Age and Growth of *Nototodarus sloanii* (Cephalopoda: Oegopsida) Based on Daily Increment Counts in Statoliths

Yuji Uozumi*¹ and Hiroe Ohara*²

(Received 21 August, 1992)

Statoliths of *Nototodarus sloanii* collected around New Zealand were examined to determine age. By comparing the increase in number of increments in statoliths with the number of days elapsed between sampling dates, the periodicity of the increment formation was validated. Estimated hatching month ranged from January to December. This result suggests that spawning occurs throughout the year. The relationship between statolith radius and dorsal mantle length suggests daily increment width must reflect squid growth well. Back-calculation was applied to compensate for the short sampling period. The differences in size at age are significant between the seasonal groups. The winter group is larger than the summer one between about 100 and 230 days old. This difference became smaller and finally the summer group became larger than the winter one at around 250 days old and after. It is suggested that differences in growth between the groups are consistent with seasonal changes in water temperature.

The resources of arrow squids, comprised of *Nototodarus sloanii* and *N. gouldi*, rapidly became one of the most important fishery resources in the 1970s, starting from an insignificant bycatch in New Zealand waters. The arrow squids are caught by both jig and trawl fisheries. A jig fishery developed by Japanese, Korean, and Taiwanese vessels around the mainland of New Zealand produced 30,000–60,000 tonnes annually in the 1980s. A trawl fishery developed by Japanese, Russian, and Korean vessels produced 30,000–60,000 tonnes in the 1980s, about half of which was taken around the Auckland Islands. The number of vessels in both fisheries, however, has decreased recently, mainly due to the shifting of their fishing grounds to the southern Atlantic Ocean to fish *Illex argentinus*.

N. sloanii is widely distributed in waters down to about 500 m in depth around New Zealand except for the north and west coast of North Island.¹⁾ *N. sloanii* is caught by both jig and trawl fisheries mainly around the South Island and the Auckland Islands, and comprises a major part of the arrow squid catch,¹⁾ while *N. gouldi* is caught by the jig fishery off the west coast of the mainland.

The biology of *N. sloanii* was summarized by Kawakami,²⁾ Mattlin *et al.*,³⁾ and Smith *et al.*¹⁾

These papers suggested a long but poorly defined spawning season and several seasonal and/or regional subpopulations. Growth was estimated from the progressive changes of modes in length composition, which were obtained from the waters around the Auckland Islands where a very clear succession of modes were observed.⁴⁾

In this paper, the growth of *N. sloanii* was estimated from aging results using daily increments in the statoliths. Growth in the younger stages before recruitment into the fisheries was estimated by back-calculation.

Materials and Methods

Samples and Data

Most of the samples for aging were collected by Japanese squid jiggers and trawlers (Table 1). About 70% of them were collected in January–April 1991 on the Snares Shelf. Samples of juvenile squid were collected by a fine mesh mid-water trawl (KMT midwater trawl net with 10 mm mesh cod-end) during a joint Japan–New Zealand squid survey by R/V *Kaiyo Maru* in July–September, 1985.⁵⁾ Localities of samples are shown in Fig. 1.

*¹ National Research Institute of Far Seas Fisheries, Shimizu 424, Japan (魚住雄二: 遠洋水産研究所).

*² Tokai University, Shimizu 424, Japan (大原啓江: 東海大学海洋学部).

Present address: Nihonsouken Company, Hamamatsu 430, Japan (日本総研).

