

## Analysis of precision in statolith derived age estimates of the tropical squid *Photololigo* (Cephalopoda: Loliginidae)

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Jackson, G. D. and Moltschaniwskyj, N. A. 1999. Analysis of precision in statolith derived age estimates of the tropical squid *Photololigo* (Cephalopoda: Loliginidae). – ICES Journal of Marine Science, 56: 221–227.

Precision in statolith derived age estimates among readers experienced in statolith age analysis was determined for both juvenile and adult individuals of the tropical loliginid squid *Photololigo* off Queensland, Australia. Juvenile age estimates were compared between two readers, while adult age estimates were compared among three readers. There was no reader effect in the age estimates of juveniles, but there was a trend of increasing age estimates with consecutive replicate counts for each reader. In the case of adult squid there was a statistically significant difference in age readings among readers, with the average greatest difference of 9.7 increments. However, this difference represented 5.6% of the lifespan of the oldest individual and 6.9% of the youngest aged adult. These differences were well within the 10% requirement of replicate counts in previous studies. Furthermore the growth curves generated on age estimates from each reader did not differ significantly.

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Key words: *Photololigo* sp., squid, statoliths, age and growth, increments, precision.

Received 8 June 1998; accepted 4 December 1998.

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### Introduction

The ability to age individual organisms at a resolution of days has been one of the most significant advances towards our understanding of the population dynamics of both fish and squid. The recognition that daily growth increments can be detected in fish otoliths and squid statoliths has provided marine researchers with a much needed tool for the development of reliable growth models. Furthermore, detailed increment analysis can provide information on growth rates, hatch dates, lifespans, and even daily fluctuations in growth performance.

In many ways squid statolith ageing research is comparable to research using fish otoliths (see parallel reviews: Campana and Neilson, 1985; Jackson, 1994). However, the small size of the squid statolith (usually less than 2 mm in length), along with potential problems with increment definition, can lead to particular difficulties in detecting and counting increments.

Ageing studies require both accuracy (i.e. the closeness of a measured or computed value to its true value, Secor *et al.*, 1995) and precision (i.e. the closeness of repeated measurements of the same quantity, Secor *et al.*, 1995). A number of validation studies have demonstrated daily periodicity in squid statolith increment formation (see Jackson, 1994; Jackson *et al.*, 1997; Arkhipkin and Bizikov, 1997). However, it is important to recognize that age data for individuals are estimates based on the enumeration of daily increments, often achieved by taking a mean of replicate counts (review Jackson, 1994). The reliability of these estimates is therefore directly related to the degree of precision in individual counts. Issues of accuracy and precision have been dealt with in the otolith literature (e.g. Kimura and Lyons, 1991; Campana and Jones, 1992; Hoenig *et al.*, 1995; Ralston *et al.*, 1996) including the comprehensive study of Campana and Moksness (1991). However, techniques employed in statolith research have generally

not caught up with the multitude of studies that have been carried out using fish otoliths.

Research continues to accelerate on the use of statolith age data in comprehensive studies of squid growth and demography (e.g. Arkhipkin, 1993, 1995, 1996; Collins *et al.*, 1995; Nigmatullin *et al.*, 1995; Arkhipkin *et al.*, 1996; Brodziak and Macy, 1996; Arkhipkin and Silvanovich, 1997; Dawe and Beck, 1997). Such studies underscore the usefulness of squid statoliths for tools in squid demography and highlight the fact that age estimates need to be reliable and repeatable for routine ecological and fisheries research.

In this study, our aim was to consider issues of precision within and among readers in squid age estimates. Statolith analysis has a subjective component and many of the problems of distinguishing between daily and sub-daily increments in fish otoliths (e.g. Campana, 1992; Nielson, 1992) are directly applicable to squids. It was therefore of interest to quantify the precision of age estimates by different readers and determine if precision varied with squid age. Ultimately we were interested in knowing if growth estimates differed among readers.

