AGE, GROWTH AND MATURITY OF JUMBO SQUID (*DOSIDICUS GIGAS* D'ORBIGNY, 1835) OFF THE WESTERN COAST OF THE BAJA CALIFORNIA PENINSULA

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ABSTRACT

Although jumbo squid (*Dosidicus gigas*) live off the western coast of Baja California, México, biological information for the species from this area is scarce. We processed the statoliths of 191 squid (144 females and 47 males) caught off western Baja California during 2004. The oldest male was 391 days old (mature at 690 mm dorsal mantle length, ML) and the oldest female was 433 days old (mature at 700 mm ML). Birth dates for both sexes were concentrated in January, indicative of a reproductive peak. Jumbo squid growth was best described by the logistic model. The largest females were larger (100 mm ML) and lived longer (1.4 months) than the largest males. The maximum daily growth rate in females was 2.09 mm per day (at 220 days; 407.6 mm ML) and in males was 2.1 mm per day (at 200 days; 365.9 mm ML). Finally, we conclude that squid from the Gulf of California grow faster than squid from off the western coast of Baja California.

INTRODUCTION

Jumbo squid (*Dosidicus gigas* d'Orbigny, 1835) is the largest and one of the most abundant species of the Ommastrephidae family and is distributed along the eastern Pacific Ocean from California (40°N) south to the southern part of Chile (45°S) (Nesis 1983; Nigmatullin et al. 2001). In México, the largest aggregations of jumbo squid occur in the Gulf of California and off the western coast of Baja California (Sato 1976; Klett-Traulsen 1996; Markaida and Sosa Nishizaki 2001).

In the Gulf of California, where a jumbo squid fishery has been established, this species has been widely studied (Klett 1982; Ehrhardt et al. 1983; Hernández-Herrera et al. 1998; Markaida et al. 2004). However, off the western coast of Baja California only exploratory studies have been conducted on the jumbo squid fishery (Sato 1976; Klett-Traulsen 1996). Recently the jumbo squid has greatly expanded its range in the eastern North Pacific Ocean and this may have important effects in the marine ecosystem (Field et al. 2007; Zeidberg and Robison 2007). The oceanographic and ecological conditions in the Gulf of California and off the western coast of Baja California differ, and such differences could influence the biological parameters (e.g., growth rate) of jumbo squid.

Currently, the jumbo squid fishery in the Gulf of California is regulated under the premise of a single cohort (Hernández-Herrera et al. 1998). However, some authors assert the existence of more than one cohort, which might imply more than one growth pattern (Ehrhardt et al. 1983; Nigmatullin et al. 2001; Markaida et al. 2004). Moreover, movements of jumbo squid within and outside the Gulf of California (Klett 1982; Ehrhardt et al. 1983; Markaida et al. 2005) are not considered in the current management strategy of the Mexican fishery.

The first works on squid age and growth were based in the modal frequency analysis (Hixon 1980; Ehrhardt et al. 1983; 1986). However, further studies have indicated that these analyses may not accurately predict length, because cephalopods, in general, have accelerated growth rates, large sizes, a short life span, partial spawning, and migratory behavior, which cause cohorts to overlap (Jackson and Choat 1992; Jackson et al. 2000). Since the 1980s, age and growth studies of squid have been performed using statolith growth increments from which individual age can be determined (Rodhouse and Hatfield 1990a).

Daily formation of growth increments in statoliths of *Dosidicus gigas* has not yet been confirmed, however, most studies that have validated age in other Ommastrephidae squid report a daily pattern (Dawe et al. 1985; Hurley et al. 1985; Lipiński 1986; Jackson et al. 1993; Lipiński et al. 1998). We thus assume that daily statolith increment deposition occurs in jumbo squid. Previous studies on jumbo squid aging through readings of statolith microstructure concluded that it lives between 1 and 2 years (Arkhipkin and Murzov 1986; Masuda et al. 1998; Markaida et al. 2004; Filauri 2005).

