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research paper

How old are giant squids? First approach to aging *Architeuthis* beaks

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Cephalopod research across scales: from molecules to ecosystems

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ABSTRACT.—The giant squid *Architeuthis dux* Steenstrup, 1857 is one of the largest and most enigmatic marine species. Its age estimation remains controversial with many estimates of maximum age ranging from 1 to 14 yrs. Successful results regarding the study of aging in cephalopod beaks for some octopod and oegopsid squids support using these structures for age estimation. We analyzed the beaks of 10 individuals, caught between 1995 and 2006, with reconstructed dorsal mantle lengths (*DMLs*) between 823 and 1418 mm. The beaks were measured and weighed, and their microstructure was analyzed in three ways: (1) in the rostrum area [rostrum sagittal sections (RSS)] for both upper and lower jaws, and the (2) inner lateral wall surfaces (LWS) and (3) inner crest surfaces (CS) for upper jaws. A constant sequence of increments was observed along the RSS, indicating that the use of lower jaws is more feasible due to the higher erosion and tighter packing of increments of upper jaws. The statolith of one individual was analyzed, resulting in 520 increments (579 increments from RSS of its lower jaw). Assuming daily deposition, the age estimations in RSS between 411 and 674 d suggest rapid growth of *A. dux*, averaging 1.97 mm *DML* d^{-1} (SD 0.45). When maximum ages were estimated by applying these results to the largest measured specimens in the literature (e.g., 2400 mm *DML*), an age of approximately 3 yrs was obtained. Analysis over a greater size range of individuals would allow more accurate age estimations of this emblematic squid.

Giant squids (family Architeuthidae) are well known as one of the largest and most enigmatic marine invertebrates. They inhabit temperate oceans and adjacent subpolar and subtropical waters worldwide. Following the description of *Architeuthis dux* Steenstrup, 1857, over 20 *Architeuthis* species have been reported from all over the world (e.g., Clarke 1966, Roper and Boss 1982) based on scant evidence (Roper et al. 2015). Förch (1998) recommended that Architeuthidae be reduced to a single genus and species, *A. dux*, consistent with the earliest adequate systematic description. Moreover, recent mitochondrial genome analyses suggest the presence of a single species with a worldwide distribution (Winkelmann et al. 2013), supporting the hypothesis that only one global species, *A. dux*, is valid (Kubodera et al. 2018).

Giant squids have long captured public and scientific attention, as they satisfy all requirements of an emblematic species (Guerra et al. 2011). However, until recently, all information about giant squids was based on specimens that had either washed ashore dead, were collected floating dead at the surface, or were found partially digested in (or regurgitated from) predator stomachs. On the other hand, cases of multiple strandings in the northeast Atlantic have been linked to geophysical prospecting using air-gun arrays with high-frequency signals, indicating that acoustic factors could cause or contribute to deaths of *A. dux* specimens (Guerra et al. 2004). Habitat preferences and specific migrations of giant squids are poorly known; *A. dux* has been associated with canyons and seamounts because (1) species from such topographical structures have been found in the stomach contents of giant squid (González et al. 2002), and (2) there have been many specimens collected in areas with such structures (Roper and Shea 2013, Escánez et al. 2018). Despite numerous records from all major oceans (e.g., Kirk 1880, Aldrich 1968, Nigmatullin 1976, Roeleveld and Lipinski 1991, Ré et al. 1998, González et al. 2002, Martins and Perez 2009, Roper and Shea 2013, Kubodera et al. 2018), the knowledge of their biology and ecology (Roper and Shea 2013, Regueira et al. 2014), and recent in situ observations (Kubodera and Mori 2005, Schrope 2013, Guerra et al. 2018), the life history of the giant squid is still largely unknown.

Techniques that are used for age and longevity estimations of giant squids are based on hard structure analysis of statoliths (e.g., Jackson et al. 1991, Gauldie et al. 1994, Brunetti et al. 1998, Lordan et al. 1998, Guerra et al. 2006), size frequency analysis of mass findings (Kubodera et al. 2018), growth models for projections of the life span (Grist and Jackson 2007), and isotopic analysis of tissue (Landman et al. 2004). However, growth and lifespan of giant squid still remain controversial and estimates of longevity range from 2 to 3 yrs (Gauldie et al. 1994, Lipiński 1997, Lordan et al. 1998, Grist and Jackson 2007) to >14 yrs (Landman et al. 2004).

The beaks of *A. dux* have been analyzed to reveal life-history traits and trophic ecology by using isotopic analysis (e.g., Cherel and Hobson 2005, Cherel et al. 2009, Guerra et al. 2010), but to our knowledge the use of beaks for age estimation has not been assessed. Successful results on age analysis of beak sections in other cephalopod species such as octopods (Raya and Hernández-González 1998, Perales-Raya et al. 2010, 2014a,b, Villegas-Bárcenas et al. 2014, Armelloni et al. 2019), oegopsids (Liu et al. 2015, 2017, Lishchenko et al. 2018b), and sepioids (Lishchenko et al. 2018a) support using these structures for age estimation in giant squids.