Table 1. Collection data for the statoliths used in this study

Sampling Date	Locality		Depth (m)	Type of Gear	No. of Specimens	Range of Size (mm ML)
85 8 4	43°18'S	168°22'E	140	M*	1	158-158
85 8 5	46°58'	168°49'	60	M	1	220-220
85 8 5	47°54'	168°19'	100	M	1	30- 30
85 8 12	44°52'	171°33'	46	M	1	32- 32
85 8 15	43°19'	175°15'	85	M	2	42- 46
85 8 15	44°13'	175°53'	380	M	1	36- 36
85 8 16	43°18'	173°23'	65	M	22	15- 65
85 9 19	43°19'	173°23'	65	M	3	48- 60
90 1 17	47°51'	166°57'	149	J	12	213-277
90 3 15	44°56'	171°48'	121	J	4	140-269
90 3 25	48°30'	166°30'	?	B	21	258-342
90 4 30	47°30'	169°35'	?	B	9	300-340
90 11 6	46°47'	166°03'	470	B	12	304-398
90 11 6	46°35'	166°08'	507	B	14	268-352
91 1 10	41°29'	170°47'	?	J	1	230-230
91 1 15	42°05'	170°40'	?	J	2	216-232
91 1 15	41°16'	171°01'	189	J	7	172-256
91 1 17	45°08'	171°28'	132	J	17	140-250
91 1 17	45°08'	171°28'	122	J	10	120-158
91 1 18	46°31'	167°18'	115	J	30	98-202
91 1 23	48°50'	166°50'	185	B	30	126-168
91 1 27	46°33'	167°18'	128	J	41	142-280
91 2 5	46°34'	167°14'	?	J	22	118-206
91 2 10	46°29'	167°16'	124	J	31	160-264
91 2 11	46°32'	167°18'	?	J	18	150-200
91 2 15	46°32'	167°17'	117	J	67	114-258
91 2 15	48°38'	167°00'	133	J	19	125-232
91 2 15	48°33'	167°00'	137	J	22	142-272
91 2 15	48°33'	167°00'	?	J	11	130-242
91 2 15	46°33'	167°19'	?	J	22	152-222
91 2 16	47°48'	167°09'	143	J	29	142-218
91 2 21	48°50'	167°03'	180	B	22	204-242
91 3 1	48°23'	168°06'	?	B	31	208-272
91 4 18	47°33'	169°07'	532	B	54	108-342
Total					601	15-398

M: fine mesh midwater trawl by R/V *Kaiyo Maru*.

B: bottom trawl by Japanese commercial vessels.

J: jigging by Japanese commercial jigging vessels.

Statolith Processing and Count of Increments

After the measurement of dorsal mantle length (ML), the statoliths were removed and stored in liquid paraffin. Aging was carried out using these statolith samples. Processing and counting procedures were according to Uozumi and Shiba.⁶⁾ Each statolith was mounted individually with the anterior concave side down on a glass slide using a single drop of super glue (cyanoacrylate adhesive). The statoliths were then ground by hand on fine waterproof sandpaper and finally polished using alumina polish. A microscope equipped with a color TV camera system was used during the grinding procedure and for viewing the incre-

ments in the statoliths. Counting was carried out on a 15-inch color TV monitor at 920x magnification.

The increments were most discernible in the dorsal dome, especially along the wing attachment area (Fig. 2). Increments were usually counted in this area from the core to the edge region. Since the increments in the terminal-most portion of the statoliths could not be counted in most samples, the number of increments in this area was derived by extrapolation based on those counted in the nearest area where counting was possible. The proportion of the estimated number of increments to the total was about 5%,

Fig. 1. The localities of samples. Solid circles show the sampling sites.

The arrow and open circle show the sampling area which was used for the validation study.

regardless of the size of statolith.

Back-calculation

The number of juvenile samples was insufficient to derive the appropriate growth curve in this study. Therefore, a back-calculation method which estimates the length at the time when the rings were formed was applied to estimate length at younger ages.⁷⁾ This method has been used commonly in studies on the growth of fishes.⁷⁾

This method needs the relationship between statolith radius and mantle length, and each monthly radius. Measurements of statolith radius and monthly radii (radius of each 30 increments) were carried out on a TV monitor using a digital map meter (COMCURVE-5, Koizumi Sokki Mfg Co., Ltd) at 920x magnification. The statolith radius and monthly radii were measured from core to tip of the dorsal dome along the curved axis shown in Fig. 3. Measurement of the statolith radius was carried out in almost all of the observed specimens which were not broken in the measurement area, while the measurement of monthly radii was carried out in 20 specimens hatched in the same month.

