf between 1986 and 1988. Specimens for full morphometric and length-at-age analysis (sample A) were frozen aboard ship and returned to the U.K. Specimens for length-at-age analysis only (sample B) were measured and dissected in the field. Dates and locations of all samples are given in table 1.

Morphometric/length-at-age analysis

Sample A for morphometric analysis ($n = 335$) was selected to represent the size range present. Specimens were dissected, sexed and assigned a maturity stage (I: juvenile; II: immature; III: preparatory; IV: maturing; V: mature) based on the appearance and

Table 1. *Position and date of capture of Illex argentinus used in morphometric, and size at age, analysis*

(Detailed information on position and date of capture not available for samples taken from vessels transhipping catch in Berkeley Sound, but these were caught North of Falkland Islands.)

date	position		n
sample A			
morphometric analysis only			
11 Mar. 1986	48° 37′ S 60° 29′ W		12
15 Mar. 1986	49° 03′ S 60° 35′ W		20
20 Mar. 1986	48° 55′ S 60° 30′ W		12
21 Mar. 1986	47° 19′ S 60° 47′ W		16
25 Mar. 1986	47° 56′ S 60° 56′ W		9
		total	69
morphometric/size at age analysis			
7 Mar. 1986	49° 45′ S 61° 09′ W		25
14 Mar. 1986	49° 15′ S 60° 03′ W		17
18 Mar. 1986	48° 47′ S 60° 26′ W		22
22 Mar. 1986	47° 21′ S 60° 48′ W		21
24 Apl 1986	no data		2
May 1986	no data		22
Jun. 1986	no data		21
25 Mar. 1987	no data		36
21 Feb. 1988	52° 50′ S 58° 50′ W		12
Mar. 1988	no data		88
		total	266
sample B			
size at age analysis only			
15 Mar. 1987	51° 05′ S 58° 02′ W		30
20 Apl 1987	50° 55′ S 62° 17′ W		50
18 May 1987	49° 32′ S 59° 55′ W		50
4 Jun. 1987	50° 33′ S 62° 01′ W		50
		total	180

relative size of the gonads and accessory reproductive organs (Lipinski 1979; Juanico 1983). The following measurements were made to the nearest millimetre: dorsal mantle length (ML), lower mandible rostral length (LRL), nidamental gland length of females (NGL), and the following measurements of mass to two decimal places (in grams): total body (BW), mantle (MW), head, including arms and tentacles (HW), digestive gland (DGW), ovary, including oviducts (OW), testis (TW), nidamental gland (NGW), oviducal gland (OGW), spermatophoric complex (SCW), and viscera, including gills, empty stomach, caecum, pancreas, ink sac (VW). The paired statoliths were dissected from the heads of a sub-sample ($n = 251$), using one of the techniques reviewed by Rodhouse & Hatfield (1990), and stored temporarily in analytical-grade glycerol.

Fecundity estimates

Fecundity was estimated in a sub-sample of 16 females from sample A (maturity stage: III, $n = 4$; IV, $n = 10$; V, $n = 2$). Ovaries and oviducts were removed, fixed in 5% formalin, to harden the eggs and make them easier to handle, and weighed. Number of eggs in the ovary and oviduct were estimated from counts in sub-samples of either 250 mg or 50 mg. Weighing before and after fixation showed that this had no appreciable effect on masses of ovaries or oviducts.

Before fixation 25 mg samples were taken from the ovary and oviducts of a fully mature female and the major axis of the eggs measured to 0.1 mm. Eggs were counted under an illuminated magnifying glass and measured with a binocular dissecting microscope equipped with an ocular micrometer.

Length-at-age analysis only

The mantle lengths of specimens from sample B, processed in the field ($n = 180$), were measured to the nearest 10 mm, sexed and assigned a maturity stage. Statolith pairs were extracted, stored in analytical-grade glycerol and returned to the U.K. for preparation and increment analysis.

Treatment of statoliths

Statolith lengths were measured from the dorsal dome to the tip of the rostrum using an eyepiece graticule. After cleaning in alcohol, each statolith pair was mounted anterior side up on a microscope slide in 'Polarbed 812' resin. Ground sections, revealing the growth rings, were prepared by wet grinding with glycerine using 1000-grade carborundum paper glued to a glass slide to provide a flat surface. Usually only one statolith from each pair was ground; where both were examined similar results were obtained. After grinding, a segment of the statolith section, showing the growth rings, was traced using a compound microscope with camera lucida attachment. Increment counts were made starting at the edge of the statolith ending at the border of the nucleus, which is assumed to be the natal increment (Dawe *et al.* 1985). In a test where four repeat counts were done on a sample of ten statoliths, the coefficient of variation about the mean count for each statolith fell in the range 0.5–3.5%.

Statistical treatment

Statistical procedures were performed using the MINITAB statistical package (Ryan *et al.* 1985). All transformations are natural logarithms.

3. RESULTS

Mantle length at age

The relation between mantle length of male and female *Illex argentinus*, and number of daily growth increments in the statolith, are shown in figure 2. All data are combined in the graphs but the two samples from table 1 are depicted with different symbols. There are significant differences ($p < 0.001$) between slopes and intercepts in the growth plots for males and females.

The date of hatching of each specimen which had been aged was back calculated from the date of capture; where the date of capture is uncertain (table 1) it was assumed to be mid-month. The distribution of hatching months is shown in figure 3. The data used in this analysis were taken from sample A, which was selected to represent the size range of squid present and from sample B, which was taken at random from the catch. Although the size selected data from sample A indicate the range of hatching dates during the three years of the study, they do not provide a reliable indication of peak hatching time. The data from sample B show that the peak of hatching occurred during July in 1987.

The data were partitioned into groups of squid from different years, with hatching dates in the same month. Linear models were fitted by regression analysis to these data, and also to the complete data set shown in figure 2. There were too few data, or the size or age range was too small, to fit the trajectories for males hatched in March, April and September or females born in February, March, April and September. No February hatched males occurred in the samples.