In the central eastern Atlantic, remains of *A. dux* specimens are occasionally reported floating in waters off the Canary Islands (Spain), a volcanic archipelago located around 100 km off the northwest African coast (28°17′29.6″N, 16°37′44.8″W). The archipelago, and specifically off the southwest coast of Tenerife Island, has a high occurrence of giant squids (Escánez et al. 2018), which is probably favored by predation of deep diving odontocetes, reported to hunt large/fast moving prey such as giant squid (Aguilar Soto et al. 2008). In the present study, the microstructure of *A. dux* beaks is used to assess, for the first time to the best of our knowledge, the use

Table 1. Catch and body measurements available for each specimen (ID). I = inmature; F = female. Reconstructed body measurements (*) from rostrum length of lower jaws using equations from Roeleveld (2000) and Paxton (2016). DML = dorsal mantle length; TL = total length; GR = estimate of growth rate (mm DML d^{-1}).

ID	Date of catch	Place of catch	DML (mm)	TL (mm)	Sex	Roeleveld (2000)		Paxton (2016)		
						*DML (mm)	GR	*DML (mm)	GR	*TL (mm)
1	7 July, 1995	South Tenerife	1,520	-	F	1,418	2.31	1,493	2.43	7.6
2	1 January, 2001	South Gran Canaria	1,060	-	F	1,014	2.11	1,272	2.65	6.5
3	5 June, 2002	South Tenerife	-	1,620	F	823	1.98	1,151	2.77	5.9
4	29 October, 2002	North Tenerife	-	-	?	1,309	1.95	1,437	2.14	7.4
5	5 July, 2003	Southeast Tenerife	1,000	-	?	1,000	1.50	1,263	1.89	6.5
6	1 June, 2006	South Tenerife	-	-	?	1,055	2.57	1,296	3.15	6.6
7	25 October, 2005	South Tenerife	1,200	7,500	I	1,314	2.65	1,439	2.90	7.4
8	3 September, 2004	South Tenerife	-	-	?	1,019	1.76	1,275	2.20	6.5
9	29 July, 2005	South Tenerife	-	-	?	1,086	1.61	1,314	1.95	6.7
10	19 October, 2005	South Tenerife	-	7,500	?	1,290	1.29	1,427	3.16	7.3
Mean	-		-	-		1,133	1.97	1,337	2.53	6.8
Max	1 June, 2006		1,520	7,500		1,418	2.65	1,493	3.16	7.6
Min	7 July, 1995		1,000	1,620		823	1.29	1,151	1.89	5.9

of these hard structures for age and lifespan estimation of giant squids. As reported in previous studies (e.g., Perales-Raya et al. 2010, 2014a,b, Liu et al. 2015, 2017) increments located at the rostrum tip could undergo a process of erosion during the feeding process, and therefore the rostrum tip should be analyzed carefully in order to prevent age underestimation. In this study, analysis and quantification of the erosion in cephalopod beaks was undertaken by developing a simple method, using the number of increments of the dorsal non-eroded region and the increment widths.

Materials and Methods

The beaks of 10 individuals were collected in the Canary Islands, central-east Atlantic, in the period of 1995–2006 and then analyzed (Table 1). All specimens were partially damaged and most of them consisted of the anterior ⅓ of the mantle, with incomplete arms and tentacles. In three cases, only the head and brachial crowns were available. Remains were mostly found floating at the sea surface, except specimens ID1 and ID4 which were recovered dead by fishermen. Positive identification as *A. dux* was always possible when observing buccal connectives and funnel-locking apparatus, if the carpal region of the tentacles was not available. We could not determine the sex of most specimens, but Specimen ID2 was female with spermatangia subcutaneously inserted around the eyes.

Dorsal mantle length (*DML*) and total length (*TL*) was reconstructed using the rostral length of lower beaks (Fig. 1A), using equations of Roeleveld (2000) and Paxton (2016), as shown in Table 1. Equations are shown below for Roeleveld model (Eq. 1) and Paxton models for *DML* (Eq. 2) and *TL* (Eq. 3):

$$DML(\text{mm}) = 10^{[(RL/11.2)+1.7232]} \qquad \text{Eq. 1}$$

$$DML(\text{m}) = e^{[-1.168+98.031\times RL]} \qquad \text{Eq. 2}$$

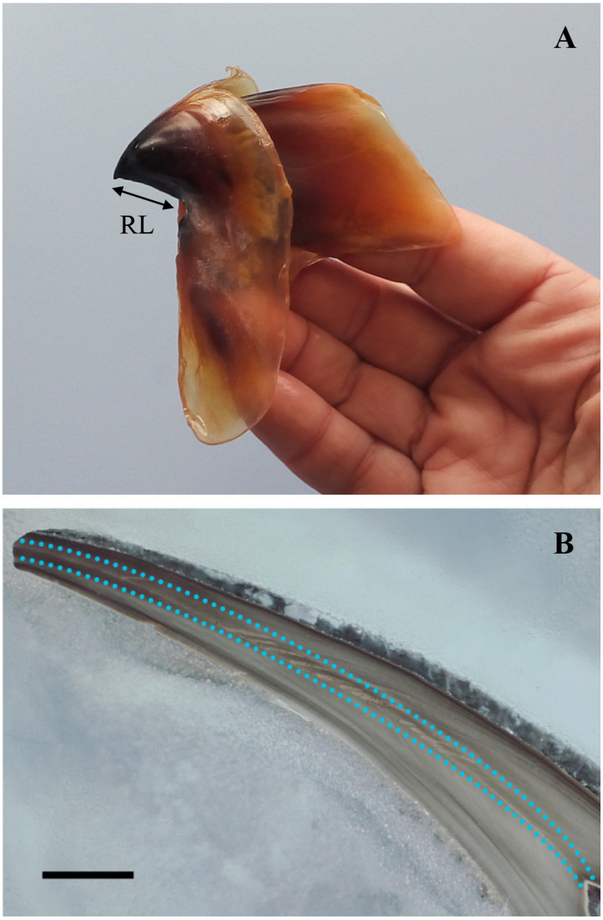

Figure 1. (A) Handheld lower beak of *Architeuthis dux* showing rostral length (RL). (B) Rostrum sagittal section of the specimen ID4 with 670 increments. Reading region delimited by dotted lines, from anterior tip with the oldest increments (left), to the posterior border with the most recent increments (right). Bar = 1 mm.