Fig. 2. Photo micrograph of the posterior convex view of a ground statolith, from *Nototodarus sloanii* with a dorsal mantle length of 200 mm.

Fig. 3. Schematic view of statolith showing the axis for the measurements.

Fig. 4. Length compositions for each five-day period around the date on which each statolith sample was collected in January-February 1991.

The shaded area shows the length range of specimens from which statoliths were extracted for the validation study.

Validation of Daily Increment Formation

For validation of the periodicity of increment formation, no direct method such as the use of a chemical marker⁹⁻¹⁰⁾ was carried out in this study. So another type of validation was tried which involved comparing the number of increments in the statoliths with the date of capture.⁶⁾

The data and specimens used in the validation were collected from a very restricted area of a 8 square miles (shown by the arrow in Fig. 1), during 29 days from 18th January to 15th February 1991. Length composition for each five-day period around the date on which each statolith sample was collected are shown in Fig. 4. Statoliths were selected from the modal region of length compositions (shaded area of Fig. 4), regardless of sex.

Statistical Analyses

A predictive regression model was applied to the analysis of the relationship between the number of increments and the sampling date. A cubic curve was fitted to the relationship between statolith radius and mantle length. A logistic curve was fitted to express the growth of squid based on Marquardt's method.¹¹⁾

Akaike's Information Criterion (AIC) was utilized

as a criterion in the selection of models for logistic growth and the relationships between statolith radius and mantle length. It is known that the model with the lowest AIC gives the best selection.¹²⁾ The two models, sex-separated and sex-combined ones, were constructed for the logistic growth and relationship between statolith radius and mantle length, respectively. Based on the AIC values, the optimal model was selected, because the parameters of the logistic curves were estimated by a non-linear method and it is difficult to apply conventional statistical methods such as covariance analysis.

The AIC for each model is expressed in equation as follows:

For sex-combined model,

$$AIC = N \cdot \ln(2\pi \cdot SS/N) + N + 2 \cdot NP$$

where N : number of specimens

$\ln$: natural logarithm

SS : sum of squares

NP : number of parameters

For sex-separated model,

$$AIC = N_1 \cdot \ln(2\pi \cdot SS_1/N_1) + N_1 + 2 \cdot NP + N_2 \cdot \ln(2\pi \cdot SS_2/N_2) + N_2 + 2 \cdot NP$$

where subscripts refer to variables for male and female, respectively.

Results

Validation of Daily Increment Formation

In sequential length composition, a gradual progression was observed in the modes from

Fig. 5. Relationship between the number of increments in the statoliths and the date on which the samples were collected in January-February 1991.

Table 2. The result of analysis of variance for the relationship between number of increments and sampling date

Factor	SS	DF	MS	F-value	F-value at 1% level
Regression	10384.20	1	10384.20	55.5	6.91
Error	17784.50	95	187.21		
Total	28168.70	96			

Table 3. The number of specimens observed with respect to the hatching month and the month in which the sampling was done

Month sampled	Hatching month												TOTAL
	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	
JAN					9	18	44	64	1				136
FEB						3	70	163	5				241
MAR					1	16	19	13	1				50
APR						1	4	20	24	7			56
MAY													0
JUN													0
JUL													0
AUG	1			20	11							1	33
SEP					1								1
OCT													0
NOV	7	7	8									2	24
DEC													0
Total	8	7	8	20	22	38	137	260	31	7	0	3	541

160 mm *ML* on 18th January to 210 mm *ML* on 15th February (Fig. 4). This progression suggested that all the samples were derived from the same cohort.

There was a linear relationship between the number of increments for these specimens and the sampling date (Fig. 5). The equation for the regression of the number of increments on sampling date was;

$$Y = 1.1X + 149 \quad (r = 0.6, n = 97)$$

where Y = the number of increments observed in the statoliths,

X = catch date expressed as the number of days since 1st January 1989,

r = correlation coefficient, and

n = number of individuals observed.

Analysis of variance showed that this regression was significant at the 1% level (Table 2) and the 95% confidence interval of the slope was 0.80–1.4. The estimated value of the slope was very close to 1, which means that the formation of each increment takes about one day.