Inspection of the slopes (b) for the growth equations in table 2 reveals that the growth rate of females is consistently greater than in males when groups hatched in the same month are compared. This is also reflected in the data for all months combined. There is also a consistent trend of increasing growth rate, of both males and females, with month of hatching between May and August, so that squid hatched early in the austral winter appear to grow more slowly than those hatched late.

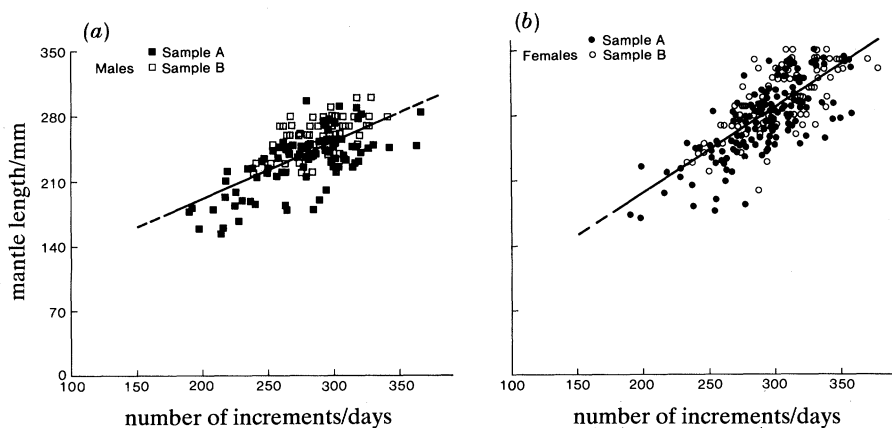The linear equations in table 2 were used to predict

Figure 2. Relation between number of growth increments in the statolith and mantle length of (*a*) male and (*b*) female *Illex argentinus*.
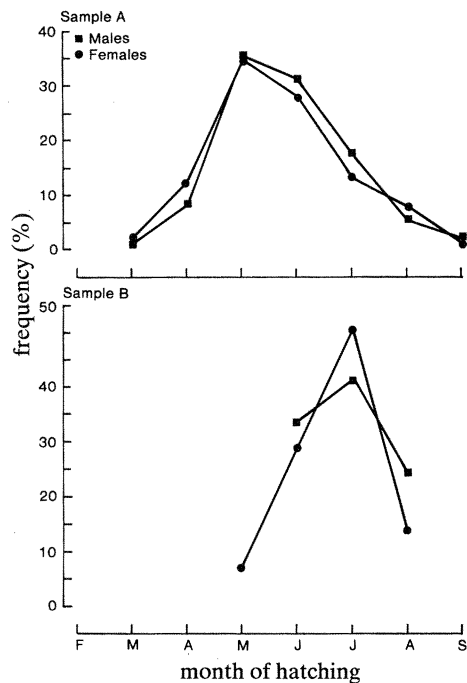
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Figure 3. Frequency distribution of hatching month of *Illex argentinus*.

mantle lengths, at age one year, of males and females hatched in each month from May to August (table 2). The data reflect the growth rate differences between squid hatching in different months so that those hatching early in the austral winter are predicted to

attain a smaller size after one year's growth than those hatching late.

Statolith length at age

There is a positive relation between the number (N) of growth increments in the statolith and statolith length (SL, in millimetres) (figure 4). The relation, for all data combined, is similar for both sexes:

males SL = 0.48 (± 0.04) + 0.0019 (± 0.001) N ($r^2 = 0.51$; $n = 164$);

females SL = 0.53 (± 0.03) + 0.0018 (± 0.001) N ($r^2 = 0.55$; $n = 267$).

There is no significant difference in the slopes of these lines but the intercepts are significantly different ($p < 0.001$).

Growth of statolith length proceeds at a relatively slower rate than mantle length and the relation between statolith growth and body growth differs between sexes. From the equations in table 2 for all months, predicted increase in mantle length between age 200 and 300 days is 32 % for males and 46 % for females whereas, from the equations above, predicted increase in statolith length for the same period is 22 % for males and 23 % for females.

Statolith length – mantle length relation

The allometric relation between statolith length (SL, in millimetres) and mantle length (millimetres) in males and females is given by the following:

males   ln SL = -2.83 (± 0.18) + 0.52 (± 0.03) ln ML ($r^2 = 0.60$; $n = 164$);

Table 2. *Intercepts* (A) *and slopes* (b) $\pm$*s.d. in linear models for size at age in post-recruit Illex argentinus for each month of hatching*: ML (mm) $= A + bT$ (days)

(Predicted mantle lengths at age 1 year ($\pm$s.d.) are also given.)

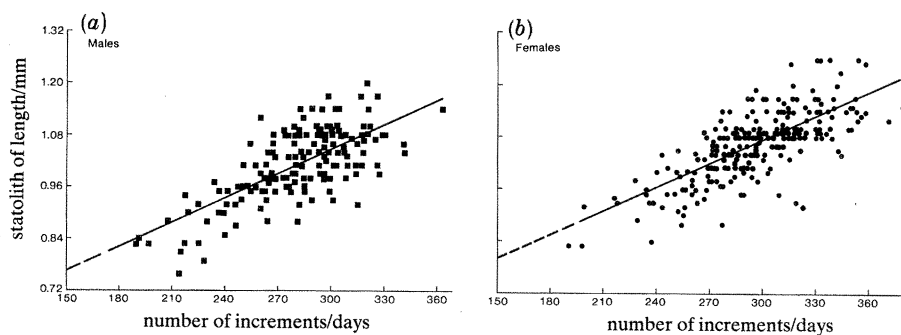|	A	b	r^2	n	predicted ML at 1 year
Males					
May	137.0 (± 58.7)	0.35 (± 0.20)	0.09	35	265 (± 14.2)
Jun.	46.1 (± 22.8)	0.70 (± 0.08)	0.59	53	301 (± 7.4)
Jly	26.6 (± 16.2)	0.81 (± 0.06)	0.82	44	320 (± 5.5)
Aug.	-9.8 (± 27.9)	1.00 (± 0.11)	0.83	21	355 (± 11.0)
all months	70.9 (± 15.2)	0.61 (± 0.05)	0.45	153	295 (± 4.8)
females					
May	-7.8 (± 32.8)	0.94 (± 0.11)	0.55	61	335 (± 7.8)
Jun.	-13.2 (± 20.4)	0.99 (± 0.07)	0.74	75	351 (± 5.3)
Jly	-10.7 (± 17.7)	1.03 (± 0.06)	0.80	78	367 (± 4.8)
Aug.	-72.6 (± 28.0)	1.30 (± 0.10)	0.88	28	402 (± 7.9)
all months	15.6 (± 14.4)	0.91 (± 0.05)	0.57	242	347 (± 3.6)