$$TL(\mathrm{m}) = 0.006 + 5.117 \times DML \qquad \text{Eq. 3}$$

Beak measurements were selected according to Clarke (1986): rostral length, hood length, and crest length. Beaks were also weighed before preparation. All beak measurements and *DML* reconstructions are shown in Table 2.

At the time of collection, beaks were cleaned and preserved in 70% ethanol. Prior to age estimation, beaks were rehydrated in distilled water for several days. The options in the rostrum area [rostrum sagittal sections (RSS)] for microstructure analysis in both upper and lower jaws were explored and assessed. Inner lateral wall surfaces (LWS) and inner crest surfaces (CS) were also examined in upper jaws. The full technique for preparing RSS and LWS are described by Perales-Raya et al. (2010). For RSS, the rostrum region of the jaw is cut and embedded in resin with the lateral side facing up. After hardening, the piece is ground with 1200-grit waterproof sand paper and subsequently polished with 1 μm diamond paste. As the rostrum region is fully

Table 2. Beak measurements (upper and lower jaws) and age estimations (days) from sections of lower jaws in each specimen (ID). Precision of beak readings (CV = Coeficient of Variation). Age estimation from statolith available in specimen ID8.

ID	Lower jaw				Upper jaw				Beak reading 1	Beak reading 2	Precision CV (%)	Statolith reading
	Crest	Hood	Rostrum	Weight	Crest	Hood	Rostrum	Weight				
1	49.0	24.0	16.0	3.9	101.0	71.5	15.0	4.5	615	582	3.9	-
2	41.0	17.7	14.4	2.0	86.9	43.8	14.3	3.1	480	457	3.5	-
3	39.9	17.1	13.4	1.7	78.3	57.0	13.3	2.5	415	403	2.1	-
4	49.7	23.8	15.6	2.8	93.9	61.2	14.5	4.2	670	646	2.6	-
5	46.9	20.0	14.3	2.7	95.9	65.2	14.7	3.9	668	651	1.8	-
6	39.3	19.3	14.6	1.6	76.1	50.1	14.0	2.3	411	410	0.1	-
7	48.8	26.9	15.6	4.1	95.8	67.1	14.9	5.4	496	483	1.9	-
8	46.0	21.6	14.4	1.9	92.3	64.2	15.7	2.8	579	544	4.4	520
9	37.0	17.3	14.7	2.3	77.5	53.4	14.1	2.3	674	660	1.0	-
10	47.6	20.5	15.5	2.8	95.3	67.8	17.5	3.3	451	446	0.5	-

tanned, the increments are visible under reflected-vertical light and it is unnecessary to sand down both sides. Regarding LWS, the jaw is sagittally sectioned with scissors to obtain two symmetrical half beaks, which are cleaned with water and their inner surfaces observed under reflected-vertical light. An obliquely reflected light beam was also used for observation of the inner surface of the crest and lateral walls.

Age was estimated by counting the increments in the RSS of lower beaks, using vertical epi-illumination and magnifications of 100× to 400×, and most commonly between 150× and 250×, using an image analysis system (IAS). The reading region is located in the central area of the RSS, at both sides of the central axis where each increment was tracked (Fig. 1B). Thus, following the increments along the central and adjacent axes increased the accuracy of readings by covering the reading direction, suggested by Liu et al. (2015) as being the closest to the statolith-determined ages in several ommastrephid squids.

In the present study, the RSS technique was tested in both upper and lower jaws. The RSS increments were counted in the high-resolution images saved by the IAS (NIS-Elements, Microscope Imaging Software, Nikon©). Each specimen was photographed multiple times (n = 9–22) to cover the whole reading region of each sample. Two experienced readers counted increments on each RSS. Age "precision" between both readings (sensu Campana 2001) was assessed using the coefficient of variation, CV (standard deviation divided by the mean number of increments in each sample; Chang 1982, Campana 2001):

$$CV(\%) = 100 \times \sqrt{(R1 - R)^2 + (R2 - R)^2}/R \qquad \text{Eq. 4}$$

$R1$ and $R2$ being the number of increments from the first and the second reading respectively, and R being the mean number of increments from both readings.