## Materials and methods

Twenty-three juvenile *Photololigo* sp. 3 (nomenclature after Yeatman and Benzie, 1994) were captured in January 1991 with light-traps from inshore sites as part of a distribution and abundance study off the Northeast Australian Coast (see Moltchanivskyj and Doherty, 1994, 1995). These were immediately preserved in 100% ethanol and the mantle length (ML), mm, of each individual was obtained after preservation. Statoliths were removed within 14 days and a whole unground statolith from each individual was placed in immersion oil on a microscope slide and viewed along the longitudinal plane with an Olympus BH high power microscope ( $\times 400$ ). Reader 1 counted the increments using a camera lucida while Reader 2 read increments directly down the microscope. Each reader made three consecutive counts of each statolith and the age estimates were compared.

To examine adult squid age estimates, statoliths were examined from 31 trawl-caught adult individuals of *Photololigo* sp. (20 males, 13 females) captured off Bundaberg, Queensland, Australia during 1995/1996. The species of *Photololigo* in Australia are yet to be named, but the adult individuals in this study were identified using electrophoresis and were the same species referred to as *Photololigo chinensis* by Yeatman and Benzie (1994) (M. Dunning, DPI Fisheries Brisbane, pers. comm.). Mantle length of each specimen was measured on defrosted individuals in the laboratory. Each statolith was mounted in the thermoplastic cement Crystal Bond<sup>™</sup> and ground with 1200 grit wet

carborundum paper and polished with 0.05  $\mu\text{m}$  alumina powder on a wet Leco LeCloth<sup>™</sup> (see Jackson, 1990a,b, 1994). Larger statoliths were ground on both the anterior and posterior surfaces along the longitudinal plane, while smaller statoliths were usually ground and polished on only one surface. Prepared statoliths were placed under an Olympus BX50 high power microscope ( $400\times$ ) and illuminated with polarized light. Increment counts were made directly from a live image on a 17" high resolution computer monitor, generated using a Pulnix<sup>™</sup> black and white video camera via an Imascan<sup>™</sup> video card in a Pentium<sup>™</sup> computer. Increment counts were undertaken three times (non-consecutively) by three readers experienced in statolith increment analysis.

## Data analysis

### Similarity of age estimates among and within readers

The data for both the juvenile and adult statoliths were analysed using a split-plot design because neither the data from the three replicate counts by each reader, nor the age estimates by the three readers are independent of one another. Two sources of variation were of interest to us. The first is the difference among the readers, given the variation within each reader. The second is whether readers were consistently under- or over-estimating the age relative to the other readers. Precision was calculated for each age estimate as (s.e./mean)\*100.

However, we needed to interpret the split-plot analysis on the basis of the residuals rather than the average age across all the individual squid, because the squid differed in age. Therefore, we calculated the average "age" of each squid given the nine replicate counts from the three readers (the grand average). The difference between each readers average from the grand average (residual) was then calculated. The average residual for each reader therefore provided an indication as to the magnitude of the difference of each readers age estimate.

Examining the number of increments counted on sequential replicates allowed us to determine if readers were perceiving more or less increments each time they viewed the statolith. If there was any directional change in the perception of sub-daily or daily increments with consecutive counts then it would be possible to detect this by examining the difference (residual) between each count and the average of the three counts for each squid. If, for example, a reader detected more increments with each examination of the statolith, the first count would have a negative residual, the second count would have a residual close to zero and the third count would have a large positive residual. If this trend was consistent among all statoliths counted, then the average residuals across the 31 squid would show this trend. With only three counts it is not possible to do a "runs test" (Zar,

Table 1. The precision (expressed as a percentage) among the three replicate counts from each juvenile squid by each reader is calculated and averaged across the 23 squid. The maximum and minimum precision is provided. R = Pearson correlation coefficient between dorsal mantle length and precision. The final column is the precision between the two readers across the 23 squid, using the mean of their three counts. \*Significant correlation at 0.05 significance level.

Reader	1	2	Between readers
Average precision	2.26	2.17	6.51
Maximum precision	1.16	0.00	0.00
Minimum precision	3.72	4.76	23.30
R	0.61*	0.05	0.03

1984) to check for any non-random sequence. Therefore, data were viewed to see if there was any linear sequence to the residuals.

