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A.

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## RESEARCH ARTICLE

Growth models fitted to *Dipturus chilensis* length-at-age data support a two-phase growthModelos de crecimiento ajustados a datos de largo a la edad de *Dipturus chilensis* confirman un crecimiento en dos fasesMARINA I. AVERSA<sup>1,\*</sup>, SILVANA L. DANS<sup>1,2</sup>, NÉSTOR A. GARCÍA<sup>1</sup> & ENRIQUE A. CRESPO<sup>1,2</sup><sup>1</sup>Laboratorio de Mamíferos Marinos, Centro Nacional Patagónico, CONICET, Boulevard Brown 2825 (CP9120) Puerto Madryn, Chubut, Argentina<sup>2</sup>Universidad Nacional de la Patagonia San Juan Bosco, Boulevard Brown 3700 (CP9120) Puerto Madryn, Chubut, Argentina

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## ABSTRACT

Age and growth for the beaked skate was estimated from bands in the vertebral centra of 689 individuals obtained from incidental catches of the Argentine hake (*Merluccius hubbsi*) fishery. Age bias plots and indices of precision indicated that ageing method was precise and unbiased (% CV = 3 % PA = 82.09 %). Edge and marginal increment analysis of the vertebrae support the hypothesis of annual band pair deposition. Three growth models were fitted to length-at-age and the two-phase growth model produced the best fit. This feature has never been described before for *D. chilensis* and can be related to changes in energy allocation and the shift from juvenile to adult phase. The unrealistic biological estimates of the von Bertalanffy growth model illustrates the importance of fitting alternative models to the data. Female beaked skates reached greater size in length ( $L_{\infty}$ ) as well as in disc width ( $L_{\infty}$  = 138.2 cm;  $DW_{\infty}$  = 92.46 cm) and have lower growth rate ( $k$  = 0.08 yr<sup>-1</sup>) than males ( $L_{\infty}$  = 106.7 cm;  $DW_{\infty}$  = 74.52 cm;  $k$  = 0.121 yr<sup>-1</sup>). This study provides basic information on age and growth for the beaked skate, *D. chilensis*, which were previously not available for its south Atlantic range of distribution.

**Key words:** beaked skate, *Dipturus chilensis*, growth, two-phase growth.

## RESUMEN

La edad y el crecimiento de la raya picuda fue estimado a partir de las bandas en los cuerpos vertebrales de 689 individuos obtenidos de las capturas incidentales de la pesquería de merluza argentina (*Merluccius hubbsi*). Gráficos de sesgos y el análisis de precisión indicaron que el método utilizado para la determinación de la edad es preciso y no sesgado (% CV = 3 % PA = 82.09 %). El análisis del tipo de borde e incremento marginal vertebral confirmó la hipótesis del depósito anual de un par de bandas. Se ajustaron tres modelos de crecimiento a los datos de largo a la edad y el modelo de dos fases produjo el mejor ajuste. Esta característica nunca antes fue descripta para *Dipturus chilensis* y podría relacionarse con un cambio en la cuota de energía y el paso de la fase juvenil a la adulta. Las estimaciones obtenidas con el modelo de Von Bertalanffy resultaron biológicamente irrealistas, lo que demuestra la importancia de ajustar modelos alternativos a los datos. Se observó que las hembras alcanzan tallas ( $L_{\infty}$  y  $DW_{\infty}$ ) más grandes ( $L_{\infty}$  = 138.2 cm;  $DW_{\infty}$  = 92.46 cm) y tienen tasas de crecimientos más bajas ( $k$  = 0.08 yr<sup>-1</sup>) que los machos ( $L_{\infty}$  = 106.7 cm;  $DW_{\infty}$  = 74.52 cm;  $k$  = 0.121 yr<sup>-1</sup>). Este estudio provee información básica de edad y crecimiento de la raya picuda, *Dipturus chilensis*, en el Atlántico sur de su rango distribución, la cual no estaba anteriormente disponible.

**Palabras clave:** crecimiento, crecimiento en dos fases, *Dipturus chilensis*, raya picuda.

## INTRODUCTION

The beaked skate *Dipturus chilensis* (Guillenot, 1848) is found along the Atlantic and Pacific coasts of South America. It has been reported to be one of the most abundant species of the Family Rajidae in northern and central Patagonian waters (Menni & Gosztanyi 1982, Menni & López 1984, García de la Rosa

1998). This species, together with other elasmobranchs, seabirds and marine mammals was usually taken as by-catch in the bottom-trawling fishery for the Argentine hake *Merluccius hubbsi* (Gosztanyi 1984, Coscarella 1997, Caille et al. 1997, Crespo et al. 1998). From the 80's until the mid 90's it was discarded with other components of the by-catch but by the end of the decade, the species

became a valuable commodity for exporting fishing companies. In the last few years, together with other species, the beaked skate increased its commercial value as a consequence of the decline of the Argentine hake captures and the development of new Asian markets for elasmobranch fins (Massa et al. 2001, 2004; Licandeo et al. 2006).

Elasmobranchs have various reproductive characteristics like delayed maturity, large energy investment in relatively few young and reproduce every one to two years, which means slow rates of replacement within population. Studies on the beaked skate during the 90's have been focused on life history parameters, in particular on sexual maturity and feeding habits (Bahamonde 1950, Koen Alonso et al. 2001, García de la Rosa 1998). Although size at first maturity has been described, age-specific fecundities and growth rates are not known, therefore, there is a lack of essential information for its management and conservation. With regard to diet studies, two important shifts were found related to over fishing in the Patagonian shelf. The first one is a change in the predatorial behavior from benthic to demersal-benthic preys, occurring at about 35 cm total length, at which consumption of a new class of prey item becomes possible. The second shift, from demersal-benthic to demersal-pelagic coincides with sexual maturation and probably is part of a larger behavioral response to maturation (Koen Alonso et al. 2001).

The knowledge of growth rates and age-specific fecundities is critical to adequately assess the impact of fishery exploitation and development of management procedures. Elasmobranchs cannot be aged using traditional fish ageing methods since they lack calcified structures (Cailliet et al. 1983). However, the most outstanding research on age determination of elasmobranchs has analyzed the opaque and translucent bands in calcified vertebral centra. Several techniques have been developed to enhance these bands so they can be easily counted (Cailliet et al. 1983, Stevens 1975, Casey et al. 1985, Ferreira & Vooren 1991). In addition, there are various methods to verify the temporal periodicity of bands formation (Holden & Vince 1973).

Age and growth rates from the beaked skate have already been study in the Pacific

range of its distribution (Fuentealba & Leible 1990, Gilli et al. 1999, Licandeo et al. 2006). With respect to its range of distribution in the Atlantic Ocean an estimation of the size at maturity and other reproductive aspects have been provided for the region between 31°00' and 39°30' S (Paesch & Oddone 2008). Since that, age and growth parameters can vary among regions and differences in life history trait have already been reported for the beaked skate along its distribution in the fjords and channels of southern Chile (Licandeo & Cerna 2007), age and growth information for *Dipturus chilensis* from Patagonia waters is necessary for population assessment of this species in this region.

In view of this background, the objective of this study was to estimate the age of *D. chilensis* captured by *Merluccius hubbsi* fishery vessels and compare different growth models to determine which model provides the best fit.

## METHODS

### *Study area and field work operations*

Beaked skates were collected onboard commercial vessels of the Argentine hake fishery where they are usually caught as by-catch. The bottom-trawling fishery for the Argentine hake operates in northern and central Patagonian waters (41°00'-46°45' S and 58°00'-65°00' W) (Fig. 1). Samplings of commercial catches were carried out between 1997 and 2007 depending on the fishery company availability thus there is no continuous record over all months and years.

On board, all skates were sexed, sized and weighed. Total length ( $L_T$  in cm) and disc width ( $DW_T$  in cm) were used as standard measurements of the beaked skate size for growth estimation.

### *Age determination*

A section of the vertebral column including the first 20 vertebral centra were removed from each specimen and kept frozen. For examination, vertebrae were defrosted with subsequent removal of connective tissue and the neural arch. The diameter of the vertebral centra was measured with an electronic caliper. The technique used to enhance the vertebral bands has produced satisfactory results with aging of marine mammals and some elasmobranch species (Crespo et al. 1994). This technique involved the examination of a stained section under transmitted light with a dissecting microscope. Each vertebra was previously decalcified in 5 % nitric acid solution between 30 minutes and 4 hours and then, rinsed in running tap water over a 24 hours period, and finally cut to 40  $\mu$ m sagittal sections using a freezing microtome (Fig. 2A). Sections were stained with Mayer's Haematoxylin and then mounted on glass slides. A dissecting microscope was used for measuring and counting vertebral bands.

The growth pattern of the vertebrae included an opaque and a translucent band that extended from the intermedialia to the corpus calcareum (Fig. 2B). Age estimation was done enumerating the opaque bands. The birth mark was identified as the first one near the focus following an angle change of the centrum.