Distances between growth marks (increment widths) were measured using the software Age&Shape 1.0. (Infaimon©) after calibrating for each magnification used. When extrapolation was necessary for some areas with poor visibility, the previous increment sequence of the same length was used in these areas with no clear increments. To mitigate tip erosion effects, the first increments located at the rostral tip of the RSS were counted in the dorsal area, where erosion was not seen. This number of dorsal increments (DI) was then used to extrapolate the eroded missing increments in the reading region, using DI and the widths of this number of previous increments in the central reading region. This allowed for estimation of the increment width of all increments in the reading region, including the increment width of the eroded tip. The total sum of all increment widths was considered an estimation of the reading length (*RL*), and the sum of eroded increment width, as the estimation of the eroded length (*EL*). For each individual, the percentage of eroded length (*E*) was calculated using *RL* and *EL,* and this equation:

$$E(\%) = \frac{EL \times 100}{RL} \qquad \text{Eq. 5}$$

Estimate growth rates (GR, mm of *DML* d^{-1}) were calculated by comparing the number of increments (*R*1) to the reconstructed *DML* of each specimen (*see* Table 2). Statoliths were mostly unavailable for the purpose of comparison, except for one statolith of specimen ID8. This statolith was placed in epoxy resin (two components, West System©) with the anterior side facing up in a glass slide, ensuring that lateral dome and dorsal dome were affected as little as possible by the convexity of the posterior side. After hardening, it was ground (1200 grinding paper) and polished (1 µm diamond paste). It was then flipped over in order to grind and polish the posterior side. The statolith was finally observed under transmitted light at 400× magnification, with the anterior side facing up, whereby a higher degree of visibility of increments was observed compared to the posterior position. Some extrapolation (7%) was necessary, mainly in the border of the lateral dome where increments were not visible and information on previous increments was considered in order to complete the statolith reading.

The analysis of sea surface temperatures (SST) in the channel between the islands of Tenerife and La Gomera was performed to explore seasonal variations in these waters. Following the methodology used in Perales-Raya et al. (2014a), daily high-resolution time series of SST from 1995 to 2011 (from the NOAA THREDDS Data Server 2017) were used to obtain a SST-time series at a daily frequency for a time horizon of 17 yrs in the study area of 28 × 28 km (center at 27°59.418´N, 17°53.472´W). These SST-time series were obtained by using an optimum interpolation method that employs an Advanced Very High Resolution Radiometer (AVHRR) for the computation of SST from infrared satellite data, which includes a large-scale adjustment of satellite biases with respect to the in situ data. These data were used in combination with in situ surface data from ships and buoys (Reynolds et al. 2007). The analyses have a spatial grid resolution of 0.25°.

Results

From the three regions (RSS, LWS, CS) that were explored for assessing increments in beaks of *A. dux*, only RSS resulted in being suitable for aging analysis (Fig. 1B). A constant sequence of microincrements was observed along the RSS in both upper and lower jaws. Lower jaws were more reliable (Fig. 2) due to the higher erosion and tighter agglomeration of microincrements of the upper jaws. Using an obliquely reflected light beam, a sequence of thick increments was found for the first time in the CS of beaks. Most of the increments continued along the LWS, where usually several

Figure 2. Image composition of the reading region shown in Figure 1 from the rostrum surface section of the lower jaw in the individual ID4. Bar = 500 µm.