Figure 4. Relation between number of growth increments in the statolith and statolith length (*a*) males and (*b*) females.

Table 3. *Slopes (b) and intercepts (A) ± s.d. for allometric equations relating mantle length and total body mass of male and female Illex argentinus to the size and mass of somatic tissues, gonads and secondary sexual organs*: ln *organ mass (or length)* = A + b ln BW; ln *organ mass (or length)* = A + b ln ML (s: *residual standard deviation about the regression lines*; r² : *adjusted proportion of variation accounted for by the variance model*)

	A	b	s	r²	n
independent variable: total body mass					
dependent variable:					
males					
mantle mass	−0.11 (±0.08)	0.88 (±0.01)	0.06	0.97	122
head mass	−1.70 (±0.12)	1.10 (±0.02)	0.10	0.96	122
viscera mass	−2.04 (±0.21)	0.81 (±0.04)	0.18	0.81	122
digestive gland mass	−3.89 (±0.21)	1.29 (±0.04)	0.18	0.91	122
testis mass	−4.34 (±0.28)	1.17 (±0.05)	0.23	0.83	122
spermatophoric complex mass	−9.62 (±0.59)	1.93 (±0.10)	0.50	0.74	122
lower rostral length	0.06 (±0.06)	0.25 (±0.01)	0.05	0.84	103
females					
mantle mass	−0.32 (±0.09)	0.92 (±0.01)	0.09	0.95	213
head mass	−1.14 (±0.09)	0.97 (±0.01)	0.09	0.95	213
viscera mass	−2.08 (±0.17)	0.84 (±0.03)	0.17	0.82	213
digestive gland mass	−4.21 (±0.18)	1.35 (±0.03)	0.18	0.91	212
ovary mass	−7.98 (±0.94)	1.76 (±0.15)	0.97	0.38	213
nidamental gland mass	−8.67 (±0.96)	1.78 (±0.16)	0.99	0.34	213
oviducal gland mass	−10.10 (±1.57)	1.57 (±0.13)	0.80	0.40	211
lower rostral length	0.23 (±0.06)	0.22 (±0.01)	0.06	0.78	157
independent variable: mantle length					
dependent variable:					
males					
total body mass	−14.3 (±0.56)	3.68 (±0.10)	0.13	0.91	122
mantle mass	−13.1 (±0.44)	3.30 (±0.08)	0.10	0.93	122
head mass	−17.0 (±0.85)	3.95 (±0.16)	0.20	0.84	122
viscera mass	−14.2 (±0.79)	3.08 (±0.15)	0.18	0.79	122
digestive gland mass	−22.0 (±1.14)	4.67 (±0.21)	0.26	0.81	122
testis mass	−21.2 (±1.21)	4.32 (±0.22)	0.28	0.76	122
spermatophoric complex mass	−34.8 (±2.71)	6.64 (±0.50)	0.63	0.60	122
lower rostral length	−3.7 (±0.26)	0.95 (±0.05)	0.06	0.79	103
females					
total body mass	−13.0 (±0.43)	3.40 (±0.08)	0.13	0.91	213
mantle mass	−12.5 (±0.43)	3.16 (±0.08)	0.14	0.89	213
head mass	−14.0 (±0.45)	3.35 (±0.08)	0.14	0.89	213
viscera mass	−13.0 (±0.64)	2.87 (±0.11)	0.20	0.75	213
digestive gland mass	−21.0 (±0.90)	4.47 (±0.16)	0.28	0.79	212
ovary mass	−29.2 (±3.23)	5.71 (±0.58)	1.02	0.32	213
nidamental gland mass	−30.3 (±3.31)	5.80 (±0.59)	1.04	0.31	213
oviducal gland mass	−29.2 (±2.80)	5.11 (±0.49)	0.84	0.34	211
nidamental gland length	−3.7 (±1.11)	1.46 (±0.20)	0.33	0.20	211
lower rostral length	−2.7 (±0.21)	0.77 (±0.04)	0.06	0.73	157

females   ln SL = −2.15 (±0.12) + 0.39 (±0.02) ln ML (r² = 0.55; n = 267).

There is a significant difference between the slopes and intercepts of these lines (p < 0.01).

The low exponents in the above equations reflect the observation that statolith growth is negatively allometric with mantle growth in both sexes, with greater divergence between the growth rates in females.

Allometry

Relation between log transformed measurements of body mass and mantle length, and size and mass of somatic tissues, gonads and secondary sexual organs were derived by linear regression analysis (table 3). In each instance regressions were highly significant.

Table 3 reveals several trends in the relative growth of *Illex argentinus*. In relation to growth in body mass, the growth of somatic tissues of mantle, head, and viscera approximates isometry (b = 1) in males and females. The digestive gland, gonad and secondary sexual organs, grow relatively faster in both sexes than the total body (b > 1). Correlation between body mass and the mass of somatic tissues is generally higher than the correlation between body mass and mass of the reproductive organs, especially in females.