Vertebral radius was measured from the focus to the distal margin of the corpus calcareum. A linear regression of total length (and disc width) as function of the vertebral radius was fitted for females and males, to determine if the structure was appropriate for estimating growth rate of the animal. The regression line for females was compared to that for males using an analysis of covariance (ANCOVA).

#### Age assessment and verification

The senior author read the number of observed bands twice without knowledge of the size and sex of each specimen. Age consensus was achieved when the two age estimates agreed, or with a third additional reading. If no consensus was reached the sample was discarded. Aging bias and precision of the resulting age estimates were examined using aged bias-plot and the coefficient of variation (Campana et al. 1995). Additionally, the percent agreement based on consensus counts was determined following Goldman (2004). Individuals were divided into 5-cm length

increment groups and perfect agreement and agreement plus or minus 1 year were calculated.

Two indirect verification types of analysis were used to validate periodicity of band formation: Centrum Edge Analysis and Marginal Increment Analysis (Cailliet et al. 2006). The former involves the qualitative characterization of the margin of the vertebrae in two distinct edge classes based on optical qualities (opaque or translucent). The marginal increment analysis was used as a quantitative assessment of band deposition following Conrath et al. (2002):  $MIR = MW / PBW$  where MW is the margin width, PBW is the width of the penultimate band pair (Fig. 2B). Mean monthly marginal increment ratios were calculated and potential differences between months of capture were compared with non parametric Kruskal-Wallis test by ranks. To carry out this analysis, skate specimens were collected on a monthly basis during one year from commercial landings of bottom trawlers for Argentinean hake *Merluccius hubbsi* and were handed over by the fishery company (Alpesca S.A.).

#### Study of growth

Three alternative growth curves were fitted for males and females length at age data. The traditional von Bertalanffy, the Gompertz, and a two phase growth model (TPGM) equations:

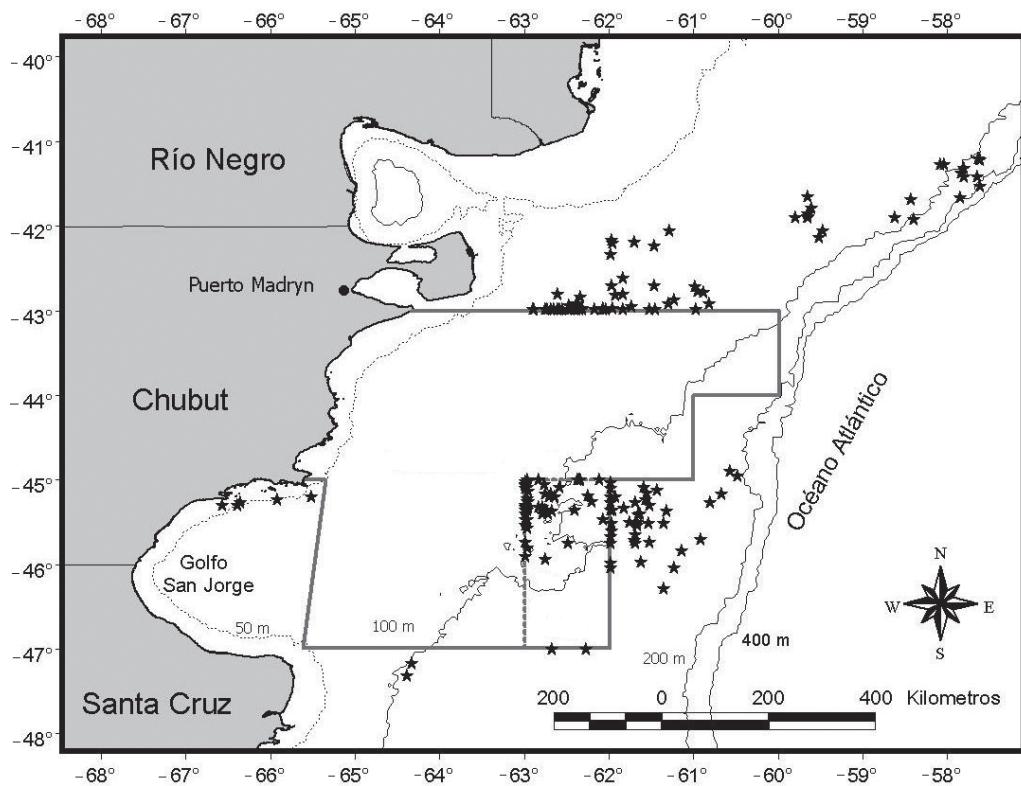


Fig. 1: Sampling zone for *D. chilensis*, showing where the bottom-trawling fishery for the Argentine hake *Merluccius hubbsi* operates. (\*) Symbols signify *D. chilensis* by-catch locations. The area where *Merluccius hubbsi* fishing is forbidden is distinguished by a square.

Zona de muestreo para *D. chilensis*, mostrando donde opera la pesquería de arrastre de fondo para merluza argentina *Merluccius hubbsi*. Los símbolos (\*) indican los lugares puntuales donde se capturaron *D. chilensis* como fauna acompañante de la pesquería. El área de veda de pesca de *Merluccius hubbsi* está marcada por las líneas que forman un cuadrado.

$$L_T = L_\infty e^{(-c_0 e^{-kt})} \quad DW_T = DW_\infty e^{(-c_0 e^{-kt})}$$

Gompertz

$$L_T = L_\infty (1 - e^{-k(t-t_0)}) \quad DW_T = D_\infty (1 - e^{-k(t-t_0)})$$

Von Bertalanffy

$$L_T = L_\infty (1 - e^{-k A_T (t-t_0)}) \quad DW_T = DW_\infty (1 - e^{-k A_T (t-t_0)})$$

Two Phase Growth model

where  $L_T$  and  $DW_T$  are the total length and the disc width at time  $t$  respectively;  $L_\infty$  and  $DW_\infty$  is the theoretical maximum total length/disc width or asymptotic length/disc width;  $k$  is the rate at which  $L_\infty$  is approached,  $c_0$  is the proportionality constant and  $t_0$  is the theoretical age at zero length (Ricker 1979). The two phase growth model is a variation of the von Bertalanffy model by Soriano et al. (1992) where  $A_T$  is a factor that modifies  $k$  when the age is increased and is given by:

$$A_T = 1 - \frac{h}{(t - t_h)^2 + 1}$$

where  $t_h$  is the age which the transition of the two phases occurs and  $h$  determines the magnitude of the maximum difference in length at age data between the Von Bertalanffy and the Two Phase Growth Model in the  $t_h$  point.

Growth equation parameters were calculated using maximum likelihood estimation. Slopes of growth estimates of males and females were tested using the maximum likelihood test (Kimura 1980, Cerrato 1990).

The Akaike's information criterion (AIC) was applied in order to rank the growth models by their ability to give the most parsimonious explanation of observed length and disc width at age data. The difference between the AIC with the higher number of parameters and the model with fewer parameters ( $\Delta AIC$ ) allows the calculation of the Akaike weight ( $w_i$ ) which represents the probability of choosing the correct model from the set of candidate models and is calculated as:

$$w_i = \frac{\exp(-\Delta AIC/2)}{\sum_{r=1}^R \exp(-\Delta AIC/2)}$$

where  $R$  is the number of candidate models.

Theoretical longevity ( $\omega$ ) was estimated as the age at which 99 % of the  $L_\infty$  (or  $DW_\infty$ ) was attained ( $7 * (\ln 2)/k$ ) (Fabens 1965); as the age at which 95 % of the  $L_\infty$  (or  $DW_\infty$ ) was reached ( $5 * (\ln 2)/k$ ) (Ricker 1979).

## RESULTS

### Age determination

A total of 796 beaked skates vertebrae were examined during this study, 105 vertebrae were considered unreadable and were discarded. Females ranged in size from 19 to 134 cm  $L_T$  ( $n = 319$ ), while males ranged from 28.7 to 101 cm  $L_T$  ( $n = 369$ , Fig. 3). Age estimates ranged from 3 to 24 for females and 3 to 17 for males. The 0-2 classes were not observed and consequently were absent in the sample.

The staining technique provided good enhancement of vertebral rings and allowed for repeatable and consistent bands counts. The bands were generally clearer along the corpus calcareum than the intermedialia, but the entire section was examined when making the band count. Vertebral centra for older skates tended to show marginal band crowding, which potentially resulted to underestimate de number of rings.