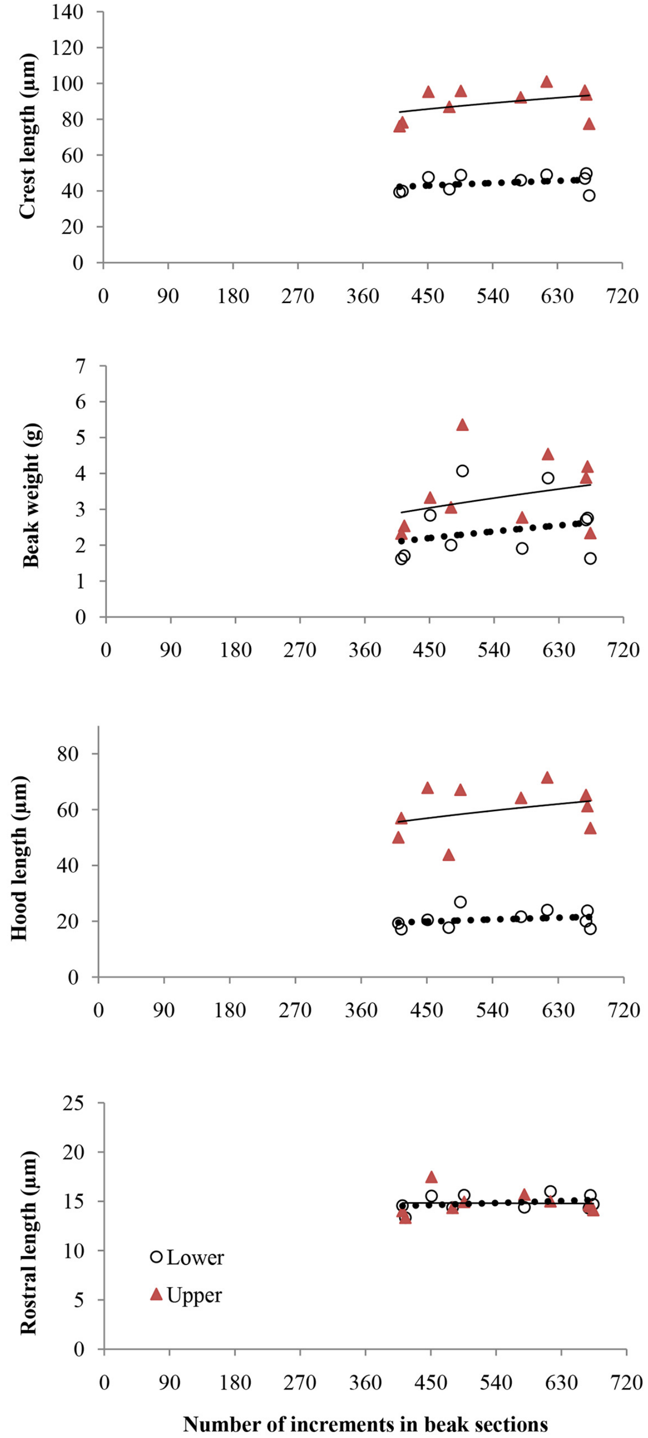

Figure 3. Relationships between the number of increments in beak sections (lower jaw) and several beak measurements (lengths in microns and weights in grams). Regression lines using a power model for upper and lower jaws ($R^2 < 0.5$).

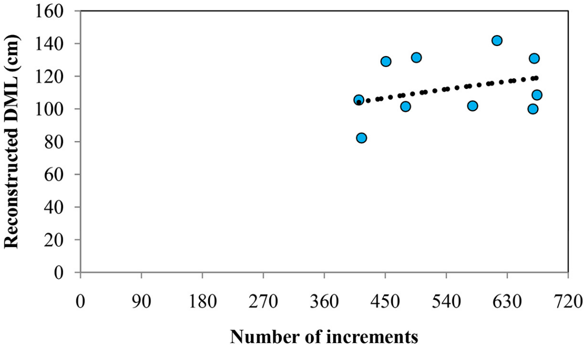

Figure 4. Relationship between the number of increments and reconstructed dorsal mantle length [using equation of Roeleveld (2000)]. Regression line (power model, $R^2 < 0.5$).

microincrements were visible in between. The microincrement sequence was clear in some areas of LWS although it was usually difficult to follow throughout the entire LWS. Both LWS and CS showed some regions with very small and clear microincrements, but there were also confusing zones with no increments observed in their surface or there were many scratches on the surface thus impeding observing a reliable sequence of increments. This was especially frequent in the anterior region of the beaks. For these reasons, both CS and LWS were finally rejected for aging analysis of beaks of the giant squid.

Assuming daily deposition in beaks of *A. dux*, age estimations in the sample for reconstructed sizes between 823 and 1418 mm *DML* (Table 1) ranged between 411 and 674 d. All reading and precision values are shown in Table 2. The mean *CV* obtained from both readings was 2.2% (SD 1.4). These results indicate that both readings were similar, therefore either of them could be selected. *R*1 was used as age estimation in days and increments identified in the images used for measuring each increment width. Statolith count of individual ID8 was 520 increments, and comparing with RSS reading 1 of the specimen (579 increments) indicates around 2 mo of difference, with around 10% fewer increments in the statolith.

Table 3. Data of increment widths, ages, and hatching dates by specimen (ID). Specimen ID2 showed broken tip and therefore eroded percentage was not estimated. SD = standard deviation.

ID	Mean increment width (µm)	SD	Total length of reading region (µm)	Number of eroded increments	Percentage of eroded distance (%)	Estimated age (days)	Estimated hatching date
1	10.0	8.0	6,040	22	3.6	615	30 October, 1993
2	8.3	3.9	3,914	-	-	480	9 September, 1999
3	12.2	6.3	4,979	43	10.4	415	16 April, 2001
4	12.9	5.3	8,499	24	3.6	670	28 December, 2000
5	11.1	5.1	7,279	33	4.9	668	5 September, 2001
6	18.6	6.9	7,594	17	4.1	411	16 April, 2005
7	19.1	8.0	9,288	30	6.0	496	16 June, 2004
8	14.2	7.2	7,934	28	4.8	579	2 February, 2003
9	9.6	4.9	6,276	40	5.9	674	24 September, 2003
10	20.7	9.6	9,031	35	7.8	451	25 July, 2004
Mean	13.7	-	7,083	30	5.7	546	