TABLE 1
Analysed statoliths from jumbo squid (*Dosidicus gigas*) caught off the western coast of Baja California, Mexico, during 2004.

Month	Both	Females	Males
January	67	56	11
April	15	11	4
July	41	32	9
October	68	45	23
Total	191	144	47

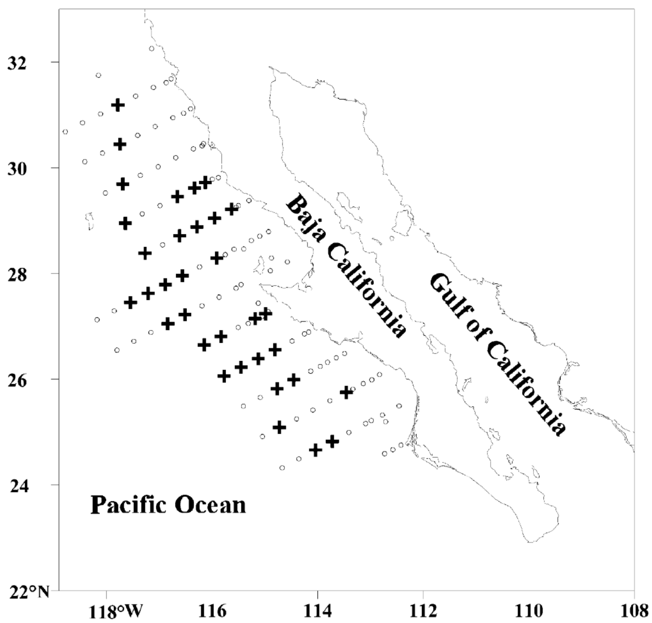

Figure 1. Grid sampling of oceanographic IMECOCAL cruises (circles) off western Baja California showing stations where jumbo squid (*Dosidicus gigas*) samples were caught in 2004 (crosses).

The aim of this work is to determinate the age and describe the growth of jumbo squid from the western coast of the Baja California peninsula using statolith increment counts.

MATERIALS AND METHODS

Jumbo squid were captured during four oceanographic cruises (tab. 1) off the western coast of Baja California during 2004 on board the BO *Francisco de Ulloa*. The cruises were developed within the IMECOCAL (Investigaciones Mexicanas de la Corriente de California http://imecocal.cicese.mx) program. The station network and the stations in which the analyzed specimens were captured are shown in Figure 1.

The squid were captured manually with jigs. Dorsal mantle length (ML) was measured to the nearest 5.0 mm. Sex was identified and reproductive condition evaluated according to the maturity scale of Lipiński and Underhill (1995): I-II (immature), III (maturing), IV-V (mature). Size-at-maturity groups were determined according to Nigmatullin et al. (2001): the small-sized group (males maturing at 130–260 mm ML, females at 140–340 mm ML), the medium-sized group (males maturing at 240–420 mm ML and females at 280–600 mm ML) and the large-sized group (males maturing at >400–500 mm ML and females at >550–650 mm ML). Squid heads were kept frozen until they were processed in the laboratory where statoliths were extracted and stored in 95% alcohol (Rodhouse and Hatfield 1990a).

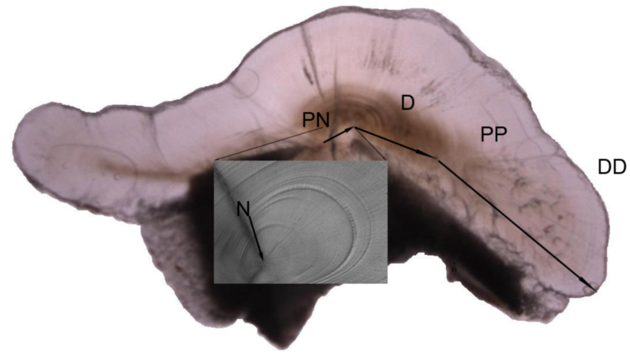

Figure 2. Growth zones in a jumbo squid (*Dosidicus gigas*) statolith between the nucleus (N) and the dorsal dome (DD): postnuclear (PN), dark (D), and peripheric (PP).