In relation to growth in mantle length, the growth of body mass exceeds the expected cubic (b = 3) relation (Forsythe & Van Heukelem 1987). Growth in mass of the somatic tissues of the mantle, head and viscera approximate a cubic relation with mantle length, except the head of the male which has a somewhat higher length exponent. The digestive gland, gonad and secondary sexual organs have length exponents that are considerably higher than for other tissues. Correlation between mantle length and the mass of
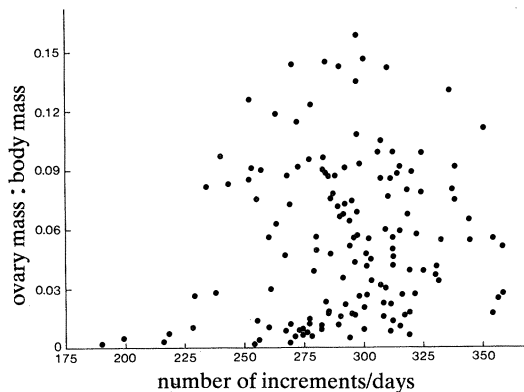
Figure 5. Relation between number of growth increments in the statolith and the ratio ow:bw.

somatic tissues is also generally higher than the correlation between mantle length and mass of the reproductive organs, especially in females.

To test whether the low correlation between ovary mass and body mass, and ovary mass and mantle length (table 3), could be attributed to the confounding effects of age, the relation between the ratio ow:bw and age was examined. The expectation being that if early hatched slow-growing females mature at the same age, but at a smaller size than late hatched, fast-growing females, a positive relation would emerge. However, no significant relation was found (figure 5),

which suggests that the relatively low predictability of ovary mass from body mass or mantle length is due to individual variation in the size at which full maturity is reached.

The relation between ovary mass and body mass, and nidamental gland and body mass, varies with maturity stage. There are significant, but non-systematic, differences among slopes when the relations are calculated for each maturity stage separately ($p < 0.01$ for ovaries; $p < 0.001$ for nidamental glands). When the common slopes (b) are fitted for each maturity stage there is a systematic increase in intercept values with maturity stage and the differences among intercept values are significant ($p < 0.001$) in the case of both ovaries and nidamental glands (table 4). These data show that both ovary mass and nidamental gland mass increase with maturity stage, independent of body mass.

Growth of the beak, in terms of lower rostral length, is approximately isometric with mantle growth in males but it grows relatively more slowly in females.

Maturity stage relations

The median number of growth increments in the statolith and median mantle length at each maturity stage for males and females are shown in figure 6. For both sexes there is significant correlation ($p < 0.01$– $p < 0.05$) between number of increments, mantle

Table 4. *Common slope (b) and intercepts (A) $\pm$ s.d. for allometric equations relating total body mass of maturity stage I–V female Illex argentinus to mass of ovary and nidamental glands*: $\ln \text{ow} = A + b \ln \text{bw}$; $\ln \text{ngw} = A + b \ln \text{bw}$ (*s: residual standard deviation about the regression lines*; r^2: *adjusted proportion of variation accounted for by the variance model*).

	A	b (common)	s (common)	r^2	n
dependent variable: ovary mass					
maturity stage[a]					
I	-6.14 (± 0.48)	1.23 (± 0.08)	0.46	0.98	10
II	-6.03 (± 0.45)	—	—	—	43
III	-4.77 (± 0.47)	—	—	—	75
IV	-3.86 (± 0.47)	—	—	—	71
V	-3.58 (± 0.49)	—	—	—	14
dependent variable: nidamental gland mass					
maturity stage[a]					
I	-6.81 (± 0.53)	1.24 (± 0.08)	0.99	0.96	10
II	-6.68 (± 0.51)	—	—	—	43
III	-5.30 (± 0.53)	—	—	—	75
IV	-4.51 (± 0.53)	—	—	—	71
V	-4.25 (± 0.55)	—	—	—	14

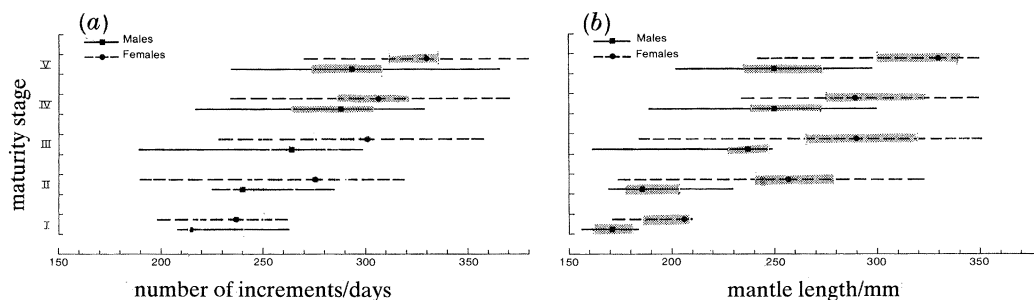[a] Differences among intercepts significant ($p < 0.001$).