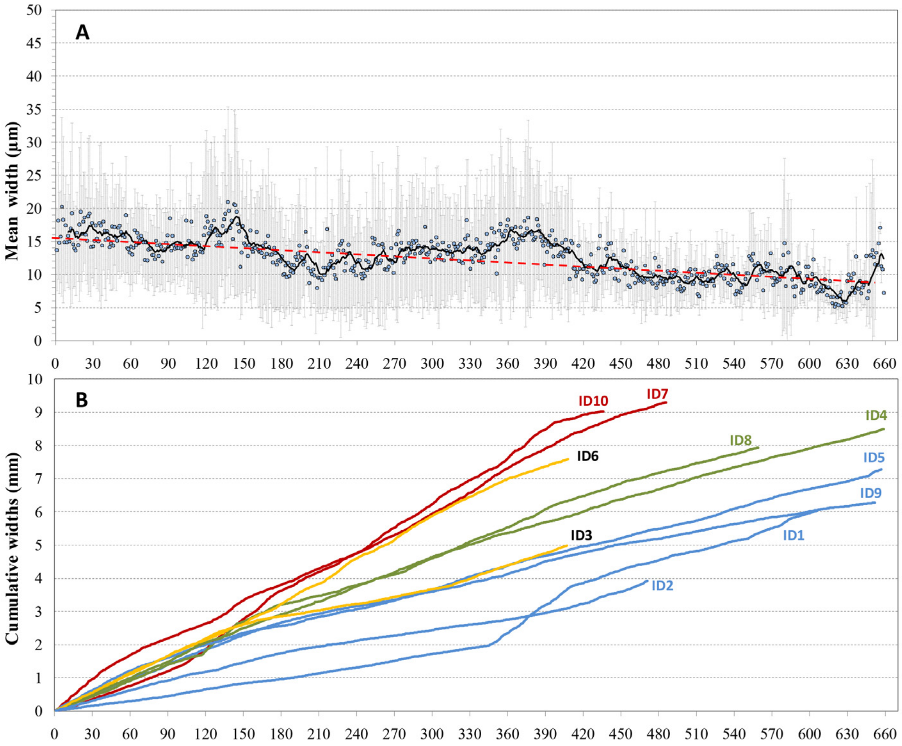

Figure 5. (A) Mean increment widths of the lower jaw sections for the 10 specimens of *Architeuthis dux* analyzed. Moving average (black line) and linear trend (red dotted line) of the mean increment widths. Error bars (SD) are shown for each mean increment value. (B) Cumulative widths for each specimen (*see* Table 3). Lines in red, blue, green, and yellow for individuals hatched in early summer (middle June–July), late summer–autumn (September–November), winter (end December–February), and spring (April), respectively.

Relationships between the number of increments in RSS (an approximation of age in days) and beak measurements in both upper and lower jaws are shown in Figure 3. Reconstructed *DML* from the equation of Roeleveld (2000) had more similarity to those estimated during sampling of the specimen in the lab (when available). For this reason, this equation was used for reconstructed *DML* and this assessed its relationship with the number of increments in RSS. The relationship with reconstructed *DML* is shown in Figure 4. In all cases, the best regression model was a potential curve, with low regression coefficients ($R^2 < 0.5$). Estimated GR suggests a rapid growth, averaging 1.97 mm *DML* d^{-1} (SD 0.45) using the equation of Roeleveld (2000) for *DML* reconstruction, and 2.53 mm *DML* d^{-1} (SD 0.47) using the equation of Paxton (2016; *see* Table 1).

Results of increment widths and erosion estimations are summarized in Table 3. The mean increment width in the sample was 13.7 µm (SD 4). The number of eroded increments in the reading region of RSS averaged 30 (SD 8). In terms of percentage (%), the mean eroded distance in the sample was 5.7% (SD 2.2) of the total reading length. For each increment, the mean value (Fig. 5A) and the cumulative width (Fig. 5B) for the 10 individuals is graphed, from the oldest increments located at the RSS tip, to the most recent increments located at the posterior end of the RSS. Error bars

(SD) are included in Figure 5A for each increment. Linear regression ($R^2 = 0.45$) indicates a decreasing trend in the increment width, from the young ages (16.4 µm of average for first 30 increments) to the oldest ages (10.2 µm for the latest 30 increments). Assuming daily deposition of increments in RSS, specimens of maximum rostrum growth in Figure 5B (ID7 and ID10) were born in early summer 2004 (middle June–July; *see* Table 3), whereas those of minimum rostrum growth (ID2, ID1, ID9, ID5) were born at the end of summer or autumn (during September and October of different years). Variable growths resulted for specimens born in spring (April for ID3 and ID6), whereas those born in winter (end December and February) showed intermediate rostrum growth.

Discussion

All sample individuals that were found dead and floating on the sea surface were caught in the warm-hot season (June–October). The higher occurrence of findings in this season could be influenced by exposition to warm water currents, because it has been suggested that giant squids may suffocate from arterial desaturation when high increases in ambient temperatures are experienced (Brix 1983). Recent studies (e.g., Romanov et al. 2017) support the observations made in the present study of severe mutilations due to predation on the specimens recovered from the sea surface, and injuries at the mantle tip suggest predation by a large animal, probably a sperm whale. Eight of the ten individuals of the present study were found in the southwest of Tenerife Island, an area with a steep deepwater canyon in the channel between the islands of Tenerife and La Gomera, hosting a resident population of shortfin pilot whales *Globicephala macrorhynchus* Gray, 1846. Their year-round presence and hunting of large prey (Aguilar Soto et al. 2008) could be explained by the high abundance of large species of squid in the area, as large squids may be a key resource for this teuthophagus cetacean.

Daily periodicity in the beak RSS has been validated in two octopus species (Perales-Raya et al. 2014b, Villegas-Bárcenas et al. 2014). Cross-verification of daily periodicity in the increments of RSS with statolith readings supports the hypothesis of one increment per day for a number of oegopsid species (Liu et al. 2015, 2017), where beak microstructure in RSS has been used for age estimation in ommastrephid and gonatid squids (Hu et al. 2016, Fang et al. 2016, Lishchenko et al. 2018b). The results for the specimen with both structures indicate around 2 mo of difference (10% fewer increments in the statolith than in beak RSS), which could be due to some underestimation in statolith counts. In other oegopsid species [*Dosidicus gigas* (Orbigny, 1835), *Ommastrephes bartramii* (Lesueur, 1821), and *Stenoteuthis oualaniensis* (Lesson, 1830)], beak counts were slightly lower than statolith counts, but not in *Illex argentinus* Castellanos, 1860 (Liu et al. 2015) and the population of *D. gigas* from Chile (Liu et al. 2017). Beak erosion has been suggested by Liu et al. (2015) as being the cause of the lower number of increments in RSS, although this is not happening in all species and when a lower number is counted in the statoliths, overlapping of very thin and closed increments in some specimens could be related to underestimation of statolith counts. Exploring upper and lower jaws could help to select the jaw with less erosion, as was undertaken in the present study, in which lower jaws were less eroded in their anterior region. Moreover, from the experiences of the present authors with respect to the aging analysis of beaks, the pattern of deposition and microstructural appearance of RSS increments observed in beaks of *A. dux* was similar and comparable to other species of octopuses, squids, and cuttlefishes that were previously analyzed in the lab where this present study was undertaken, supporting the hypothesis of daily deposition.