Statolith length (SL), the distance between the extreme parts of the dorsal dome and the rostrum, was measured to within 1.0 µm (Arkhipkin and Murzov 1986) using an image analysis system and Image Pro Plus (Version 4.5.29) software. Statoliths were mounted on microscopic slides, ground (1000–1500 grit waterproof sandpaper), and polished (0.3 µm alumina powder) on both sides. The ground statolith was then embedded in Canada balsam under a coverslip and left to dry overnight at 70°C, according to the Arkhipkin method (Dawe and Natsukari 1991).

Two readers conducted the statolith increment counts independently using an optical microscope with a polarized light filter at 40×. The number of increments for each growth zone, postnuclear, dark and peripheric, were counted from the nucleus up to the border of the dorsal dome of the statolith (fig. 2; Arkhipkin and Perez 1998). The age of each squid was calculated as the average of both reader counts. When the difference between counts was >10% the statoliths were read again until a consensus was reached (Pierce et al. 2001).

The utility of the statolith in describing the jumbo squid growth pattern was evaluated by fitting a linear regression of SL to ML data for each sex. Six growth models were fitted to age-ML data (Markaida et al. 2004) for each sex. The model with the largest coefficient of determination (r^2) and the least coefficient of variance

(CV) in estimated parameters was chosen to describe growth (Arkhipkin et al. 2000).

Comparisons among selected growth curves per sex were performed by an *F* test (Arkhipkin et al. 2000):

$$F = \frac{\left[\dfrac{(SS_t - SS_p)}{(m+1)(k-1)}\right]}{\left[\dfrac{SS_p}{DF_p}\right]}, \qquad (1)$$

$$DF_p = \sum_{t=1}^{k} n_t - k(m+1), \qquad (2)$$

where $(m+1)(k-1)$ and DF_p are the degrees of freedom, SS_t is the total residual sum of squares, SS_p is the pooled residual sum of squares for k compared regressions, m is the number of variables to estimate (two for the curves considered here), and DF_p is the pooled degrees of freedom.

Absolute daily growth rates (DGRs, mm) were calculated for each 20-day interval by sex (Arkhipkin and Mikheev 1992):

$$\mathrm{DGR} = \frac{ML_2 - ML_1}{\Delta T}, \qquad (3)$$

where ML_1 and ML_2 are the calculated MLs at the beginning and the end of each interval of time (ΔT = 20 days).

Jumbo squid hatching dates were obtained by subtracting the age from the date of capture (Campana and Jones, 1992). Squid were grouped by month and sex.

RESULTS

A total of 207 pairs of statoliths from 154 females and 53 males were collected. Statoliths were readable for 144 females and 47 males (tab. 1), which represented 92% and 87%, respectively, of the total sample. The size distribution of females indicated that at medium sizes (240–340 mm ML), they were mostly immature with a few maturing, and at large sizes (620–820 mm ML) were maturing and mature. Maturing and mature males were distributed into two size groups: medium (220–320 mm ML) and large (520–680 mm ML) (fig. 3).

The SL and ML relationship was highly significant ($r^2 = 0.89$, $p < 0.001$), indicating that growth is proportional in both variables and justifying the use of statoliths for describing the growth in ML of jumbo squid.

No significant differences were detected in the number of growth increments between the left and right statolith ($\chi^2 = 19.17$; d.f. = 20; $p > 0.05$), which validates using either statolith. Consequently, the right statolith was used in this study and, when not readable, the left was used.