Another problem related to the interpretation of the number of increments is determining the age (or stage) of initiation of increment formation.

It is impossible to resolve this problem until statoliths from reared larval squid can be obtained. Therefore, it was assumed that increment formation begins at the time of hatching. Under this assumption, the number of increments signifies age in days after hatching.

Hatching Month and Growth of Overall Samples

In total, 541 specimens were aged successfully. Following the validation, the day of hatching of each specimen can be estimated from age in days (number of increments) and the date of the sample. These results were compiled into hatching month composition (Table 3). Hatching month ranged from January to December, except for November. The wide range of hatching month distribution suggested that spawning occurs throughout the year.

The relationship between age in days and *ML* is shown in Fig. 6 according to sex. The ages of the specimens ranged from 88 to 318 days old. Figure 6 suggests that there might be one inflection point in the growth curve. The logistic curves were estimated for the two models, *i.e.* sex-separated and sex-combined models, excluding the unsexed specimens. The *AIC* calculated for each

Fig. 6. Relationship between age and dorsal mantle length for all specimens aged in the study according to sex.

Open and solid circles show females and males, respectively, while triangles show unsexed specimens. Solid curve shows the final growth curve for the sex-combined model.

Table 4. *AIC* values for the sex-separated and sex-combined models in logistic growth equation

	Number	Sum of square	<i>AIC</i>
Sex-separated			4,725.5
Male	257	143,114	(2,362.0)
Female	252	169,263	(2,363.5)
Sex-combined	509	313,618	4,721.8

model suggested that the sex-combined model was the optimal one for the present study (Table 4). The final equation was estimated using the sex-combined data including unsexed specimens. The resulting equation is as follows:

$$ML = 355.7 / (1 + e^{-0.021(t-186.5)})$$

where *ML* = dorsal mantle length (mm)

t = age in days.

The optimal growth curve is shown in Fig. 6. It is clear that the growth curve expressed growth between 150 and 300 days old very well, but there are some discrepancies between observed and estimated sizes at ages younger than 150 days old.

There is a possibility that this overestimation of growth in younger ages may be caused by the insufficient number of younger squid samples and seasonal variability in growth, because the hatching month is widely distributed throughout the year (Table 3).

Fig. 7. Relationship between dorsal mantle length and statolith radius.

Open and solid circles show females and males, respectively, while triangles show unsexed specimens. Solid curve shows the final cubic curve for the sex-combined model.

Table 5. *AIC* values for the sex-separated and sex-combined models in relationship between statolith radius and mantle length

	Number	Sum of square	<i>AIC</i>
Sex-separated			5,052.6
Male	231	598,721	(2,481.1)
Female	236	715,081	(2,571.5)
Sex-combined	467	1,313,800	5,044.0

Back-calculation

To analyze the growth in the younger stages, back-calculation was applied. The relationship between statolith radius and mantle length is shown in Fig. 7 according to sex. Cubical parabolas were estimated for the two models, *i.e.* sex-separated and sex-combined models, excluding the unsexed specimens. The *AIC* calculated for each model suggested that the sex-combined model was the optimal one for the present study (Table 5). The final equation was estimated using the sex-combined data including unsexed specimens. The resulting equation is as follows:

$$ML = -0.11 - 0.22SR + 0.018SR^2 - 1.1 \cdot 10^{-6}SR^3$$

($n=501$, $R=0.97$)

where *ML* = dorsal mantle length in mm,

SR = statolith radius in μm ,

n = number of specimens, and

R = multiple correlation coefficient.