The higher degree of erosion and agglomeration of microincrements observed in RSS of upper jaws prevented using them in the giant squid, despite being suitable in other oegopsid squids (Liu et al. 2015, 2017, Fang et al. 2016, Hu et al. 2016) or octopuses, where no significant difference was found between RSS of upper and lower jaws (Perales-Raya et al. 2010). In addition, the upper jaw has been successfully used for age estimation in LWS of the common octopus (e.g., Hernández-López et al. 2001 Canali et al. 2011, Cuccu et al. 2013, Perales-Raya et al. 2014a,b). Nevertheless, the abundance of deep scratches observed in the anterior surface of lateral walls and crest in the upper jaws of giant squid made it difficult to perform a complete count of increments in these areas. These observations suggest that predation activity of giant squid could be more active and aggressive in the upper jaw, thus increasing the prevalence of scratches and the erosion in the anterior part of LWS and RSS of this jaw. Therefore, the selection of upper jaw or lower jaw should be tested when assessing age estimation from RSS beaks of a species for the first time.

The low regression coefficients obtained in Figure 3 for beak measurements and in Figure 4 for reconstructed *DML* could be related to the heterogeneity of the sample, with individuals caught in different years and seasons. We hypothesize that the ages obtained in the sample (411–674 increments) in this study correspond to individuals in their latest growth phase when a slower growth rate would be more feasible. Gauldie et al. (1994) observed a rapid early growth and an apparent asymptotic growth in size-at-time data for the 24 specimens reported around New Zealand, in which large, faster-growing squid mature, spawn, and die in advance of slower growing members of their cohort. Results from size frequencies of mass findings within a relatively short period of time (Kubodera et al. 2018) suggest a very rapid growth and an inclination towards an S-growth curve, with lower growth rates in earlier and later life stages. In the present study, the results from increment analysis indicate decreasing mean widths (*see* Fig. 5A), supporting a decreasing growth trend, at least in the rostrum beak. When analyzing the cumulative widths individually (*see* Fig. 5B), the decreasing growth trend is more evident in some specimens (e.g., ID9, ID3, ID7, ID4, ID5) or some periods such as later life stages (ID10, ID6). Individuals hatched in early summer 2004 (*see* ID7 and ID10 of Fig. 5B) could have grown faster due to more favorable conditions during their first life stage. In the Canary Basin, several studies have indicated seasonal mass transport behavior of the North Atlantic Central Water (0–700 m depth) which reaches its maximum average value during summer (Machín et al. 2006, Mason et al. 2011). These physical conditions are favorable for the formation of cyclonic eddies (0–700 m depth) which increase the primary production to 3.5 times that of the nearby waters (Arístegui et al. 1994). These mesoscale structures could have increased the food availability during the first stages for specimens born in the early summer, resulting in larger rostrum sizes for similar ages (*see* Fig. 5B). Moreover, the summer of 2004 was significantly warmer compared with the 17 yrs of daily SST time series analyzed (1995–2011), reinforcing the hypothesis of favorable environmental conditions for high primary production in the area. Conversely, specimens born from September (*see* ID1, ID2, ID5, ID9 of Fig. 5B) could have found less favorable conditions during first stages, since the integrated

Table 4. Estimation of maximum ages (years) from the largest specimen measured (2400 mm DML, Norman and Lu 2007) and estimates of growth rates (GR) from the present study (*see* Table 1). DML reconstruction from Roeleveld (2000)[1] and Paxton (2016)[2].

	GR[1]	Years[1]	GR[2]	Years[2]
Age from mean GR	1.97	3.3	2.53	2.6
Age from minimum GR	1.29	5.1	1.89	3.5
Age from maximum GR	2.65	2.5	3.16	2.1

mass transport decreases in autumn and reaches its minimum value during winter (Mason et al. 2011). When comparing individual growth lines of Figure 5B with mean SST values during the first three months after hatching (data not shown), all cases showed that rostrum growth was faster in individuals hatched in warmer years. However, a detailed analysis would be needed in order to draw definitive conclusions regarding this issue.

In the present study, mean RSS increment width in *A. dux* (13.7 μm) was similar to the estimated value by Liu et al. (2015) for the oegopsids species *D. gigas* from the southeastern Pacific (13.6 μm), *I. argentinus* from the southwestern Atlantic (13.4 μm), and *O. bartramii* from the northwestern Pacific (12.4 μm). The standard deviations of these species were lower than the value obtained in the present study for *A. dux*, indicating a higher variation of increment widths in the giant squid. The two highest values of widths seem to occur in the 4–5 and 12–13 mo of life, although the variability of data (*see* error bars of Fig. 5A and SD in Table 3) prevent definitive conclusions about growth peaks in the increment widths.