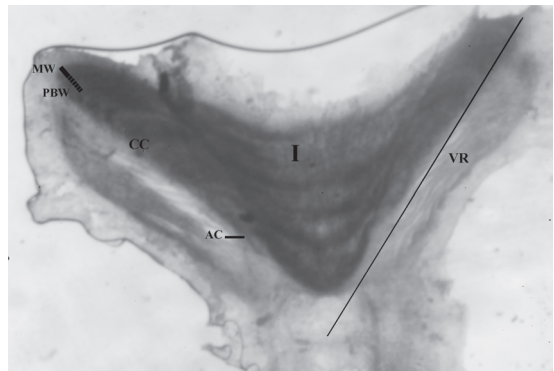
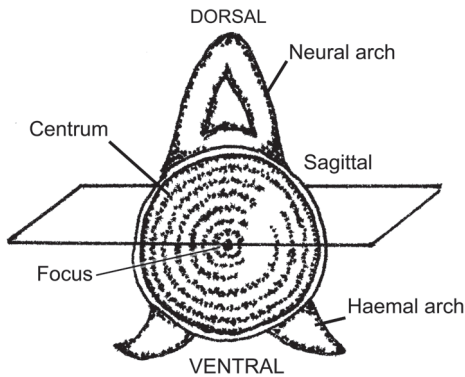


Fig. 2: (A) Sectioning plane used on *D. chilensis* vertebral centra. (B) *D. chilensis* vertebra showing the calculation of the marginal increment ratio. MW = Margin width; PBW = Previous band width; AC = Angle change indicating birthmark; VR = Vertebral radius; CC = Corpus calcareum; I = Intermedialia

(A) Plano de corte utilizado en las vertebrae de *D. chilensis*. (B) Vértebra de *D. chilensis* mostrando el cálculo de la relación de incremento marginal. MW = Ancho del margen; PBW = Ancho de la banda previa; AC = Cambio de ángulo indicando la marca de nacimiento; VR = Radio vertebral; CC = Corpus calcareum; I = Intermedialia.



Relationships between total length ( $L_T$ ) and vertebral radius ( $V_R$ ) and disc width ( $DW$ ) and vertebral radius ( $V_R$ ), for females and males were not significantly different (ANCOVA,  $n = 124$ ,  $P > 0.05$ ) therefore, these data were combined into a single regression. Both relationships,  $L_T$  vs.  $V_R$  and  $DW$  vs.  $V_R$ , were non-linear and a natural logarithm transformed data provided a better linear fit passing through the origin (Fig. 4A, 4B).

#### Age assessment and verification

To test for precision, a subsample of 234 vertebrae was read. Count comparisons between readings indicated no bias (Fig. 5). The coefficient of variation (% CV) was around 3 % which is a high level of precision. Percentage agreement between the two sets of band counts was 82.06 % exact counts and 96.86 % within one band (Table 1).

To assess the temporal periodicity of band deposition, edge marginal analysis was conducted on 126 samples that were determined to have unambiguous edge types. The proportion of edge types varied among all months examined (Fig. 6). While a high proportion of opaque edges were observed during summer (December, February) and fall (March, May) months, most of the samples collected during winter (July, August) and

spring months (September, October, November) showed translucent edges. Opaque edges were correlated with the season average sea surface temperature for the area where the Argentine hake fishery operates. A higher proportion of opaque edges corresponded with the highest sea surface temperatures, while translucent edges were more frequent at lower sea surface temperature (Fig. 6).

Mean MIR ratios were calculated from 110 beaked skate vertebrae collected during a year. The sample was not large enough to plot the age groups separately, so monthly mean marginal increments were combined. The marginal increment tended to decrease from February onwards showing a minimum seasonal increment during October; and increased sharply during November (Fig. 7). There were significant differences in the marginal increment analysis (MIR) between months (Kruskal-Wallis test:  $H(8, N = 110) = 58.85230$ ,  $P < 0.0001$ ). Contrast 'z' comparisons found that September and October were significantly different from February, March, May and December ( $P < 0.05$ ).

#### Study of growth

While the von Bertalanffy (VBGM) provided the worst fit to the length-at-age data, the two phase growth model (TPGM) was the best

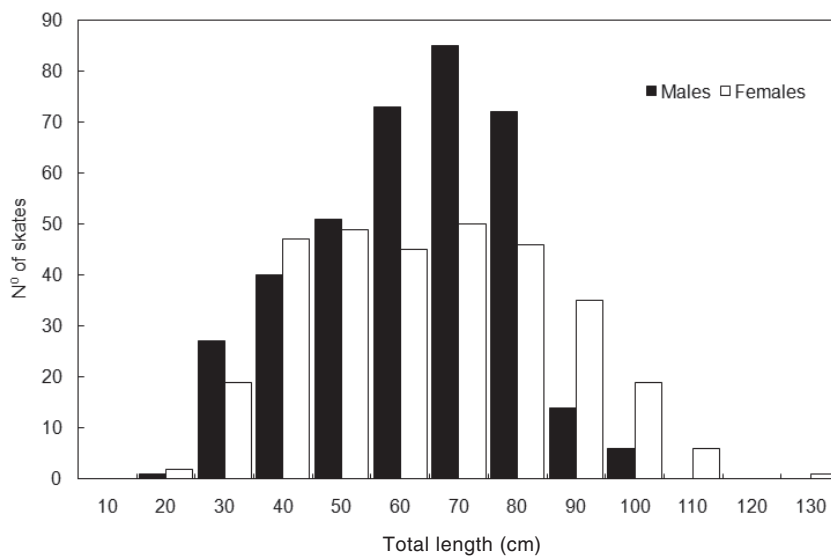
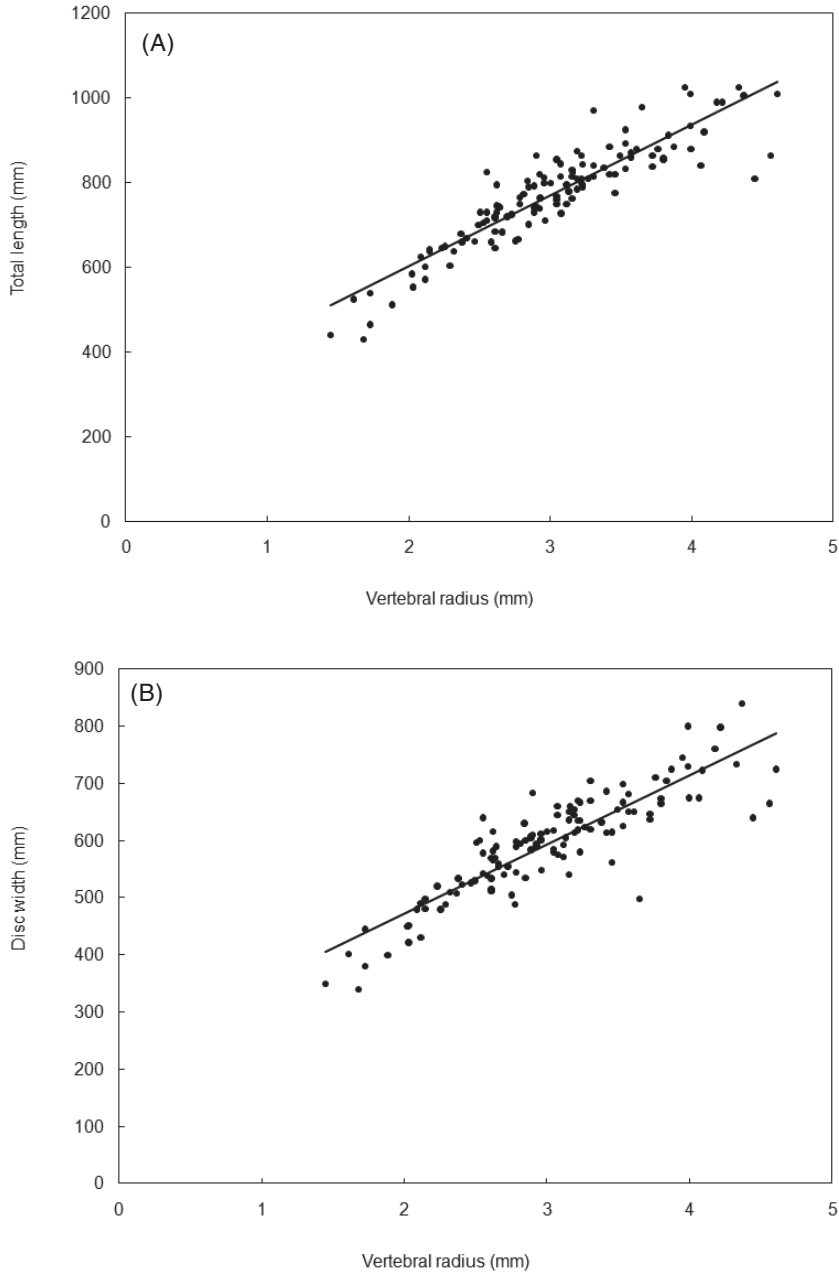


Fig. 3: Total length frequency of females and males beaked skate *D. chilensis*.

Frecuencias totales de hembras y machos de raya picuda *D. chilensis*.

among the growth equations fitted, with an Akaike weight ( $w_i$ ) of 0.99 (Table 2). Estimates of the asymptotic length or disc width varied depending on the model. The VBGM produced estimates of  $L_\infty$  and  $DW_\infty$  greater than the maximum sizes collected

during this study ( $L_\infty = 151.38$ ;  $DW_\infty = 139.35$ ). While estimates of  $L_\infty$  and  $DW_\infty$  using Gompertz (GGM) and the two phase growth equation (TPGM), were similar to the maximum sizes for both sexes observed in this study (Table 2).