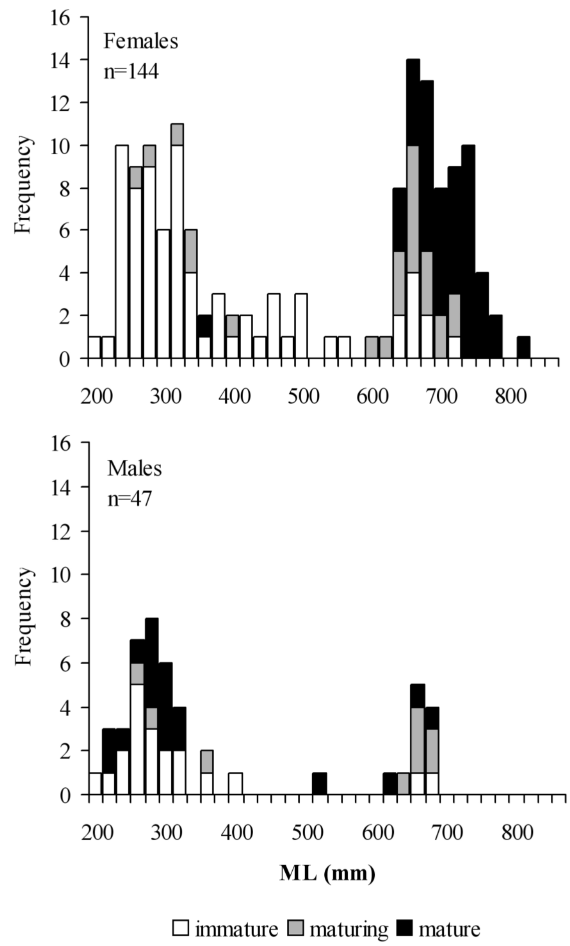

Figure 3. Mantle length (ML) frequency distribution by maturity stage and sex for jumbo squid (*Dosidicus gigas*) caught off the western coast of Baja California during 2004.

Age

The youngest male was 125 days old (at 210 mm ML) and immature; the oldest male was 391 days old, and was mature at 690 mm ML. The youngest female was 105 days old (at 240 mm ML) and immature; the oldest female was 433 days old (at 700 mm ML) and mature; and the largest female (830 mm ML) was 425 days old and mature.

Growth

The model that best fit age-ML data was the logistic model for both sexes ($r^2 = 0.98$, CV% 3.15 for females; $r^2 = 0.97$, CV% 7.4 for males) (fig. 4). The difference between the growth curves of both sexes was highly significant ($F_{3,182} = 2.25$, $p < 0.001$) (tab. 2). The asymptotic MLs calculated by the model were $Y\infty = 877.5$ mm ML for females and $Y\infty = 792.1$ mm ML for males.

TABLE 2
Statistical comparison of jumbo squid (*Docidicus gigas*) growth curves between sex and areas, western coast of BC (WC) 2004 and Gulf of California (GC) 1995–1997, from the logistic growth model. *n* = number of squid; RSS = residual sum of squares; RMS = residual mean square. Data are from Markaida et al. (2004).

	n	RSS	RMS	*F*	*p*
WC					
Females	142	1255.39	8.90	$F_{3,182}$ = 2.2591	$p < 0.001$
Males	46	328.49	7.46		
Females					
WC	142	1255.39	8.90	$F_{3,383}$ = 51.50	$p < 0.001$
GC	247	489250	2005		
Males					
WC	46	328.49	7.46	$F_{3,173}$ = 12.24	$p < 0.001$
GC	133	236077	1815		

Growth was larger for female jumbo squid; at 15 months old, females reached 767 mm ML and males 732 mm ML. Differences in growth between squid from the Gulf of California (Markaida et al. 2004) and from off the western coast of Baja California were highly significant for both sexes (tab. 2).