Mean values of 2.2% for *CV* indicate high precision, comparable with other beak studies carried out in RSS of other oegopsid squids where *CV* values ranged from 2.86% to 4.98% in four ommastrephid species caught in the Atlantic Ocean and the Pacific Ocean (Liu et al. 2015). The estimate of *CV* from rostrum readings (RSS in adults and rostrum surfaces in paralarvae) in octopods has shown values ranging from 1% to 4% (Perales-Raya et al. 2010, 2014a,b, Villegas-Bárcenas et al. 2014, Perales-Raya et al. 2018). In the specimen of *A. dux* where both statolith and RSS beak were analyzed, a difference of 59 fewer increments was observed in the statolith compared with RSS. Statolith and RSS readings were cross-verified in other oegopsid species, supporting the hypothesis of daily deposition but suggesting that some underestimation due to feeding erosion of the rostrum cannot be ignored (Liu et al. 2015). Comparisons in *D. gigas* showed significant linear relationships, where the values of the regression slopes were close to one and the intercepts were close to zero (Liu et al. 2017). In the gonatid squid *Berryteuthis magister* (Berry, 1913), preliminary results showed that the number of increments on the RSS of lower jaws exceeded the value of statolith sections by approximately 35% (Lishchenko et al. 2018b). Those authors reported that lower jaws are larger and bear wider-spaced increments than upper jaws, suggesting that the complex structure of gonatid statoliths can lead to mistakes and age underestimations. The results of the present study are preliminary, as only one individual was cross-verified using a statolith reading, but interspecific differences may contribute to explaining the differences as the selection of upper/lower jaw can be relevant in some species to minimize the erosion effect on the age underestimation.

Based on the assumption that one RSS increment is laid down each day, the results of this study indicate an estimated GR range of between 1.29 and 2.65 mm *DML* d^{-1}

[using the equation of Roeleveld (2000) for the reconstruction of *DML*, *see* Table 4], which are lower but comparable with the growth rates reported by Jackson et al. (1991; 2.76 mm in a juvenile specimen) and Lordan et al. (1998; 2.6–3.5 mm *DML* d^{-1}) based on statolith counts of daily increments. On the contrary, results of GR using equation of Paxton (2016) indicate higher values of GR (1.89–3.16 mm d^{-1}, *see* Table 4), which are more in line with higher estimates of GR that varied from 3.9 to 5.6 mm *DML* d^{-1} (Gauldie et al. 1994, Fernández-Núñez and Hernández-González 1995, Lipiński 1997, Brunetti et al. 1998). O'Shea (2000) obtained intermediate values of 2.5–4.1 mm *DML* d^{-1}. All these studies are also based on statolith counts. Estimated GR of this species appears to be very rapid (although it can vary), and males and females may have different growth rates, as suggested by Guerra et al. (2006) and Grist and Jackson (2007) from statolith readings. Approximate value of maximum age as an estimation of the lifespan of *A. dux* was calculated in the present study by applying these results to the largest measured specimen to date, i.e., 2400 mm *DML* (Norman and Lu 1997), obtaining mean values of approximately 3.3 yrs of age [using the equation of Roeleveld (2000) for the reconstruction of *DML*, *see* Table 4].

The existence of one global species of giant squid *A. dux*, with a worldwide distribution and low level of genetic diversity, as suggested by Winkelmann et al. (2013), indicates a considerable morphological variation within the species (Roper and Shea 2013). Geographical variations may influence the life-span duration from different locations and therefore the maximum ages in the present study from the largest individual measured (*see* Table 4) should be taken with caution, as the specimen was caught off the coast of southern Australia (Norman and Lu 1997). Nonetheless, a maximum lifespan of around 3 yrs is plausible in the species, in accordance with previous studies suggesting a longevity of 2 yrs for males and 3 yrs for females based on modal size frequency distribution of mass findings (Kubodera et al. 2018) and statolith ages (e.g., Jackson et al. 1991, Fernández-Núñez and Hernández-González 1995, Lordan et al. 1998) in both the Pacific Ocean and the Atlantic Ocean. Guerra et al. (2006) summarized the age estimation of *A. dux* from different approaches and suggested lifespan durations between 1 and 3 yrs. They also found a marked sexual dimorphism in *A. dux* and suggested that males have a lifecycle of around 1 yr and are much smaller than females. Females are larger, mature later, and live for 2 to 3 yrs. Regarding those authors, it seems unlikely that females reach greater ages. The results of the present study are not in line with long life-span estimations of many years from isotopic analysis on statoliths of three specimens from Tasmanian waters (Landman et al. 2004). Ages derived from the model fell between 13 and 38 yrs, with <14 yrs cited as being most likely; however, the parameters are extremely dependent on assumptions of depth and statolith growth patterns, making the age estimates highly uncertain (Roper and Shea 2013).

To our knowledge, the quantification of erosion in cephalopod beaks has been assessed for the first time in the present study. Therefore, the results of 5.7% of reading length eroded, and averaged value of 30 d cannot be compared with previous studies. However, it means that in giant squids a mean of 30 d has to be counted in the dorsal area (where a clear sequence of very thin increments was usually observed) and higher magnification is sometimes necessary to prevent age underestimation. Although analysis of more different-sized individuals and cross-verification of readings from several hard structures is advisable, the results of the present study, in line with Guerra et al. (2006) and Kubodera et al. (2018), move the research a little closer towards answering the question of how old giant squids are.

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