**Fig. 4:** (A) Relationship between total length and vertebral radius for both male and female *D. chilensis* used in this study. The curve was fitted by  $L_T = 364.48 V_R^{0.683}$ . (B) Relationship between disc width and vertebral radius for both male and female *D. chilensis* used in this study. The curve was fitted by  $D_W = 296.1 V_R^{0.635}$ .

(A) Relación entre el largo total y el radio vertebral para machos y hembras de *D. chilensis* utilizados en este estudio. La curva ajustada fue  $L_T = 364.48 V_R^{0.683}$ . (B) Relación entre el ancho de disco y el radio vertebral para machos y hembras de *D. chilensis* utilizados en este estudio. La curva ajustada fue  $D_W = 296.1 V_R^{0.635}$ .

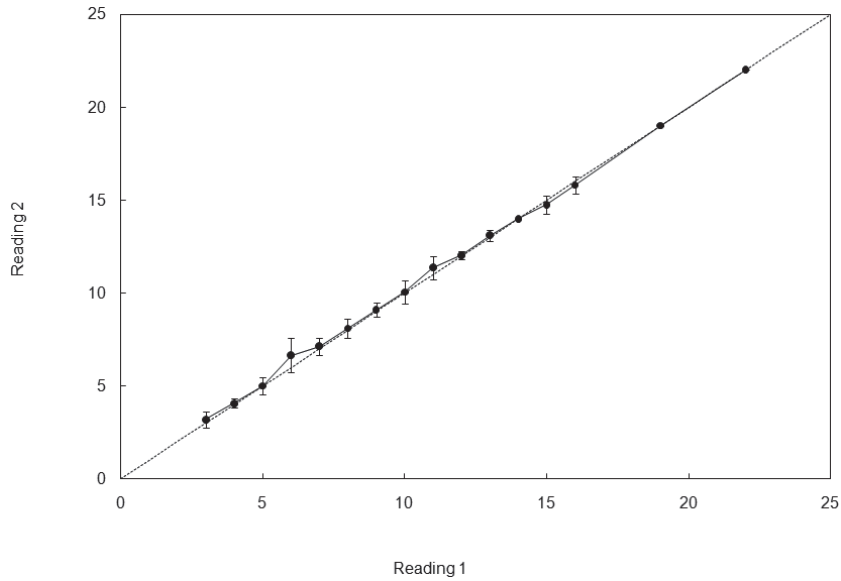


Fig. 5: Age bias plot for pair-wise comparison vertebral counts of beaked skates, *D. chilensis*. The one-to-one equivalence line is also presented.

Gráficos de las comparaciones entre los pares de lecturas de la raya picuda, *D. chilensis*. También se presenta la línea de equivalencia uno a uno.

TABLE 1

Percentage agreement (PA) between consensus band-pair counts.

Porcentaje de coincidencia (PA) entre los pares de bandas contabilizados.

| Size group<br>(cm) | Total vertebrae<br>read | N° of vertebrae<br>aged in agreement | N° of vertebrae aged<br>in agreement $\pm 1$ year | % PA  | % PA $\pm 1$ year |
|--------------------|-------------------------|--------------------------------------|---|-------|-------------------|
| 25.1-30            | 2                       | 2                                    | 2   | 100   | 100               |
| 30.1-35            | 13                      | 12                                   | 13  | 92.31 | 100               |
| 35.1-40            | 5                       | 5                                    | 5   | 100   | 100               |
| 40.1-45            | 5                       | 3                                    | 4   | 60    | 80                |
| 45.1-50            | 5                       | 5                                    | 5   | 100   | 100               |
| 50.1-55            | 11                      | 10                                   | 11  | 90.91 | 100               |
| 55.1-60            | 20                      | 14                                   | 16  | 70    | 80                |
| 60.1-65            | 23                      | 17                                   | 23  | 73.91 | 100               |
| 65.1-70            | 18                      | 15                                   | 18  | 83.33 | 100               |
| 70.1-75            | 29                      | 24                                   | 29  | 82.76 | 100               |
| 75.1-80            | 20                      | 17                                   | 20  | 85    | 100               |
| 80.1-85            | 24                      | 19                                   | 24  | 79.17 | 100               |
| 85.1-90            | 12                      | 10                                   | 11  | 83.33 | 91.67             |
| 90.1-95            | 11                      | 11                                   | 11  | 100   | 100               |
| 95.1-100           | 9                       | 5                                    | 8   | 55.56 | 88.89             |
| 100.1-105          | 6                       | 6                                    | 6   | 100   | 100               |
| 105.1-110          | 6                       | 5                                    | 6   | 83.33 | 100               |
| 110.1-115          | 4                       | 3                                    | 4   | 75    | 100               |
| Total              |                         |                                      |   | 82.06 | 96.86             |



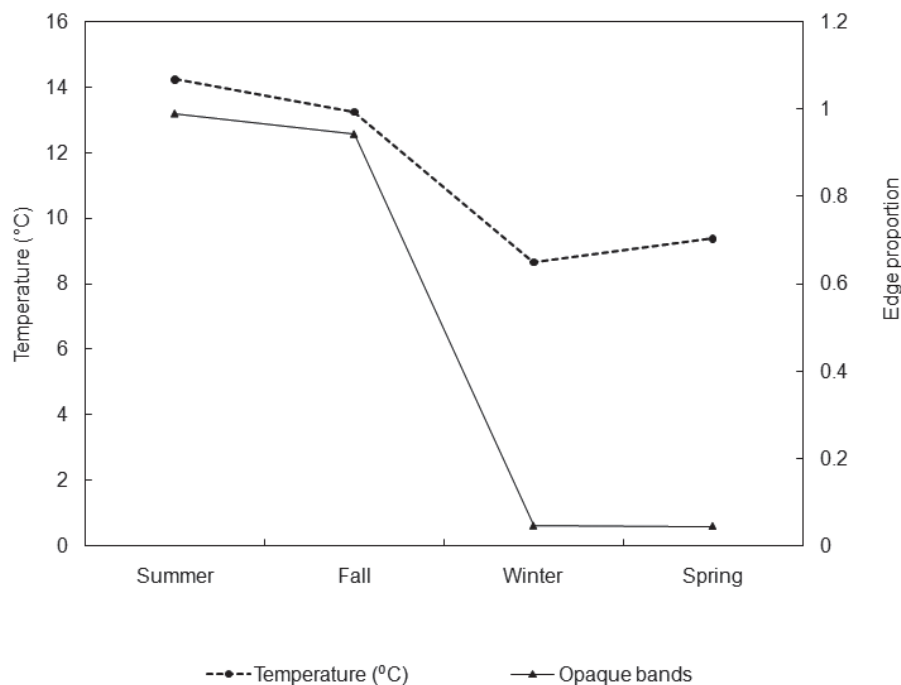


Fig. 6: Seasonal variation in centrum edge type ( $\blacktriangle$ ) from vertebral sections containing 8 to 14 growth rings in *D. chilensis*. Seasonal mean sea surface temperature ( $\bullet$ ) from the area where Argentine hake fishery operates.

Variaciones por temporadas en el tipo de margen del centrum ( $\blacktriangle$ ) en las secciones vertebrales con 8 a 14 anillos de crecimiento en *D. chilensis*. Medias temporales de la temperatura superficial del mar ( $\bullet$ ) del área donde opera la pesquería de merluza argentina.

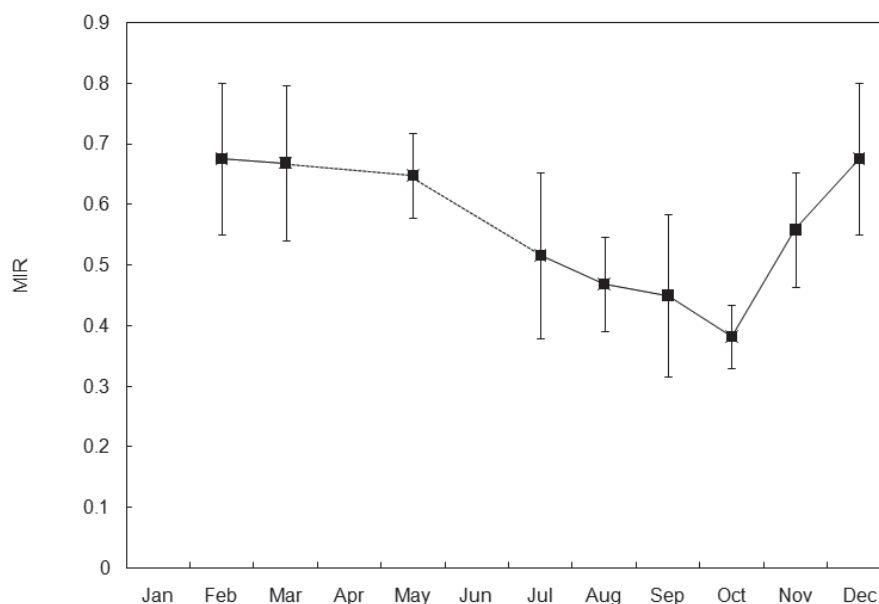


Fig. 7: Mean monthly marginal increment ratios determined from pooled sexes and sizes (70 to 90 cm  $L_T$ ).