### Growth estimates

All length-at-age relationships were linear due to the limited length range in our adult data set. An analysis of covariance was used to compare the slopes of the relationships, using length as the response variable, reader as the treatment, and age as the covariate. The inclusion of the interaction between age and treatment in the linear model is the test of different slopes.

## Results

### Juveniles

The mantle length and weight of the juveniles ranged from 7.1 to 38.1 mm and the estimated ages ranged from 19 to 41 days. The relatively high average precision value of 6.51 across all readers (Table 1) revealed that the age estimates of the juveniles were less precise than age estimates obtained for the adults below. There was also a significant relationship between squid size and precision of the age estimate for Reader 1 but not for Reader 2. There was a small (1.7 day) and non-significant reader effect in the age estimates (Table 2 –

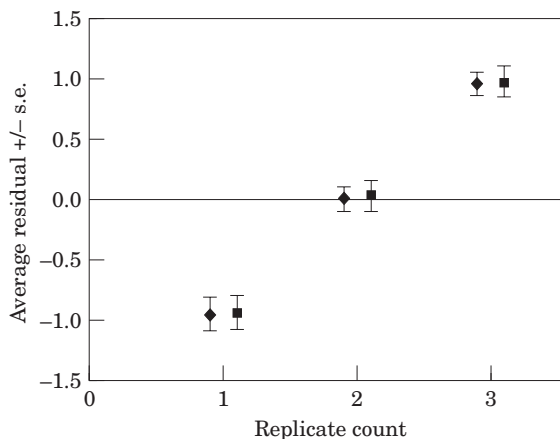


Figure 1. The difference between each replicate count for an individual and the final age estimate for that individual, averaged across all individuals. The two readers are plotted separately.

reader effect). This difference represented 4.5% of the age of the oldest individual and 8.5% of the age of the youngest individual. However, there was a significant difference among the replicate increment counts of each reader (Table 2 – time effect). Both readers consistently counted fewest increments on the first count and the greatest number of increments on the last count (Fig. 1). On average, the number of increments increased by 1.9 between the first and third counts.

### Adults

#### Similarity of age estimates among and within readers

Across the 31 adult squid there was evidence that the three readers were counting different numbers of increments in the statoliths (Table 3). At the most extreme end of the scale, we found that on average there was a 9.7 increment difference in age estimates. This represents 5.6 and 6.9%, respectively, of the age of the youngest and oldest individuals aged. However, given the absence of “real” age information we used the grand average ( $n=9$ ) as the closest real estimate of age for each individual. In this case the average absolute difference

Table 2. Results from the split-plot ANOVA examining the differences between two readers estimating the age of the 23 juvenile squid.

Source	SS	d.f.	MS	F-ratio	Prob>F
Reader	47.543	1	47.543	1.236	0.2783
Individual	3330.217	22	151.374	3.937	0.0011
Error 1	845.957	22	38.453		
Time	86.101	2	43.051	81.382	<0.0001
Reader*time	0.043	2	0.022	0.041	0.9487
Error 2	46.522	88	0.529		

Table 3. Results from the split-plot ANOVA examining the differences among three readers estimating the age of 31 adult squid.

Source	SS	d.f.	MS	F-ratio	Prob>F
Reader	910.373	2	455.186	4.55	0.0143
Individual	33 701.577	30	1 123.386	11.22	<0.0001
Error 1	6006.294	60	100.105		
Time	99.108	2	49.509	1.47	0.2312
Reader*time	418.358	4	104.590	3.37	0.0110
Error 2	5587.290	180	31.041		

between a reader and the average of the three readers ranged from 0.13 to 2.27 increments (Table 4). In the worst case (2.27), this represents 1.6% of the age of the youngest adult and 1.3% of age of the oldest individual.

The average precision of the age estimates showed minimal difference among the three readers (Table 5). Reader 3 was the most precise with the replicate counts, while Reader 1 was the least precise. Among the three readers the average precision was 2.04%, suggesting that readers were obtaining very similar estimates of age, especially when compared to the precision of the estimates obtained by each reader. There was no evidence of a correlation between the size of the squid and precision of the age estimate.