Age-size relationship at maturity

Squid from the medium size group were younger than squid from the large size group. Medium-sized females maturing and mature at 260–400 mm ML were 105 to 205 days old. Large females (>600 mm ML) were mostly mature at >350 days old (fig. 4). Medium-sized mature males (<400 mm ML) were <200 days old. Males from the large size group (>600 mm ML) were mostly maturing and >350 days old (fig. 4).

Growth rate

The daily growth rate (DGR) of ML (fig. 5) in young females (100 days) was 1.46 mm per day at 201 mm ML, while the maximum DGR (1.97 mm per day) was found in females 220 days old (409.4 mm ML). After this age, DGR decreased gradually to a minimum of 0.87 mm per day in squid 440 days old (758 mm ML). The DGR in young males (100 days old) was 1.57 mm per day at 181 mm ML. Maximum DGR for ML was 2.1 mm per day (at 200 days) at 365.9 mm ML; as squid aged, DGR decreased to a minimum of 0.59 mm per day (at 440 days and 726 mm ML). In general, jumbo squid from off the western coast of Baja California grow rapidly during the first 200 days, after which growth decreases gradually. Differences in growth by sex are evident when comparing DGR at similar ages; at 120 days, females grow slower (1.59 mm per day ML) than males (1.73 mm per day ML). The point of inflection in the DGR curve indicates that males reach their maximum growth rate before females. Finally, the decrease in DGR after the point of inflection is more accelerated in males (0.70 mm per day at 420 days) than in females (0.99 mm per day at 420 days).

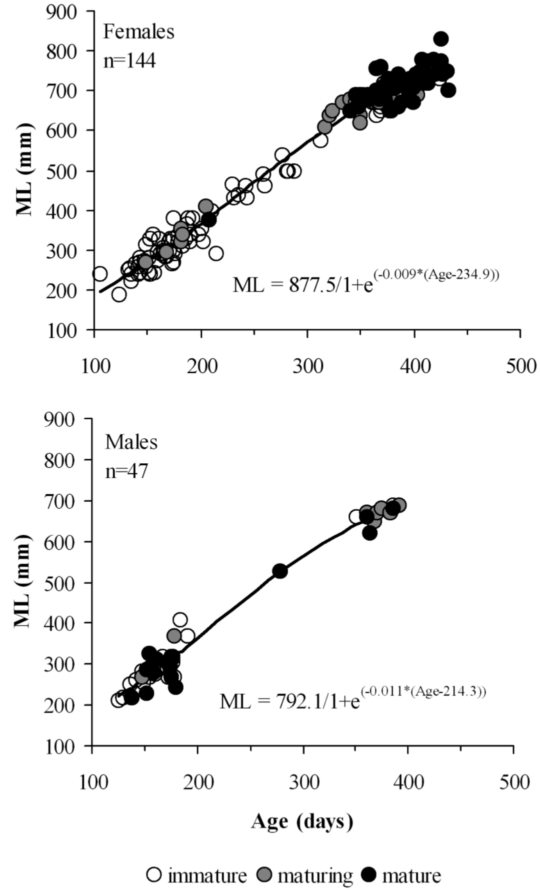

Figure 4. Relationship between age and mantle length (ML) and logistic growth curves for jumbo squid (*Dosidicus gigas*) caught off the western coast of Baja California during 2004.

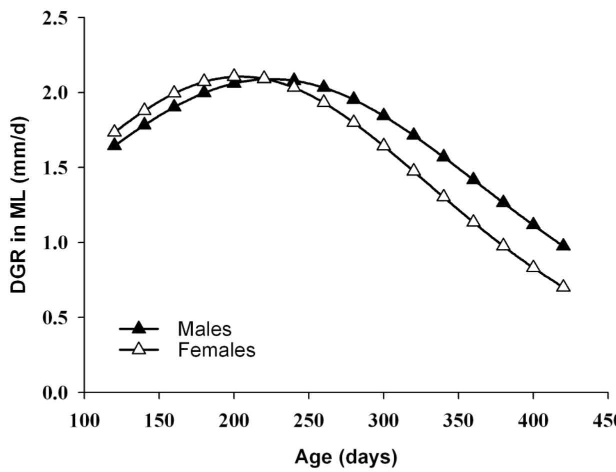

Figure 5. Daily growth rates (DGR) in mantle length (ML) (mm/d) of jumbo squid (*Dosidicus gigas*).