Medias mensuales de la relación de incremento marginal determinados a partir de datos de sexos y tallas (70 a 90 cm  $L_T$ ) agrupados.

TABLE 2

Growth parameters estimates from length and disc width based models of female and male *Dipturus chilensis* age data. AIC, Akaike Information Criterion;  $\Delta$ AIC differences between models;  $w_i$  Akaike weights.

Estimaciones de los parámetros de los modelos de crecimiento a partir de datos de longitud y ancho total del disco de *Dipturus chilensis*. AIC, Criterio de Información de Akaike;  $\Delta$ AIC diferencias entre modelos;  $w_i$  pesos de Akaike.

| Parameter     | Two Phase Growth Model |        | Gompertz  |        | Von Bertalanffy |        |
|---------------|------------------------|--------|-----------|--------|-----------------|--------|
|               | Females                | Males  | Females   | Males  | Females         | Males  |
| $L_{\infty}$  | 138.22                 | 106.67 | 123.08    | 108.01 | 151.38          | 139.35 |
| k             | 0.075                  | 0.121  | 0.139     | 0.156  | 0.064           | 0.066  |
| $t_0/c_0$     | -0.712                 | -0.122 | 1.986     | 1.798  | -0.071          | -1.397 |
| $DW_{\infty}$ | 96.46                  | 74.52  | 92.16     | 74.47  | 109.96          | 84.839 |
| k             | 0.096                  | 0.154  | 0.150     | 0.195  | 0.074           | 0.105  |
| $t_0/c_0$     | -0.153                 | 0.168  | 2.026     | 1.891  | -0.421          | -0.434 |
| N             | 319                    | 369    | 319       | 369    | 319             | 369    |
| AIC           | 1468.485               |        | 1499.7335 |        | 1505.0046       |        |
| $\Delta$ AIC  | 0                      |        | 31.24     |        | 36.5            |        |
| $w_i$         | 0.99                   |        | < 0.001   |        | < 0.001         |        |

Therefore the TPGM was used to construct the growth curves for both sexes (Fig. 8). Maximum likelihood tests indicated that the model constructed for males and females separately described data of the beaked skate better than that with both sexes combined.

Growth curves derived from this technique indicated that female beaked skates reach greater size in length as well as in disc width and have lower growth rates than males (138 cm of  $L_{\infty}$  vs. 106 cm of  $L_{\infty}$ ; 96.46 cm of  $DW_{\infty}$  vs. 74.52 cm of  $DW_{\infty}$  and  $k = 0.08$  vs.  $k = 0.121$ ; Table 2).

The VBGM produced the lowest growth coefficients for females and males ( $k_{\phi} = 0.06$  and  $k_{\sigma} = 0.07$ ). Growth coefficients for males were higher and similar for the TPGM and GGM ( $k_{\sigma\text{TPGM}} = 0.121$ ;  $k_{\sigma\text{GGM}} = 0.150$ ). Growth coefficients for females estimated by the TPGM and the GGM were also higher ( $k_{\phi\text{TPGM}} = 0.08$ ;  $k_{\phi\text{GGM}} = 0.139$ ) (Table 2).

The theoretical estimates of longevity ( $\omega$ ) produced values greater than the maximum observed ages (Table 3). Both theoretical methods indicated that females reach greater ages than males.

## DISCUSSION

This study presents the first age and growth estimates for the beaked skate in the Southern Atlantic Ocean. Growth bands were relatively clear along the corpus calcareum of the vertebrae of the beaked skate and less clear in the intermedialia region. Good readability of the growth zones on the centra led to good agreement between readers as % CV and % PA methods indicated. Although the aging technique provided a high level of reproducibility, as a result of bands for the largest and older animals to be compressed, bands near the centrum margin caused some difficulties in ageing skates. This was particularly found in adult skates even on vertebral sections that were exceptionally clear. Series of readings produced closer agreement. Although the ageing technique provided satisfactory results, it has shortcomings. In particular, it is very time consuming mainly due to decalcification process. Also, it demands extreme care when manipulating and mounting the sections to prevent that margins fold up and excessive

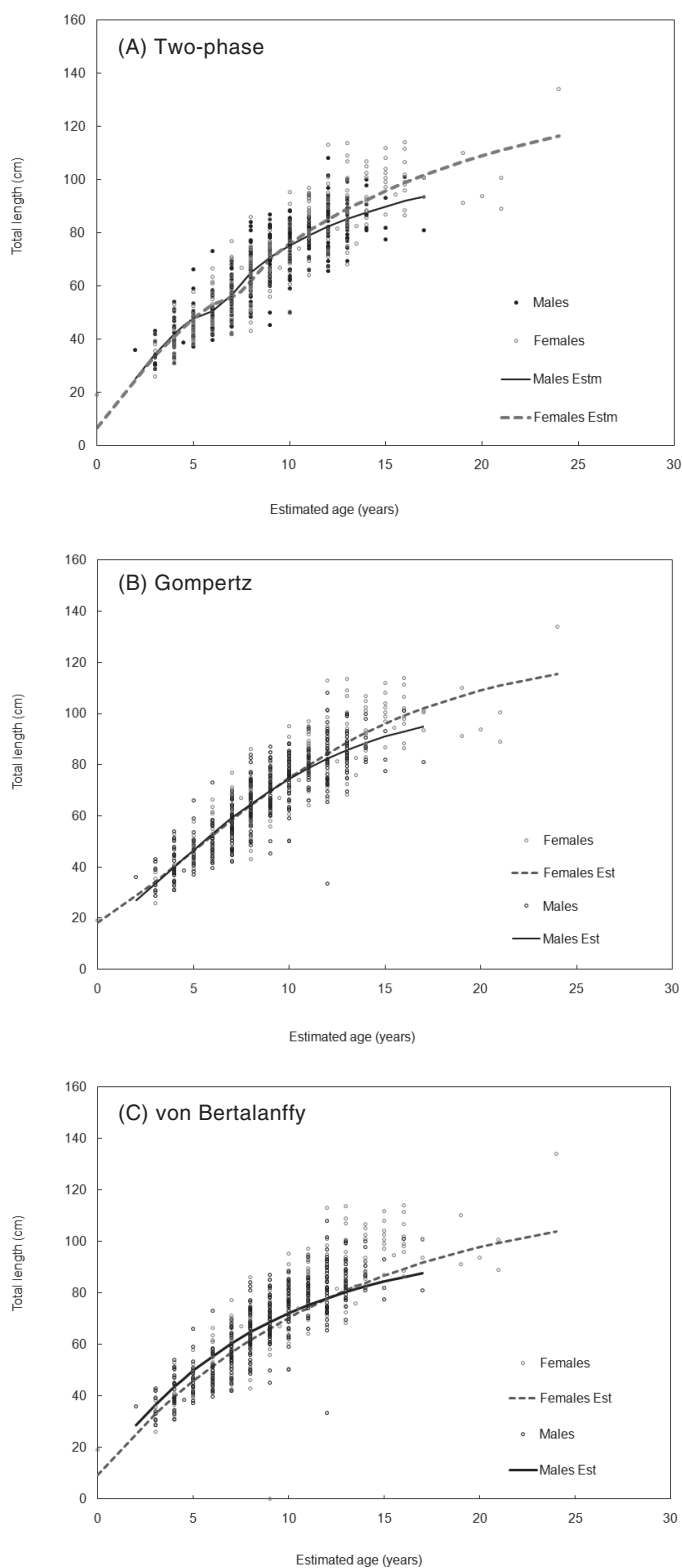


Fig. 8: Growth model curves of males and females *Dipturus chilensis* and observed lengths-at-age. (A) TPGM, (B) GGM, (C) vBGM

Curvas del modelo de crecimiento para machos y hembras de *Dipturus chilensis* y longitudes totales a la edad. (A) TPGM, (B) GGM, (C) vBGM

dehydration. Therefore, that may be taking it into account when initiating any study. Vertebral ring formation for *Dipturus chilensis* provides a continuous record of growth. This is supported by regression data showing that increases in total length and disc width are accompanied by increases in centrum diameter. Similar results were found in *D. chilensis* in the South-East Pacific (Licandeo et al. 2006) and several others skates (Neer & Cailliet 2001, Sulikowski et al. 2003, Smith et al. 2007).

Results of centrum edge characteristics suggest that an opaque band is formed during summer months and a translucent band is formed during winter months, which is indicative of the annual periodicity of band formation in the vertebrae. The correlation of band deposition with the sea surface temperature found in this study may indicate that banding patterns could be related to environmental changes. In this view, temperature fluctuations, photoperiod or food availability may cause differences in nutrients absorption which may explain the banding pattern found in the vertebrae.