Figure 6. (a) Relation between number of growth increments in the statolith and male and female maturity stage; (b) relation between mantle length and male and female maturity stage (horizontal bars: range and interquartile range).
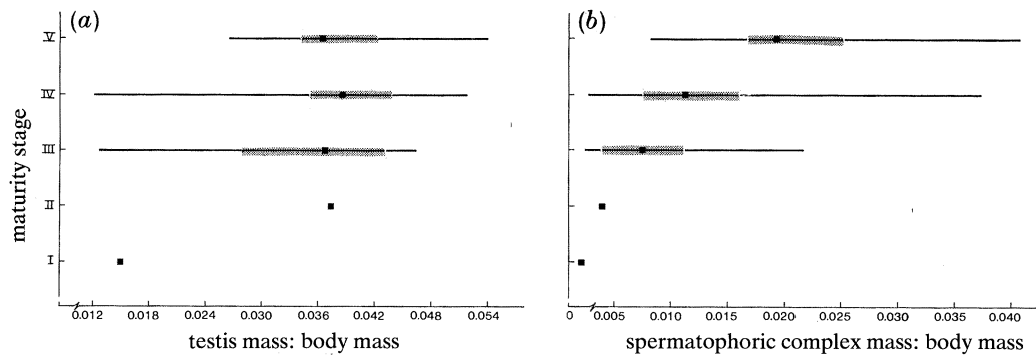
Figure 7. (*a*) Relation between medians of the ratio TW:BW and maturity stage in males; (*b*) relation between medians of the ratio SCW:BW and maturity stage in males (horizontal bars: range and interquartile range).
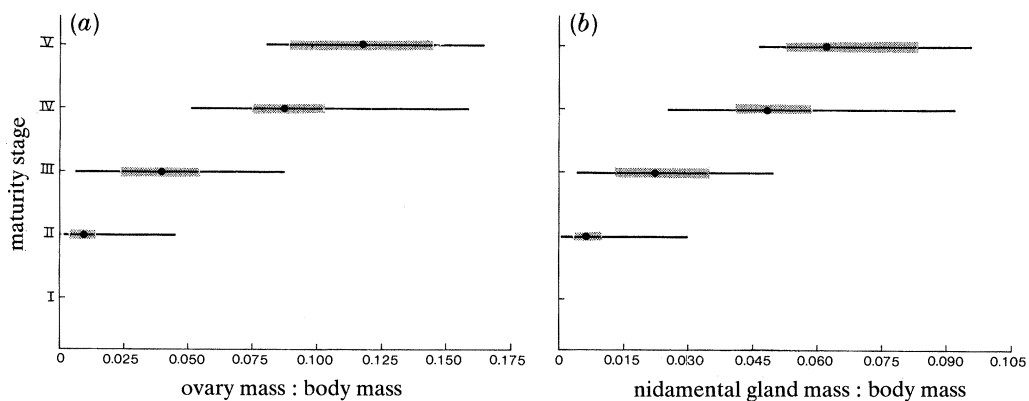

Figure 8. (*a*) Relation between medians of the ratio OW:BW and maturity stage in females; (*b*) relation between medians of the ratio NGW:BW and maturity stage in females (horizontal bars: range and interquartile range).
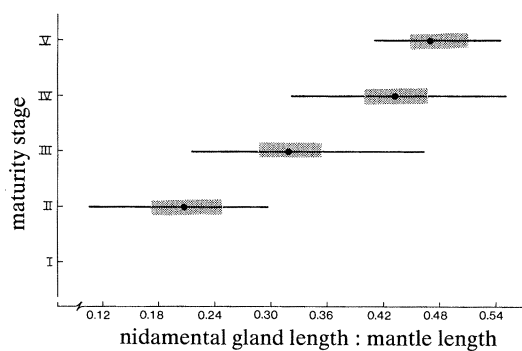

Figure 9. Relation between medians of the ratio NGL:ML and maturity stage in females (horizontal bars: range and interquartile range).

length and maturity stage. Males attain full maturity at a smaller size and earlier age than females.

The relations between male maturity stage and the ratios, TW:BW and SCW:BW are shown in figure 7. Very few males recruit into the fishery before attaining maturity stage III. Within stages III, IV and V the ratio TW:BW is very variable and there is no significant correlation between ratio medians and maturity. There is also variation in the ratio SCW:BW within maturity stages III, IV and V, but there is evidence of an asymptotic relation between ratio medians and maturity. There is significant correlation ($p < 0.01$) between the SCW:BW ratio and maturity stage.

The relations between female maturity stage and the ratios, OW:BW, NGW:BW and NGL:ML are shown in figures 8 and 9. The form of the relation between the

median of each ratio and maturity stage suggests that the major changes in relative size of the sexual and secondary sexual organs take place between maturity stages II and IV and that the differences between maturity stages I and II, and to a lesser extent IV and V are more qualitative than quantitative. There is significant correlation between OW:BW, NGW:BW and maturity stage ($p < 0.01$) and NGL:ML and maturity stage ($p < 0.05$).

Mating

Of 213 females dissected for the morphometrics data set only one had mated. This specimen had several spermatophores, with a total mass of 0.71 g, attached to the base of the gill. The mantle length of the specimen was 290 mm; body mass 539.76 g; OW:BW 0.105; NGW:BW 0.065; NGL:ML 0.50.

Fecundity

Mean individual masses of eggs in ovaries and oviducts of females between maturity stage III and V and estimated total numbers of eggs present are given in table 5. There are no data for the oviducts of stage III females as these do not start to fill until stage IV (Lipinski 1979). During female maturation there is a small increase in the mean mass of ovary and oviduct eggs. The major-axis length–frequency distribution of eggs in the ovary and oviducts of a stage V female is shown in figure 10 illustrating the shift of eggs into the oviduct as they enlarge and mature.

Table 5. *Fecundity and maturity stage relations in a sample of maturing and mature Illex argentinus* ($\pm s.d.$).

(Eggs are not present in the oviduct until stage IV.)