Furthermore, no one reader consistently under- or over-counted when compared with the other readers (Fig. 2). Neither was there any evidence that the

Table 4. The summary of the differences (residuals) between each readers estimate of age (based on three replicate counts) and the overall estimate of age based on the nine counts among the readers.

Reader	1	2	3
Average residual	2.15	-0.13	2.27
Maximum residual	9.89	13.56	13.3
Minimum residual	-6.6	-6.78	-13

Table 5. The precision (expression as a percentage) among the three replicate counts from each squid by each reader is calculated and averaged across the 31 squid. The maximum and minimum precision for the 31 squid is provided. R=Pearson correlation coefficient between dorsal mantle length and precision. The final column is the precision among the three readers across the 31 squid, using the mean of their three counts.

Reader	1	2	3	Among readers
Average precision	2.44	1.58	1.0	2.044
Maximum precision	0.58	0.24	0.42	0.420
Minimum precision	4.97	4.81	3.14	4.190
R	-0.122	0.034	0.138	0.040

magnitude or the direction of the residual for each reader was correlated with the size of the animal (Reader 1:  $r=0.05$ ,  $p=0.785$ ; Reader 2:  $r=0.31$ ,  $p=0.084$ ; Reader 3:  $r=0.20$ ,  $p=0.272$ ;  $n=31$  for all readers).

#### Number of increments counted with consecutive replicate counts

The average difference for each reader across 31 squid between each replicate count and the final age estimate derived from the three replicate counts varied among readers (Table 6). With only three counts it is not possible to do a "runs test" to see if there is any non-random sequence to the direction of the residuals of the replicate. However, from looking at the data in Table 6 there is no suggestion for any of the readers that there is a systematic change in the residuals.

#### Linear growth rates

Using age estimates from each reader, calculated linear growth rates ranged from 0.34 to 0.47 mm per day (Table 7). However, there was no evidence of a difference among the three growth rates estimated by each reader (Table 8). Therefore, while significant inter-observer differences in the age estimates of adult squid were detected, they did not result in significant differences to the biological results when length-at-age data were analysed.

## Discussion

Statolith ageing is becoming a routine tool for obtaining age estimates of squids. While there is an ongoing need for validation work to verify the presence of daily increments in statoliths (i.e. to address issues of accuracy), there is also the need to maintain rigour in increment counts to ensure precision. Recent analyses of accuracy and precision in squid statolith age estimates provides strong support that loliginid squid statoliths can be used as accurate and reliable ageing structures (González *et al.*, 1998).

The ease with which daily increments can be identified differs among species. While statoliths of some species have increments that are easily seen, those of other

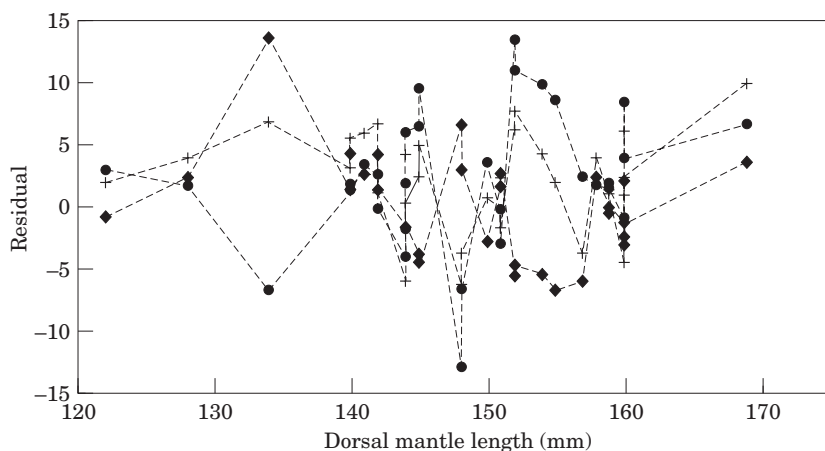


Figure 2. The residuals, or difference between the average of the three readers and the average of each single reader, plotted against the dorsal mantle length of each of the 31 adult squid. +, Reader 1; ●, Reader 2; ◆, Reader 3.

species have increments that are poorly defined and difficult or impossible to count (e.g. Jackson and Lu, 1994; Bizikov and Arkhipkin, 1997). Further difficulties are associated with distinguishing between daily and sub-daily increments, and determining where to commence counting increments (i.e. identifying the natal ring).