The drop of the MIR values from February onwards and the abrupt increase during November suggested a new ring formation starting in spring. Verification of the annual band periodicity in *D. chilensis* has already been attempted by Licandeo et al. (2006) in the south-eastern Pacific and a similar pattern was observed. Annual band formation has been validated in related species using marginal increment analysis, oxytetracycline injection and corroborated using growth rate estimates (Holden & Vince 1973, Ryland & Ajayi 1984;

Natanson et al. 2002, Zeiner & Wolf 1993, Sulikowski et al. 2003, Sulikowski et al. 2005). Although these results are similar to other studies outcomes (Cailliet et al. 1986, Cerna & Licandeo 2009) vertebral edge and MIR data were not categorized by age group to show that both younger and older beaked skates exhibit the same time of opaque band formation. The specimens used in this study ranged sizes of 70 to 90 cm of total length and age classes were grouped. Is important to notice that the range sizes that were available for this analysis corresponds to the vertebrae which edge types were more difficult to identify. The annual nature of the growth bands was verified for these lengths groups only. For these reasons, further research with a wide range sizes available, using tag-recaptured methods and chemical markers, are necessary for a complete validation study.

According to the goodness of fit criterion used (AIC), the best model for both sexes was the two phase growth model (TPGM). Traditionally, the von Bertalanffy growth equation (VBGM) has been applied to describe growth in elasmobranch fishes and only few studies have examined alternative models (Carlson & Baremore 2005). VBGM is still in force mainly because its biological premise that the size of the organism at any moments depends on the resultant of anabolism and catabolism, allows for much easier comparison between populations. The Gompertz growth equation (GGM) is an S-shaped function that may be a better option for organism that hatch from eggs (Mollet et al. 2002), when body mass may be distributed differently and would continue to increase but not greatly in length

TABLE 3

Estimates (years) based on two theoretical methods for *D. chilensis*.

Estimaciones de longevidad (años) para *D. chilensis* basados en dos métodos teóricos.

| Method                                      |   | Two Phase Growth Model | Gompertz | Von Bertalanffy |
|---|---|------------------------|----------|-----------------|
| $\omega$ (95 % $L_{\infty}$ ) Ricker (1979) | ♀ | 45 yr                  | 26 yr    | 58 yr           |
|   | ♂ | 28 yr                  | 20 yr    | 38 yr           |
| $\omega$ (99 % $L_{\infty}$ ) Fabens (1965) | ♀ | 64 yr                  | 36 yr    | 82 yr           |
|   | ♂ | 40 yr                  | 28 yr    | 53 yr           |
| Maximum observed                            | ♀ | 24 yr                  | 24 yr    | 24 yr           |
|   | ♂ | 17 yr                  | 17 yr    | 17 yr           |

once they reached a large size (Cailliet & Goldman 2004). Gompertz best fit at size at age data was suggested for batoids, such as the Pacific electric ray, *Torpedo californica* (Neer & Cailliet 2001) and the cownose ray, *Rhinoptera bonasus* (Neer & Thompson 2005).

Most recent studies proposed the use of the TPGM along with other models in order to best estimate elasmobranch life history parameters (Carlson & Baremore 2005, Araya & Cubillos 2006, Braccini et al. 2007). The TPGM allows growth to be divided into two phases that can be related to changes in habitat, feeding habits or changes in energy allocation (e.g., energy invested in growth, as for juveniles, to energy invested in growth and reproduction as in adults). The shift from juvenile to adult phase should approximate biological age at maturity. In *Dipturus chilensis*, age at maturity occurs at about 9-10 years in males and 10-11 years in females (Aversa Unpub. data) and as reported by Koen Alonso et al. (2001) there is a shift in the diet that corresponds with sexual maturation. However, there is a discrepancy between the estimated ages at which the transition of the two phases occurs,  $t_h$  (6.4 and 7.4 years from males and females, respectively) and the estimated age of  $L_{0.5}$  maturity, so the change was slightly before the onset of maturity. An alternative explanation relies on the idea that the process of maturation begins a few years before reproduction actually takes place. Besides it must be taking into account that though growth models represent beaked skate growth properly, sample size, or underrepresented age classes may affect growth estimates.

The asymptotic length ( $L_\infty$ ) values estimated by VBGM exceeded the largest specimens in the field collection for both males and females. The largest beaked skate found in this study were close to the  $L_\infty$  values predicted by the TPGM and the GGM. However, overestimation of  $L_\infty$  values has been documented before in several age and growth studies using the VBGM equation (Walmsley-Hart 1999, Sulikowski et al. 2003). It has been suggested that smallest and largest specimens are the most influential in the estimation of growth (Campana 2001) so the rareness of these individuals could be responsible for the overestimation of  $L_\infty$ . Owing to gear selection

and marketable hake size, it is quite possible that the smaller and larger size classes of the beaked skate could be underrepresented which led to the augmented  $L_\infty$  in the VBGM. It has also been suggested that because of the relationship between  $L_\infty$  and  $k$ , the VBGM tends to estimate lower  $k$  values (Carlson & Baremore 2005, Araya & Cubillos 2006). Results like these may result in biases in population models because indirect estimates such as, natural mortality and longevity rely on accurate estimates of  $k$  from growth models (Fabens 1965, Chen & Watanabe 1989, Jensen 1996). The unrealistic biological estimates of the VBGM for the beaked skate illustrate the importance of fitting alternative models to the data. In spite of this, estimates of the VBGM are presented in order to compare growth parameters of the beaked skate with other studies published (Table 4).

Theoretical estimates of longevity made using the  $k$  parameter indicate that the TPGM and the Gompertz estimates are more biologically realistic than VBGM estimates.

The oldest ages estimated in this study were 17 and 24 years (81 cm  $L_T$  and 134 cm  $L_T$ ) for males and females respectively. These ages are similar to those reported by Gilli et al. (1999) and Licandeo et al. (2006) for *D. chilensis* in Chile; both suggested that females tend to live longer than males (Table 4). The theoretical estimates of longevity suggest that males and females live for 20 and 28 years. Licandeo et al. (2006) reported ages of 27 years in *D. chilensis* in the south-east Pacific; Francis et al. (2001) 24 years in *D. innominatus* and Walmsley-Hart et al. (1999) 18 years in *D. pullopunctata*. *Dipturus* species appears to be long-lived among the Rajidae Family.

Growth rates estimated by the TPGM and the GGM are comparable to those reported for other skates of similar size (Holden & Vince 1973, Ryland & Ajayi 1984, Sulikowski et al. 2003, Licandeo et al. 2006, Table 4). Moreover, the oldest ages obtained for the beaked skate are in agreement with the assumption that larger batoids live longer and grow slower than smaller species.

*D. chilensis* growth parameters, as determined by this study, suggested that females attain larger asymptotic length and disc width, and grow slower than males (Table

TABLE 4

Comparison of age and growth parameters among *Dipturus* species. Growth data are based on fits on von Bertalanffy growth equation in order to be comparable.

Comparación de los parámetros de crecimiento entre las especies del género *Dipturus*. Los datos de crecimiento están basados en ajustes a la ecuación de Von Bertalanffy de modo que puedan compararse.

| Species                 | Maximum age | N   | sex | k(year <sup>-1</sup> ) | L <sub>∞</sub> (cm) | DW <sub>∞</sub> (cm) | L <sub>T</sub> ranges (cm) | Location of study                         | Source                      |
|-------------------------|-------------|-----|-----|------------------------|---------------------|----------------------|----------------------------|---|-----------------------------|
| <i>D. chilensis</i>     | 25          | 85  | ♀   | 0.127                  | 0.123               | --                   | 25-125                     | Golfo de Arauco                           | Fuentelba & Leible (1989)   |
|                         | 26          | 44  | ♂   | 0.123                  | 118.9               | --                   | 16-116                     |   |                             |
|                         | 44          | 717 | ♀   | 0.073                  | 143.8               |                      | 25-117                     |   |                             |
| <i>D. chilensis</i>     | 41          | 368 | ♂   | 0.079                  | 131.9               |                      | 42-108                     | Chile, VIII to X region                   | Gili et al. (1999)          |
|                         | 27          | 216 | ♀   | 0.112                  | 128.3               | ---                  | 23-124                     |   |                             |
| <i>D. chilensis</i>     | 23          | 186 | ♂   | 0.134                  | 107.8               | ---                  | 36-106                     | South-Eastern Pacific                     | Licandeo et al. (2006)      |
|                         | 32          |     | SC  | 0.098                  | 130.4               | ---                  |                            |   |                             |
|                         | 52          | 87  | ♀   | 0.06                   | --                  | 77.1                 | 13-74.7 D <sub>W</sub>     |   |                             |
| <i>D. pullopunctata</i> | 40          | 93  | ♂   | 0.08                   | --                  | 133                  | 17.7-69.6 D <sub>W</sub>   | Aghulas Bank, South Africa                | Walmsley-Hart et al. (1999) |
|                         | 39          |     | SC  | 0.08                   | --                  | 87.3                 |                            |   |                             |
| <i>D. nasatus</i>       | 20          | 134 | SC  | 0.16                   | 91.3                | -                    | 15-75 PL                   | South Island, New Zealand                 | Francis et al. (2001)       |
| <i>D. innominatus</i>   | 33          | 98  | SC  | 0.095                  | 150.5               | -                    | 19-133 PL                  | South Island, New Zealand                 | Francis et al. (2001)       |
| <i>D. chilensis</i>     | 24          | 319 | ♀   | 0.064                  | 151.38              | 109.9                | 19-134                     | Patagonian waters, South-Eastern Atlantic | This study                  |
|                         | 17          | 369 | ♂   | 0.066                  | 139.35              | 84.84                | 28-101.5                   |   |                             |

SC = sexes combined



2). This trend seems to be a common pattern in batoids and many shark species as well. Fuentealba & Leible (1990), Gilli et al. (1999), Mariotti et al. (2003) and Licandeo et al. (2006) also found differences in growth parameters in males and females, and reported that males reach sexual maturity before females (Table 4). This could be related to a reproductive strategy where females attain larger sizes to accommodate the eggs inside their body cavities and males grow faster to reach sexual maturity before (Holden & Vince 1973).