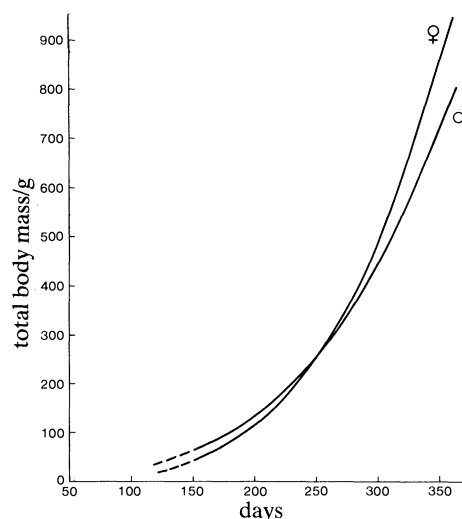|	maturity stage III	IV	V
mantle length/mm	233 (± 17)	280 (± 18)	279 (± 4)
body mass/g	248.7 (± 57.2)	460.9 (± 102.7)	470.9 (± 20.8)
age/days	270 (± 18)	310 (± 30)	277 (± 10)
n	4	10	2
ovary mass/g	11.5 (± 5.3)	28.2 (± 6.8)	30.6 (± 5.6)
oviduct mass/g	0.45 (± 0.24)	23.2 (± 12.6)	37.6 (± 3.0)
total ovary mass/g	11.9 (± 5.32)	51.4 (± 17.6)	68.2 (± 2.6)
OW:BW	0.051 (± 0.026)	0.112 (± 0.029)	0.145 (± 0.001)
NGL:ML	0.03 (± 0.06)	0.47 (± 0.03)	0.54 (± 0.01)
mean ovary egg mass/g	0.22 (± 0.04)	0.26 (± 0.04)	0.27 (± 0.06)
mean oviduct egg mass/g	no data	0.38 (± 0.03)	0.43 (± 0.02)
ovary egg count	50813 (± 21616)	106270 (± 27225)	112583 (± 46160)
oviduct egg count	no data	60159 (± 30301)	90121 (± 14816)
total ovary egg count	50813 (± 21616)	166429 (± 49028)	202704 (± 31344)
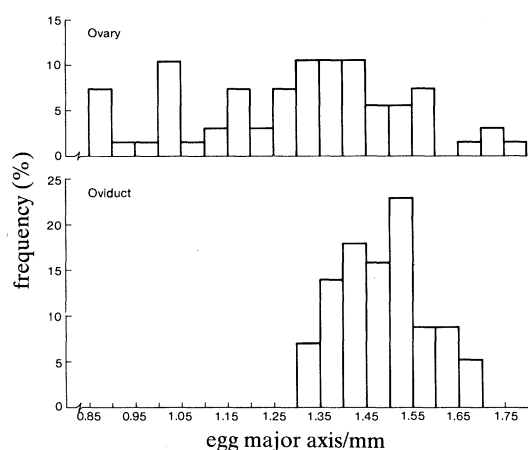
Figure 10. Major-axis length–frequency distribution of eggs in the ovary and oviduct of a mature *Illex argentinus* (25 g samples; $n = 67$ for ovary; $n = 57$ for oviduct).

Figure 11. Modelled body mass growth of male and female *Illex argentinus*.

Total ovary masses in the sample of stage V females shown in figure 6 fell in the range 38.3–82.8 g (ML = 243–278 mm) from which it can be calculated that total fecundity of these fully mature females lies in the range 113835–246098 eggs.

An abnormality was noted in one female which only had a single oviduct and oviducal gland.

Modelling post-recruitment growth

To model the average post-recruitment growth of winter spawned *Illex argentinus* the growth parameters for squid hatched in June are used as these represent most winter spawned recruits (figure 3). These data are combined with the parameters from the allometric equations in table 3 which were derived from the sample for which data about mass were collected. Growth is predicted from age 150 to 350 days. Modelled body mass growth of males and females is shown in figure 11. Percentage gain in mass per day, or instantaneous relative growth rate, G, (d ln BW/dt)·100, for the 200 day period is estimated to be 1.2 for males and 1.5 for females.

Modelled growth of somatic tissues, gonads and secondary sexual organs of males and females is shown in figure 12. Throughout life the mantle and head contribute most of the squid's mass. In both sexes the digestive gland and gonad grow relatively fast after recruitment. Modelled changes in male and female maturity indices (TW:BW, SCW:BW, OW:BW, NGW:BW, MGL:ML) with age are given in table 6. Male indices at 350 days are in reasonable agreement with observed values at maturity stage V and fall well within the observed ranges (figure 7). Female indices at 350 days are in poor agreement with observed values at maturity stage V and fall outside the observed ranges (figures 8 and 9). This reflects the overall poor correlation between ovary mass and body mass, and mass of secondary sexual organs and body mass (table 3) which is associated with systematic variation with maturity stage table 4. In the specimens examined during this investigation the most mature stage V females, with highest maturity indices, were not necessarily the largest (figure 6). Therefore, although the model predicts the average ovary, nidamental
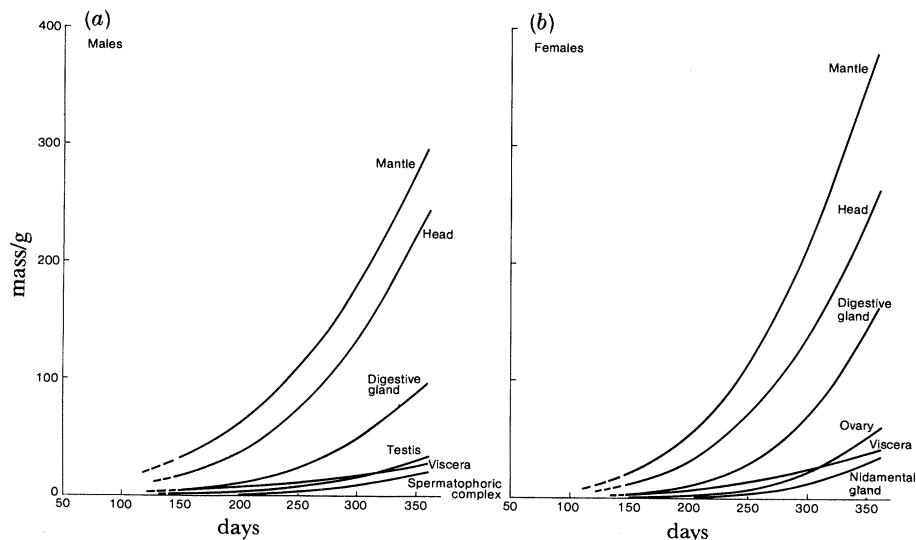
Figure 12. Modelled growth in mass of the somatic and reproductive organs of (*a*) male and (*b*) female *Illex argentinus*.