This equation was used for back-calculation of *ML* at the time when each monthly radius was formed. Because this equation expressed the relationship between 200 and 780 μm in statolith

Table 6. Back-calculated mantle length at each 30 days old by hatching months

Hatching month	Back-calculated mean mantle length (mm) at each age (days)							Number of specimens
	90	120	150	180	210	240	270	
December/January	12.0	37.3	74.3	117.0	164.3	214.5	268.3	7
February/March	14.0	45.3	88.9	135.5	186.0	228.7	—	10
April	—	—	—	—	—	—	—	—
May	14.1	43.1	81.4	126.9	180.0	—	—	8
June	14.5	46.8	88.8	138.3	—	—	—	20
July	21.5	60.2	107.7	—	—	—	—	20
August	16.6	54.8	107.7	—	—	—	—	20
September	20.1	56.1	104.4	140.0	—	—	—	18
October	18.0	52.8	96.4	151.8	—	—	—	5
November	—	—	—	—	—	—	—	—

radius, application of back-calculation was limited in this range. Thus, the lower limit roughly corresponded to 90 days of age.

Growth of Summer and Winter Hatching Groups

The *ML* at each monthly radius was estimated starting from 90 days for each hatching month group, though the sample numbers were variable from group to group (Table 6). The samples of December/January and February/March hatching month groups were pooled due to the small sample number and the mean *ML* at each month radius was calculated for each hatching month group, while the aging results were also pooled for each hatching month group and the mean *ML* at every ten-day interval was calculated.

The hatching month groups were grouped into two seasonal groups arbitrarily, namely austral summer (December/March) and austral winter (June/September) hatching groups, because the number of samples in each hatching month group was insufficient for the estimation of the growth curve for each one. The relationship between age and *ML* is shown in Fig. 8. This figure indicates that the size at age estimated by the two methods, counting increments and back-calculation are consistent with each other in each seasonal group. The logistic curves were fitted to each seasonal group (Fig. 8). The estimated equations are as follows:

Austral summer group:

$$ML = 393.8 / (1 + e^{-0.023(t-212.5)})$$

Austral winter group:

$$ML = 336.6 / (1 + e^{-0.024(t-170.5)})$$

where *ML* = dorsal mantle length (mm)
t = age in days.

Fig. 8. Relationships between age and dorsal mantle length for summer and winter groups.

Solid triangle and circle, summer group; open triangle and circle, winter group. Triangles show the means by back-calculation and circles show the means by counting increments. Solid and broken curves show the estimated logistic curves for summer and winter groups, respectively.

The growth equations express the growths of both seasonal groups very well. They are more appropriate than the growth equation estimated for all samples combined (Figs. 6 and 8).

The growth of both seasonal groups gradually became faster at younger ages until about 150 days, and the rate of growth was the fastest at around 180 days, reaching about 40–60 mm per month, and then becomes slower at older ages. The differences in size at age are significant between the groups. The winter group is larger than the summer group between about 100 and 230 days old, especially around 180 days old and the maximum difference was about 40 mm. This difference became smaller at older ages, until finally the summer group became larger than the winter

one at around 250 days old and thereafter.

Discussion

By comparing the increase in the number of increments in statoliths with the number of days elapsed between sampling dates, the periodicity of increment formation was validated under the assumption that the samples were collected from the same cohort. The results indicate that the increments observed in this study are formed daily. Daily formation of the increments has been directly validated in other ommastrephid species (*Illex illecebrosus* and *Todarodes pacificus*) with a chemical marker.^{8,10)} It is desirable that a direct method of validation should be applied to aging methods for *N. sloanii*.

The period between formation of statocysts and hatching in *Todarodes pacificus* is short (about one day at 14–20°C).¹³⁾ Immediate post-hatching paralarvae of *Illex illecebrosus* from the laboratory had one or no increments in their statoliths.¹⁴⁾ These results suggested that the number of increments represents the number of days after hatching in ommastrephid squids. Therefore, there is a high possibility that the number of increments signifies age in days after hatching in *N. sloanii*.

The life span of *N. sloanii* has appeared to be about one year, based on length composition data.^{2,3)} Length composition data showed that the maximum length reaches nearly 400 mm *ML*.^{2–4)} In this study the age of the oldest specimen was 318 days and its length was 386 mm *ML*. The age of the specimens which attained more than 350 mm *ML* ranged from 260 to 318 days. The results indicate that the life span of this species may be about one year, though the number of larger specimens was not sufficient to estimate the exact life span.