The analysis of growth of the beaked skate indicates that future studies should investigate the use of alternative growth models to best describe growth because the VBGM not always apply. Many elasmobranch fishes follow a growth pattern characterized by a decrease in growth rates which could be related to the onset of maturity (Araya & Cubillos 2006) or other factors, and the use of the VBGM derived estimates, may result in biases in stock assessments.

Historically the idea of sustainable fisheries for elasmobranchs has been questioned based on the linear relationship between stock and recruitment for most elasmobranchs (Holden 1974, 1977). Currently, that idea has been questioned, and recruitment is viewed as largely independent of stock size. The response of the population to harvesting depends not only on the amount of fishing effort expended in a fishery, but also on the peculiarities of the species biology and behaviour. Although there are several sustainable chondrichthyan fisheries, they should be managed with caution. Skates are poorly known and their life history strategies make them very vulnerable to over exploitation that certain populations may continue to decline for some time even if fishing pressures were removed immediately (Holts 1988). Fisheries would have really important effects on species assemblage. The nonselective captures of several stocks which differ in growth and maturity rates should lead to changes in species composition, since species will not have the same response to fishing pressure (Hilborn & Walters 1992). In this view, species with higher  $L_{\infty}$  and age at maturity and probably lower growth rates will be replaced by species with lower  $L_{\infty}$  and age at maturity, since they should be able to sustain

higher fishing pressures. This would lead to changes in species composition in the catch and also changes in the mean size in the catch. Observations of these characteristics have already occurred for *D. chilensis* in Malvinas/Falkland Island (Agnew et al. 2000), and a change in size-at-maturity have been reported in the Atlantic Ocean (between latitudes of 37°00'-39°00' S, Paesch & Oddone 2008), and in the north-east Atlantic for skate species *D. batis*, *R. clavata*, *R. brachyura* and *L. fullonica* which their declines of abundances were accompanied by increases in abundance of smaller species like *L. naevus* and *R. radiata* (Dulvy et al. 2000).

In the South Atlantic Ocean the beaked skate population is holding on a non selective fishery exploitation which in a future may lead to growth changes in younger animals and also changes in the capture of larger animals that will make mean size and age fall down. Indirectly, this disturbance on the demography structure may trigger changes on growth and reproduction. It is crucial to have a better understanding of age and growth process that will lead to a better understanding of the potential for *D. chilensis* populations to grow, especially in response to additional sources of mortality from fisheries. Organisms that have late age of maturity and high longevities, as *D. chilensis*, often also have low population growth rates, resulting in population turnover times that may not be able to respond to fishing mortality as well as those with high population growth rates, early maturity and low longevity.

This study provides basic information on age and growth for the beaked skate, *D. chilensis*, which were previously not available for its south Atlantic range of distribution. In order to explore the impact of exploitation on the population, future research should apply these results to carry out demographic analysis and evaluate population growth rates.

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## LITERATURE CITED

- AGNEW DJ, CP NOLAN, JR BEDDINGTON & R BARANOWSKI (2000) Approaches to the assessment and management of multispecies skate and ray fisheries using the Falkland Islands Fishery as an example. *Canadian Journal of Fisheries and Aquatic Sciences* 57: 429-440.
- ARAYA M & LA CUBILLOS (2006) Evidence of two-phase growth in elasmobranchs. *Environmental Biology of Fishes* 77: 293-300.
- BAHAMONDE NN (1950) VIII. Alimentación de la raya (*Raja flavirostris*) Philippi, 1892. *Investigaciones Zoológicas Chilenas* (Fasc. 1): 4-6.
- BRACCINI JM, BM GILLANDERS & TJ WALKER (2007) Comparison of deterministic growth model fitted to length-at-age data of the picked spurdog (*Squalus megalops*) in south-eastern Australia. *Marine and Freshwater Research* 58: 24-33.
- CAILLE G, R GONZÁLEZ, A GOSZTONYI & N CIOCCO (1997) Especies capturadas por las flotas de pesca costera en Patagonia programa de biólogos observadores a bordo, 1993-1996. Puerto Madryn. Fundación Patagonia Natural. Informe técnico N° 27.
- CAILLIET G, L MARTIN, D KUSHER, P WOLF & B WELDEN (1983) Techniques for enhancing vertebral bands in age estimation of California elasmobranchs. NOAA Technical Report. 8: 157-165.
- CAILLIET, G & KJ GOLDMAN (2004) Age determination and validation in chondrichthyan fishes. In: J Carrier, JA Musick & MR Heithaus (eds) *Biology of sharks and their relatives*. CRC Press LLC, Boca Raton Florida.
- CAILLIET G, WD SMITH, HF MOLLET & KJ GOLDMAN (2006) Age and growth studies of chondrichthyan fishes: the need for consistency in terminology, verification, validation, and growth function fitting. *Environmental Biology of Fishes* 77: 211-228.
- CAMPANA SE (1990) How reliable are growth back-calculations based on otoliths? *Canadian Journal of Fisheries and Aquatic Science* 47: 2219-2227.
- CAMPANA SE (2001) Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *Journal of Fish Biology* 59: 197-242.
- CAMPANA SE, CM ANNAND & JL MCMILLAN (1995) Graphical and statistical methods for determining the consistency of age validations methods. *Transactions of the American Fisheries Society* 124: 131-138.
- CARLSON JK. & IE BAREMORE (2005) Growth dynamics of the spinner shark (*Carcharhinus brevipinna*) off the United States southwest and Gulf of Mexico coasts: A comparison of methods. *Fishery Bulletin* 103: 280-291.
- CASEY J, JR PRATT & C STILLWELL (1985) Age and growth of the sandbar shark (*Carcharhinus plumbeus*) from the Western North Atlantic. *Canadian Journal of Fisheries and Aquatic Science* 42: 963-975.
- CEDROLA, PV, AM GONZÁLEZ & AD PETTOVELLO (2005) By-catch of skates (Elasmobranchii: Arhynchobatidae, Rajidae) in the Patagonian red shrimp fishery. *Fisheries Research* 71: 141-150.
- CERNA F & R LICANDEO (2009) Age and growth of the shortfin mako (*Isurus oxyrinchus*) in the south-eastern Pacific off Chile. *Marine and Freshwater Research* 60: 394-403.
- CERRATO RM (1990) Interpetable statistical test of growth comparisons using parameters in the von Bertalanffy equation. *Canadian Journal of Fisheries and Aquatic Science* 47: 1416-1426.
- CHEN S & S WATANABE (1989) Age dependence of natural mortality coefficient in fish population dynamics. *Nippon Suisan Gakkaishi* 55: 2490-2501.
- CONRATH LC, J GELSLEICHTER & JA MUSICK (2002) Age and growth of the smooth dogfish, *Mustelus canis*, in the northwest Atlantic Ocean. *Fishery Bulletin* 100: 674-682.
- COSCARELLA MA (1997) Estudio de la fauna acompañante en la flota pesquera operando en Patagonia Norte y su interacción con mamíferos marinos. Grade thesis, Universidad Nacional de la Patagonia San Juan Bosco.
- CRESPO EA, SN PEDRAZA, SL DANS, M KOEN ALONSO, L REYES, N GARCÍA, MA COSCARELLA & A SCHIAVINI (1998) Efectos de las pesquerías sobre la fauna y al ambiente en el norte y centro de Patagonia. Informe Final del PI N° 195. Universidad Nacional de la Patagonia San Juan Bosco.
- CRESPO EA, A SCHIAVINI, G PÉREZ MACRI, L REYES & SL DANS (1994) Estudios sobre determinación de edad en mamíferos marinos del Atlántico Sudoccidental. In: Oporto JA (ed) *Anales IV Reunión de Trabajo de Especialistas en Mamíferos Acuáticos de América del Sur*: 31-55.
- DULVY NK, JD METCALFE, J GLANVILLE, MG PAWSON & JD REYNOLDS (2000) Fishery stability, local extinctions and shifts in community structure in skate. *Conservation Biology* 14: 283-293.
- FABENS AJ (1965) Properties and fitting of the von Bertalanffy growth curve. *Growth* 29: 265-289.
- FERREIRA B & C VOOREN (1991) Age, growth, and structure of vertebra in school shark *Galeorhinus galeus* (Linnaeus, 1758) from Brazil. *Fishery Bulletin* 89: 19-31.
- FRANCIS M, CO MAOLAGAIN & D STEVENS (2001) Age, growth and sexual maturity of two New Zealand endemic skates, *Dipturus nasutus* and *D. innominatus*. *New Zealand Journal of Marine and Freshwater Research* 35: 831-842.
- FUENTEALBA M & M LEIBLE (1990) Perspectivas de la pesquería de la raya volatin Raja (*Dipturus*) chilensis: Estudio de edad, crecimiento y algunos aspectos reproductivos. In: Barbieri MA (ed) *Perspectivas de la actividad pesquera en Chile*. Escuela de Ciencias del Mar, Universidad Católica de Valparaíso.
- GARCÍA DE LA ROSA SB (1998) Estudios de las interrelaciones tróficas de dos elasmobranchios de la plataforma continental del Mar Argentino, en relación con las variaciones espacio-temporales y ambientales. *Squalus acanthias* (Squalidae) y *Raja flavirostris* (Rajidae). Phd Thesis, Universidad Nacional de Mar del Plata.
- GILLI R, M DONOSO, V OJEDA, A LÓPEZ & H