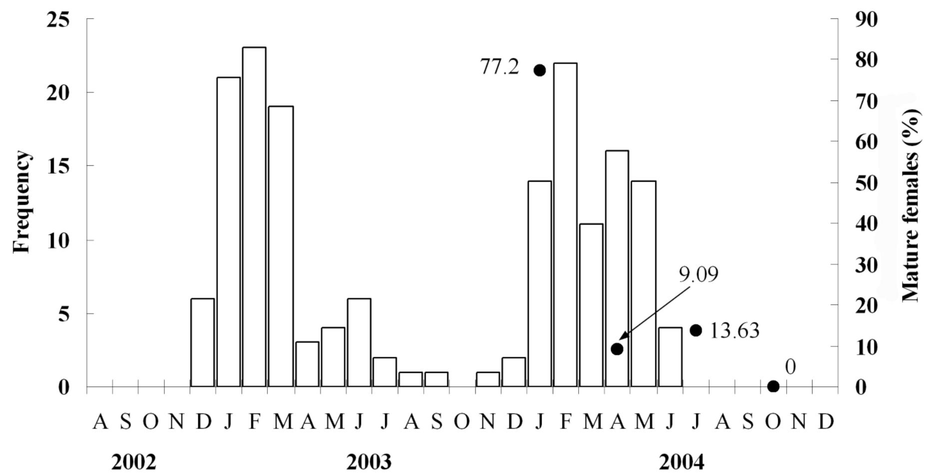

Figure 6. Monthly hatch date frequency distribution (bars, left axis) and percentages of mature female (dots, right axis) jumbo squid (*Dosidicus gigas*) caught off western coast of Baja California during 2004.

Hatching time

Jumbo squid hatch dates occurred from December 2002 to June 2004 and hatching modes occurred between January and March for 2003 and 2004 (fig. 6). In 2004, the hatching period extended to June. In January 2004, 77.2% of the females were mature which coincides with the beginning of the hatching season. Low mature female proportion in April 2004, however, did not correspond with the end of that hatching season.

DISCUSSION

Age

Maximum calculated ages from this study (433 days for females and 391 days for males) are similar to those in which jumbo squid between 1 and 1.5 years old were aged using statoliths (Arkhipkin and Murzov 1986; Masuda et al. 1998; Yatsu 2000; Markaida et al. 2004; Filauri 2005). In the Gulf of California, Markaida et al. (2004) found maximum ages of 442 days for females and 372 for males, similar to Filauri (2005) with ages of 450 and 385 days, respectively.

Growth

Accelerated growth and a short life span (0.5–2 years) are characteristic of most cephalopods. Growth differs between sexes, year, geographic area, and ontogenetic stage (Rodhouse and Hatfield 1990b; Yatsu 2000; Boyle and Rodhouse 2005). Factors which influence growth are: high rate of food consumption with a high capacity of converting energy into somatic growth (Boyle and Rodhouse 2005), a high temperature which accelerates growth rate, and migratory activity that limits potential energy for growth.

Different models have been used to describe subadult and adult jumbo squid growth, such as the von Bertalanffy in-size modal-distribution analysis (Ehrhardt et al. 1982; 1986), lineal (Masuda et al. 1998; Yatsu 2000), exponential, including juveniles (Arkhipkin and Murzov 1986), and logistic models (Markaida et al. 2004; Filauri 2005). The logistic model has also been used to describe the growth of other Ommastrephidae squid species (Arkhipkin and Silvanovich 1997; Arkhipkin et al. 1999; Arkhipkin et al. 2000). This study, however, was limited by the lack of intermediate-sized males (400–600 mm ML) to adequately complete their growth curve.