Back-calculation was applied to compensate for the short sampling period (mainly from January to April) compared to the life span. Campana and Neilson¹⁵⁾ suggested the potential value of back-calculation using daily increments. The growth patterns of statolith length and mantle length were described by a smooth-monotonic curve in *N. sloanii*. This relationship suggested that daily increment width must reflect squid growth well. Applying back-calculation, it is easy to estimate the growth of smaller squid before recruitment to the fishery. There was little discrepancy between the results of back calculation

and actual aging (Fig. 8) and these results also indicated differences in the growth of younger stages between seasonal groups.

In the present study the logistic curve was applied to the growth of *N. sloanii*, because this model is the most popular one for expressing growth which has one inflection point. The logistic curve expresses the growth of each seasonal group very well through the range of ages observed. Figures 6 and 8 suggested that growth might not be asymptotic, though there was an insufficient number of samples larger than 300 mm *ML*. This result suggested that parameter L_{∞} of the logistic model has little biological meaning.

The present results show that there is no significant difference in growth between the sexes. Uozumi and Kuroiwa⁴⁾ indicated that there was no significant difference in modal lengths between the sexes for squid smaller than about 20 cm *ML* but that the modal size of female squid is 2–3 cm larger than that of males of sizes larger than 30 cm *ML*. They suggested that there is a difference in growth between the sexes, especially in older ages based on the difference in modal lengths. In the present study, most of the specimens were smaller than 25 cm *ML*, and there were not enough specimens of larger sizes than about 25 cm *ML* to investigate the difference in growth between the sexes. Therefore, it is necessary to collect a sufficient number of samples for older squid and to investigate the difference in size at age at older ages between the sexes, before a final conclusion on the difference in growth between the sexes can be reached.

The speed of growth in length is a maximum of around 180 days old in the whole life span of the squid, and reaches 40–60 mm/month. This suggests that only one month delay in birth would result in well-separated modes in length distribution. It is usually observed that there are some well-separated modes in length composition.^{3,16,17)} It is commonly understood that different modes indicate different seasonal cohorts. But judging from the fast-growing characteristics of the squid shown in the present study, there is a possibility that the well separated modes may be due to only one or two months' delay in hatching.

The growth of the winter group, around 180 days old, is faster than that of the summer group. The winter group spends a period of around 180 days in the summer season, while the summer group spends this period in the winter season. At ages of more than about 250 days, the growth of

the summer group becomes faster than that of the winter one. Water temperature in the area sampled show clear seasonal changes. A high temperature (about 15°C) is observed in the austral summer from December to March, while a low temperature (around 10°C) is observed in the austral winter from July to August.¹⁸⁾ It is clear that the growth rate is higher in summer than in winter at the same age. Differences in growth between the seasonal groups are consistent with the seasonal changes in water temperature, though there is no direct evidence for a relationship between temperature and growth.

The length-based method has usually been applied to the study of squid growth,^{4,19)} on the assumption that the individuals which comprised the corresponding mode observed in the time series should belong to the same cohort. However, it is difficult to validate this assumption without aging. Uozumi and Shiba⁶⁾ pointed out that this assumption may not hold in species which migrate with growth. Furthermore, there are difficulties in following the corresponding modes in a time series, especially for species such as *N. sloanii* which have a wide spawning season, several modes in length composition, and a high growth rate. The aging technique using statoliths makes it possible to validate the assumption of the length-based method and to easily follow the same cohort in a time series precisely even for species which have a complex stock structure.

Acknowledgments

We extend special thanks Dr. P. Rodhouse (British Antarctic Survey, United Kingdom), Drs. H. Hatanaka and S. Kawahara (National Research Institute of Far Seas Fisheries, Japan), Prof. S. Ueyanagi (Tokai University) and Dr. T. Kubodera (National Science Museum, Tokyo) for their critical reading of the manuscript and helpful comments. We wish to express our thanks to Dr. K. Hiramatsu (National Research Institute of Far Seas Fisheries) for his valuable advice on the statistical treatment of the data.

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