- MIRANDA (1999) Parámetros poblacionales de la raya volatin VIII a X Regiones y métodos de asignación de edades. Instituto de Fomento Pesquero, Informe Final Proyecto FIP1997-20. IFOP.
- GOLDMAN KJ (2004) Age and growth of elasmobranch fishes. In: Musick JA & R Bonfil (eds) Elasmobranch fisheries management techniques: 97-132. Asia Pacific Cooperation, Singapore.
- GOSZTONYI AE (1984) La alimentación del pingüino magallánico (*Spheniscus magellanicus*) en las adyacencias de Punta Tombo, Chubut, Argentina. Contribución N° 95. Centro Nacional Patagónico.
- HILBORN R & CJ WALTERS (1992) Quantitative Fisheries Stock Assessment: Choice, dynamics and uncertainty. Chapman and Hall, New York.
- HOLDEN M (1974) Problems in the rational exploitation of elasmobranchs populations and some suggested solutions. In: FR Harden Jones (ed) Sea Fisheries Research. John Wiley & Sons, New York.
- HOLDEN M (1977) Elasmobranchs. In: JA Gulland (ed) Fish population dynamics. J Wiley & Sons, New York, New York.
- HOLDEN M & M VINCE (1973) Age validation studies on the centra of *Raja clavata* using tetracycline. Journal du Conseil International pour l'Exploration de la Mer 35: 13-17.
- HOLTS DB (1988) Review of the west coast commercial shark fisheries. Marine Fisheries Review 50: 1-8.
- JENSEN AL (1996) Beverton and Holt life history invariants result from optimal trade-off of reproduction and survival. Canadian Journal of Fisheries and Aquatic Science 53: 820-822.
- KIMURA D (1980) Likelihood methods for the Von Bertalanffy growth curve. Fishery Bulletin 77: 765-766.
- KOEN ALONSO M, EA CRESPO, N A GARCÍA, SN PEDRAZA, PA MARIOTTI, B BERÓN-VERA & NJ MORA (2001) Food habits of the beaked skate *Dipturus chilensis* off Patagonia, Argentina. ICES Journal of Marine Science 58: 288-297.
- LICANDEO RR, JG LAMINILLA, PG RUBILAR & RM VEGA (2006) Age, growth, and sexual maturity of the yellownose skate, *Dipturus chilensis*, in the south-eastern Pacific. Journal of Fish Biology 68: 488-506.
- LICANDEO R & FT CERNA (2007) Geographic variation in life history traits of endemic kite skate, *Dipturus chilensis*, (Batoidea: Rajidae), along its distribution in the fjords and channels of southern Chile. Journal of Fish Biology 71: 421-440.
- MARIOTTI P, SL DANS, SN PEDRAZA, EA CRESPO, NA GARCÍA & MI AVERSA (2003) Aspectos reproductivos de la raya picuda *Dipturus chilensis* en el norte y centro de Patagonia. In: Resúmenes de las V Jornadas Nacionales de Ciencias del Mar, Mar del Plata, Argentina. 8-12 Diciembre 2003. Universidad Nacional de Mar del Plata.
- MASSA AM, NM HOZBOR & C LASTA (2001) Explotación de rayas en la plataforma Argentina. Informe Técnico Instituto Nacional de Investigación y Desarrollo Pesquero INIDEP 53-7.
- MASSA AM, L LUCÍFORA & NM HOZBOR (2004) Condrictios de la región costera bonaerense y uruguaya. In: Sánchez RP & SI Bezzi (eds) El mar argentino y sus recursos pesqueros 4. Los peces marinos de interés pesquero caracterización biológica y estado de explotación. INIDEP, Mar del Plata.
- MENNI R & AE GOSZTONYI (1982) Benthic and semidemersal fish association in the Argentine sea. Stud. Neotrop. Fauna Environmental 17: 19.
- MENNI R & HL LÓPEZ (1984) Distributional patterns of Argentine marine fishes. Physis 42 A: 71-85.
- MOLLET HF, JM EZCURRA & JB O'SULLIVAN (2002) Captive biology of the pelagic stingray, *Dasyatis violacea*, (Bonaparte, 1832). Marine and Freshwater Research 53: 531-541.
- NATANSON L, J CASEY & N KOHLER (1994) Age and growth estimates for the dusky shark, *Carcharhinus obscurus*, in the Western Atlantic Ocean. Fishery Bulletin 93: 116-126.
- NATANSON LJ, JJ MELLO & S CAMPANA (2002) Validated age and growth of the porbeagle shark (*Lamna nasus*) in the western North Atlantic Ocean. Fishery Bulletin 100: 266-278.
- NEER JA & GM CAILLIET (2001) Aspects of the life history of the Pacific electric ray, *Torpedo californica* (Ayres). Copeia 2001: 842-847.
- NEER JA. & BA THOMPSON (2005) Life history of the cownose ray, *Rhinoptera bonasus*, in the northern Gulf of Mexico, with comments on geographic variability in life history traits. Environmental Biology of Fishes 73: 321-331.
- PAESCH L & MC ODDONE (2008) Change in size-at-maturity of the yellow skate *Dipturus chilensis* (Guichenot, 1848) (Elasmobranchii: Rajidae) in the South West Atlantic. Neotropical Ichthyology 6: 223-230.
- RICKER WE (1975) Computation and interpretation of biological statistics of fish populations. Bulletin of the Fisheries Research Board of Canada 191.
- RICKER WE (1979) Growth rates and models. In: Fish physiology Vol 8, chapter 11. Academic Press, Inc.
- RYLAND JS & TO AJAYI (1984) Growth and population dynamics of three Raja species (Batoidei) in Carmarthen Bay, British Isles. Journal du Conseil International pour l'Exploration de la Mer 41: 111-120.
- SMITH WD, GM CAILLIET & EM MELÉNDEZ (2007) Maturity and growth characteristics of a commercially exploited stingray, *Dasyatis dipterura*. Marine and Freshwater Research 58: 54-66.
- SORIANO M, J MOREAU, JM HOENIG & D PAULY (1992) New functions for the analysis of two-phase growth of juvenile and adult fishes with application to Nile perch. Transactions of the American Fisheries Society 121: 486-492.
- STEVENS J (1975) Vertebral rings as means of age determination in the blue shark (*Prionace glauca* L.). Journal of Marine Biology Assessment UK 55: 957-665.
- SULIKOWSKI JA, MD MORIN, SH SUK & WH HOWELL (2003) Age and Growth estimates of winter skate (*Leucoraja ocellata*) in the western Gulf of Maine. Fishery Bulletin 101: 405-413.
- SULIKOWSKI JA, J KNEEBONE, S ELZEY, J JUREK, PD DENLEY, WH HOWELL & PC W. TSANG (2005) Age and growth of the thorny skate, *Amblyraja radiata*, in the western Gulf of Maine. Fishery Bulletin 103: 161-168.

- WALKER TI, RA OFFICER, JG CLEMENT & LP BROWN (1995) Southern age validation: Part 1-Project overview, vertebral structure and formation of growth increment bands used for age determination. In: Final report to Fisheries Research and Development Corporation. Department of Conservation and Natural Resources.
- WALMSLEY-HART SA, WHH SAUER & CD BUXTON (1999) The biology of the skates *Raja wallacei* and *R. pullopunctata* (Batoidea: Rajidae) on the Angulhas bank, South Africa. South African Journal of Marine Science 21: 165-179.
- WINTNER S, FJ DUDLEY, N KISTNASAMY & B EVERETT (2002) Age and growth estimates for the Zambezi shark, *Carcharhinus leucas*, from the east coast of South Africa. Marine and Freshwater Research 53: 557-566.
- ZEINER SJ & P WOLF (1993) Growth characteristics and estimates of age at maturity of two species of skates, *Raja binoculata* and *Raja rhina*, from Monterey Bay, California. NOAA Technical Report NMFS 115: 87-99.

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