Table 6. *Modelled male and female maturity indices for Illex argentinus between age 150 and 350 days*

(Indices in parentheses calculated from allometric equations for maturity stage V females only.)

age/days	males TW:BW	SCW:BW	females OW:BW	NGW:BW	NGL:ML
150	0.025	0.003	0.008	0.005	0.24
200	0.029	0.007	0.017	0.009	0.27
250	0.031	0.011	0.027	0.016	0.30
300	0.036	0.018	0.042	0.024	0.33
350	0.038	0.025	0.062	0.035	0.36
(350)	—	—	(0.128)	(0.071)	(0.43)

gland and somatic growth of a June-hatched female it has no utility in predicting female maturity indices at age.

Female maturity indices at age 350 days were calculated from ovary and nidamental gland masses estimated by using the equations in table 4 for stage V females. They are shown in parentheses in table 6. These estimates are in good agreement with the indices in figures 8 and 9 for females at maturity stage V.

4. DISCUSSION
Growth

The growth data presented here confirm previous reports that *Illex argentinus* has a lifespan of approximately one year, that most of the population hatches in the mid-part of the austral winter and that females grow faster, and attain a larger size than males. No summer hatched specimens were present in the samples examined. Squid hatched later in the austral winter appear to grow faster than squid hatched early and this may reflect the fact that late hatching squid will have experienced a higher average water temperature and different feeding conditions during their lifetime than early hatching specimens of the same age. These differential growth rates may reduce the size range of squid in a cohort towards the end of its life by allowing late hatchers to catch up with early hatchers. Although the data in table 2 show that late hatchers are

predicted to reach a larger size at age 1 year it has not been confirmed that late hatchers live for a full year. It is possible that they spawn at a younger age than early hatchers.

There is no evidence that mantle length growth is asymptotic over the size or age range examined so there is no justification for fitting von Bertalanffy or Gompertz models. The observation of linear growth, derived from statolith data, is consistent with other data for ommastrephid species, including *Illex argentinus*, *Illex illecebrosus* and *Todarodes sagittatus* (Rosenberg *et al.* 1981; Radtke 1983; Wiborg & Beck 1984; Koronkiewicz 1986) and the gonatid *Gonatus fabricii* (Kristensen 1983; Wiborg *et al.* 1984).

These growth data for *Illex argentinus*, support the argument for avoiding use of asymptotic equations to describe growth of wild cephalopods (Forsythe & Van Heukelem 1987; Saville 1987). Field data for squid growth, based on shifts in size–frequency modes with time, may provide evidence of decrease in growth rate towards the end of life and this has led to the conclusion that the von Bertalanffy function is an appropriate model of cephalopod growth (Kooijman 1988). An apparent asymptote in such data may be artifactual, arising from a manifestation of Lee's phenomenon in which larger, faster growing, squid mature, spawn and die in advance of slower growing members of the cohort (Rodhouse *et al.* 1988). The most appropriate growth model for the entire life cycle of *Illex argentinus*

will emerge when further material is available, representing the periods before recruitment and after migration from the fishing grounds.

Statolith length increases with age in *Illex argentinus* but there is negative allometry between statolith size and body size in both males and females. A similar relation occurs in *Illex illecebrosus* (Hurley & Beck 1979), *Todarodes sagittatus* (Wiborg & Beck 1984) and *Gonatus fabricii* (Wiborg *et al.* 1984), indicating that statolith growth generally proceeds more slowly than, but in accord with, the rest of the squid body. In *Illex argentinus* females, which have a higher growth rate than males, there is greater divergence between the growth rate of the body and that of the statolith, than in the slower growing males. The relation between the statolith growth and body growth is clearly complex and there are interrelated effects of growth rate and sex which deserve further attention.

Dilly (1976) found no regular correlation between body size and statolith size in four species of cephalopod but he gives no information on the size of specimens examined. If the size range was limited this would explain the lack of a clear relation given that statolith growth proceeds relatively slowly in comparison with the whole body.

Allometry

Allometric, or scaling, studies allow an analysis of the role of absolute body size on ontogenetic trends in an organism's form and physiology (Gould 1966). Use of variables such as whole body mass versus organ mass in scaling studies is problematical because whole body mass includes the mass of the organ, resulting in a distorted scaling relation and an inflated correlation coefficient (LaBarbera 1989). In this study whole body mass has been used as an independent variable in the analysis of allometric relations because it is the only weight variable against which all other variables of mass can be compared. Equations relating organ mass to body mass also provide a convenient means of estimating the percentage contribution of the organ to body mass.

Growth of the soma, apart from the digestive gland, is approximately isometric with the whole body. The head is treated as a single entity here but it consists of several tissues (brain, eyes, and the muscles of the arms, tentacles and buccal mass) which may have different allometries. There is evidence of sexual dimorphism in head growth, which is probably related to greater arm length in males (Roper *et al.* 1984).

The digestive gland grows at a relatively faster rate than the rest of the soma. This organ has three functions: digestive-enzyme synthesis, absorption and storage (Boucaud-Camou & Bouchet-Rodoni 1983; Bouchet-Rodoni *et al.* 1987). Of these, the efficiency of the last two functions are probably most influenced by size. The Illicinae are characterized by high feeding rates and conversion efficiencies which are maintained throughout life (O'Dor *et al.* 1980; Hirtle *et al.* 1981) and a high mass exponent for metabolic rate (DeMont & O'Dor 1984). This implies that the relative absorptive capacity of the digestive gland must be maintained throughout life, which in turn requires that its relative mass should increase with growth because of scaling effects of absorptive surface on mass. The storage capacity of the digestive gland also increases with mass. *Illex argentinus* probably meets its energy and nutrient requirements for gametogenesis and maturation directly from the diet as it is clearly growing and maturing simultaneously (figure 6b) on the fishing grounds, but energy reserves in the digestive gland may be drawn upon during the migration to the spawning grounds.