The increasing age estimates with replicate counts of the juvenile squid statoliths in this study may be due to readers tending to count sub-daily increments as opposed to daily increments. This appears to be a problem in juvenile statoliths (e.g. Jackson *et al.*, 1993). The statoliths of very small, juvenile loliginids are often very translucent, with considerable fine structure. This

makes identification of daily increments difficult. However, in larger and thicker statoliths, translucency is decreased due to a greater amount of calcification, which helps to mask the finer structures. These differences between small and larger statoliths are probably also responsible for the greater level of precision in the adult age estimates as opposed to the juveniles. The combination of a smaller number of increments, difficulties in delineating both daily increments and the natal ring are all probable reasons contributing to the lower degree of precision in juvenile age estimates.

It is possible that sub-daily increments are present in other species, such as *Beryteuthis magister* (Arkhipkin *et al.*, 1996) and *Todarodes angolensis* (Villanueva, 1992; Lipinski *et al.*, 1993). For these species there is more than one opinion on delineating what constitutes a daily increment (see summary in Jackson, 1994).

Different techniques may also result in different age estimates. Lipinski and Durholtz (1994) found that using light microscopy produced age estimates for *Loligo vulgaris reynaudii* that differed from those obtained from scanning electron microscopy (SEM) because more increments were visible using SEM. Significant differences were also found among readers using light microscopy, but no significant differences among readers using SEM. González *et al.*, 1998 also found that different growth equations were obtained for *Illex coindetii* depending on whether statolith increments were counted manually or by semi-automatic image analysis techniques.

Differences in the age estimates for the adult squid in our study were probably due to a combination of factors such as discerning between sub-daily and daily increments, correctly identifying the natal increment and clearly identifying all increments from the natal increment to the edge. However, age estimates obtained

Table 6. The average difference between each replicate count and the mean of the three replicate counts across the 31 squid for each reader.

Reader	1	2	3
First replicate count	1.355	0.430	-0.097
Second replicate count	-2.806	1.075	-0.742
Third replicate count	1.452	-1.505	0.839

Table 7. Linear growth coefficients generated for 31 adult squid by each reader from age-at-size data, with age data  $\log_{10}$  transformed to linearize exponential relationships.

Reader	Growth coefficient	s.e. of coefficient	$r^2$
1	0.47	0.14	0.54
2	0.34	0.15	0.39
3	0.35	0.14	0.42



Table 8. Results from ANCOVA comparing the three linear growth equations generated by the three readers (see Table 6 for more information).

Source	SS	d.f.	MS	F-ratio	Prob>F
Reader	51.971	5	25.985	0.304	0.739
Age (covariate)	1963.553	1	1963.553	22.974	<0.001
Slope	46.090	2	23.045	0.270	0.764
Error	5587.290	180	31.041		

by readers were well within 10% of each other, a value that is used as the cut-off in repeated counts in other studies (e.g. Jackson *et al.*, 1997). Furthermore, the age estimates made by the different readers did not result in significantly different growth equations. These growth results are similar to results of other species of *Photololigo* in Australia which also complete their life cycle in less than 200 d (Jackson and Choat, 1992; Moltschanivskyj, 1995; Jackson and Yeatman, 1996).

Our study reveals that with a certain level of experience and competency it is possible to produce repeatable age estimates with a high degree of precision in *Photololigo* in Australian waters. The very short lifespans (<200 d in many species Jackson, 1994) and the fact that increments appear to be laid down throughout the lifespan in loliginids (e.g. Jackson *et al.*, 1993, 1997; González *et al.*, 1998) suggests that age-based population methods can be accurately applied to loliginid squids.

## Acknowledgements

The authors would like to thank Malcolm Dunning for providing statoliths from known species of *Photololigo* collected off Bundaberg. This research was funded by the ARC Large Grants Scheme, Grant No. A09601512 awarded to G. D. Jackson and N. A. Moltschanivskyj.

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