Comparison of growth curves

Males of the squid family Ommastrephidae start maturing before females, leading to a differential growth between sexes; thus females reach larger sizes (Arkhipkin and Murzov 1986; Rodhouse and Hatfield 1990b; Arkhipkin 2004; Markaida et al. 2004). Masuda et al. (1998), however, found statistically sexual differences in growth in only one out of three seasons analyzed.

Squid born in different seasons and areas experience different conditions, such as temperature and food availability, which influence their growth and can lead to temporal and spatial differentiations (Arkhipkin et al. 2000; Arkhipkin 2004). In squid from the Gulf of California (Markaida et al. 2004) and from off the western coast of Baja California, the growth rate differed between sexes. Squid from the Gulf of California, regardless of sex, grow more rapidly than squid from off western Baja California. Arkhipkin et al. (2000) also found differences in growth of the squid *Illex coindetii* from two different areas. Differences in growth in squid born during different seasons have also been observed, supporting our hypothesis that squid are influenced by seasonally oceanographic conditions (Masuda et al. 1998; Argüelles et al. 2001; Markaida et al. 2004). However, squid are a short-lived species sensitive to spatial and temporal variations. Therefore, the differences in growth we found between samples from the Gulf of California and off western Baja California collected with nearly a decade of separation may be an artifact of environment, year, etc., rather than due to location.

Growth rate

Growth rate is the proportion of increase in weight or length during an interval of time, and varies according to corporal dimensions (size or weight), age, sex, season, number of cohorts, geographic area, and hatching year (Arkhipkin and Perez 1998; Boyle and Rodhouse 2005). DGRs calculated for jumbo squid from the Gulf of California using statolith analysis range from 2 to 2.65 mm per day ML for squid 84 to 386 days old (108 mm to 875 mm ML) (Markaida et al. 2004) and from 1.47 to 2.26 mm per day ML for squid 158 to 450 days old (230 to 910 mm ML) (Filauri 2005). Both estimates are higher than our DGRs for squid of similar ages from off the western coast of Baja California (0.99–2.10 mm per day). Maximum DGRs for squid from the Gulf of California were 2.65 mm per day ML (230–250 days) in females and 2.44 mm per day ML (210–230 days) in males (Markaida et al. 2004). Thus, squid from the Gulf of California grow at a faster rate than those caught off western Baja California. However, jumbo squid tagging and recapture experiments in the Gulf of California yielded smaller DGRs of 1.0–1.5 mm per day at 500–700 mm ML (Markaida et al. 2005). This suggests that the longevity estimates given above might be underestimated.

In general, jumbo squid have higher growth rates than other squid of the Ommastrephidae family: 0.3–1 mm per day ML for *Illex illecebrosus* (Arkhipkin and Fetisov 2000), and 0.8–0.9 mm per day ML in *Todarodes pacificus* (Jackson and Choat 1992).

Hatching time

Counts of statolith growth increment allows hatching dates to be backcalculated. The presence of both a large number of hatching dates and a high proportion of mature individuals indicates massive spawning periods (Bigelow and Landgraf 1993). In the central Gulf of California multiple reproductive peaks have been identified for jumbo squid using modal distribution analysis (Ehrhardt et al. 1983; 1986; Klett-Traulsen 1996; Hernández-Herrera et al. 1998). Statolith analysis work in the same area did not identify reproductive peaks and suggests that jumbo squid reproduce all year in the Gulf of California (Markaida et al. 2004; Filauri 2005). In this study, we identified a hatching season of January–March for 2003 and 2004. While the sampling of only four months in a year limits our assumptions, this seasonality agrees with the reproductive peak described by Ehrhardt et al. (1983) in winter off the southwestern coast of Baja California.

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