Strong positive allometry of the reproductive organs is not unexpected in a short-lived semelparous organism and it reflects a shift between allocation of resources to somatic growth in early life and gonad growth later. There is high variance in the relation between the mass of female reproductive organs and body mass. This is explained statistically as the consequence of variation in maturity with size (table 4). The biological explanation is less apparent. If maturity were strongly related to age then body mass:ovary mass variability might be related to differences in growth rate associated with hatching date. However, there is no relation between maturity, expressed as the ow:bw ratio, and age of squid with a range of hatching dates. Therefore the variability can only be attributed to individual differences in the timing of onset, and/or rate of, maturation. Such differences could be due to inter-individual differences in thermal, photoperiod and feeding history (Mangold *et al.* 1975; Rowe & Mangold 1975; Arnold & Williams 1977).

Maturation

Classification of cephalopod sexual maturity into stages imposes artificial discontinuities onto what is in reality a continuous process. It is therefore to be expected that each maturity stage will encompass a broad range of body size, age and indices of maturity based on ratios.

Maturity stages are not directly comparable between sexes but male *Illex argentinus* are apparently more mature when they recruit into the fishery and reach approximately equivalent degrees of maturity and full maturation at a younger age and smaller size than females (figure 6). It has been suggested that male *Illex argentinus*, and other squid species, continue producing spermatozoa and spermatophores after reaching maturity and by inference mate more than once (Juanico 1983; Schuldt 1979; Rodhouse *et al.* 1988). *Illex argentinus* does not begin mating to any great extent until after departure from the fishing grounds; only one mated female was found during this study. Good correlation between the mass of testis and body mass, and the mass of spermatophoric complex and body mass (table 3) confirm that depletion of the gonad had not commenced in the samples examined.

Fully mature males and females encompass a wide size range, providing evidence that there is considerable inter-individual variation in the size and age of onset of maturation and maturation rate. Because this population does not start to mate and spawn on

the Patagonian Shelf between February and June when it is exploited, it is likely that mature females in the samples are precocious and possibly not representative of the whole population. It is clear from figure 6 that, if any further growth takes place, many females will mature at a greater age and larger size than those already at stage V on the feeding grounds. Therefore estimates of average population fecundity at the spawning grounds, based on these mature females, may be somewhat low.

There is no evidence that any of the samples examined were spent, or had spawned and were recovering, and apart from one female no mating had taken place. However, the presence of an appreciable proportion of stage V specimens in the samples suggests that the feeding grounds, where squid are caught by the fishery, are relatively close to the spawning grounds. This is in contrast to the situation in the *Illex illecebrosus* fishery, in the Northwest Atlantic off Newfoundland and Nova Scotia, where few mature squid are taken. This species is thought to spawn off the coasts of Florida and the Carolinas (O'Dor 1983). There is no evidence of multiple spawning as has recently been observed for the tropical ommastrephid squid *Stenoteuthis oualaniensis* (Harman *et al.* 1989).

The growth model

The growth model presented for male and female *Illex argentinus* provides a useful representation of average growth in whole body mass and tissue masses for males and females. However, modelled growth of female gonad and accessory reproductive organs is in poor agreement with observed values because of poor correlation in the allometric relation between size of these organs and body size.

During the period when the squid are commercially exploited, daily body mass growth rates are on average predicted to be 1.2 % for males and 1.5 % for females. These rates correspond closely with growth rates of *Illex illecebrosus* in the North Atlantic (O'Dor *et al.* 1980; Hirtle *et al.* 1981).

The model makes realistic predictions of male maturity indices but although it predicts average growth of female reproductive organs these do not give realistic female maturity indices for squid reaching their maximum age and size. However, using the allometric equations for the reproductive organs of stage V females only, it can be predicted that at maximum maturity the ovaries constitute some 12.8 % of total body mass and the nidamental glands 7.1 %. These values agree closely with observed proportions. The total body tissue given to gonad and accessory reproductive organs, reproductive investment, is thus about 20 %. These data are similar to comparable data for *Illex illecebrosus* (Durward *et al.* 1980) but they represent a somewhat smaller investment than by a loliginid squid, *Alloteuthis subulata*, for which comparable data are available (Rodhouse *et al.* 1988). This species invests some 25 % of mature female body mass in ovary, not including accessory sexual organs.

General discussion

This analysis considers the growth and maturation of *Illex argentinus* from the age of approximately six months when they start to recruit into the fishery until they approach maturity at one year old and depart from the feeding grounds, where they are exploited, for the spawning grounds. It is evident from the growth data collected from this phase of the life cycle over three years that there is considerable variability in the population about the time of hatching, rate of growth, rate of maturation and probably time of onset of maturation. During the fishing season, which lasts from February–March to June–July (Csirke 1987) a single generation is exploited and, for the years for which data are available, escapement has been approximately 32 % (Anon. 1989). If there is selectivity, imposed by the jigging and trawling gear employed in the fishery, it must be anticipated that artificial selection pressures will be imposed on the genetic component of variability in growth and maturation processes within this stock. Experience with exploited fish species, which generally have a longer generation time than cephalopods, has shown that exploitation has driven artificial selection for smaller size and presumably lower growth rate (Kirpichnikov 1981). If similar artificial selection pressures are imposed on exploited squid stocks then, given their short generation time, selection effects might be manifested early in the history of the fishery.

Advances in the use of growth rings in the statoliths for ageing squid and deriving growth data present opportunities for research which have not been possible until recently. Their use in fisheries and ecological research is becoming established and the physiological mechanism governing increment formation in the statolith has been examined (Morris 1988). However, the environmental cues entraining the diel rhythm of increment formation have not been determined. It has been verified that growth rings are formed daily in the closely related *Illex illecebrosus*, and that there is a firmly entrained diel rhythm of production of rings. It is likely that cues responsible for entraining the rhythm are associated with the squids diel vertical migrations and feeding cycle, but the extent to which growth ring formation can be disrupted by natural environmental perturbations is not known.

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