Master of Science
Course ***ISATEC***

M.Sc. Thesis in International Studies in Aquatic Tropical Ecology

Age and growth of skates of the genus *Bathyraja* in Argentina

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Resumen

La pesca dirigida a tiburones y rayas aumentó notablemente en los últimos veinte años en todo el mundo. Sin embargo, en la mayoría de las especies todavía se desconocen parámetros biológicos y poblacionales como la tasa de crecimiento, la mortalidad, la fecundidad etc., resultando en un manejo pesquero inadecuado. En el presente trabajo fueron investigados los métodos mas apropriados para la determinación de edad como tambien fueron estimados los parámetros de crecimiento para diez especies del género *Bathyraja* en el Atlántico Suroccidental. Se disponía de 720 ejemplares capturados en campañas de investigación realizadas entre 2003 y 2005 por el Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP). Teñir secciones longitudinales de las vértebras con cristal violeta y permanganato de potasio resultó ser el método más efectivo para facilitar la lectura de los anillos en la mayoría de las especies. Las lecturas realizadas en espinas fueron similares a las lecturas de las vértebras. Se pudieron determinar parámetros de crecimiento en seis especies, y hacer estimaciones en las otras cuatro especies. La tasa de crecimiento de las especies de talla mayor fue menor que aquella de las especies más pequeñas. No existieron diferencias latidudinales en la tasa de crecimiento pero una comparación con muestras de otros trabajos mostró que el largo total de las *Bathyraja* parece ser mayor alrededor de las Malvinas.

Palabras clave: Bathyraja, parámetros de crecimiento, Atlántico Suroccidental, Argentina, pesca de tiburones y rays,

Abstract

In the last 20 years directed shark and ray fishery has increased alarmingly everywhere in the world. For most species though, no data on growth rate, mortality, fecundity and other life history aspects exist as of now and management of the fishery is therefore insufficient. Also there still exist methodological difficulties in the age determination of elasmobranchs fishes, a fact which complicates the investigation of growth parameters. This study tried to identify the best ageing methods and estimate growth parameters for ten skate species of the genus *Bathyraja*, all occurring in the southwest Atlantic in depths of 50m and more. 720 samples were collected on board of argentine research vessels in between 2003 and 2005. Crystal violet and a new staining method using potassium permanganate, both applied on sagittal sections of vertebral centra, proved to be most effective in enhancing the banding pattern in most of the species. Thorns were also tested and readings were consistent with the ones made on vertebral sections. Growth parameters could be derived for six species and for the other four estimates could be made. Growth rate as well as infinite length varied between species, with those attaining bigger sizes having lower growth rates. No latitudinal differences in growth rate could be detected but a comparison with samples from other studies showed that total lengths were always reported to be higher around the Falkland Islands.

Key words: Bathyraja, growth parameters, southwest Atlantic, Argentina, shark and ray fishery

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1 Introduction

Overview

1.1 Life history aspects of elasmobranchs with focus on age and growth

Sharks and rays have been classified as "equilibrium" life history strategists (KING & MCFARLANE 2003, FRISK et al. 2001). They attain sexual maturity rather late in their life, have a slow embryonic development of several months to a year (CAMHI et al. 1998) and are slow growing, all of which makes them extremely vulnerable to over fishing (HOENIG & GRUBER 1990).

There is a great variability though in the rebound potential of elasmobranch fishes (FRISK et al. 2002, WALKER & HEESSEN 1996, SMITH et al. 1998) and this might result in different responses of species to a multi-species fishery. While aggregated catch statistics may exhibit stable trends, population declines of individual species could be masked by population increase of other species (DULVY et al. 2000).

In general, growth rates (k) of skates (family Rajidae), which mostly range between 0.05 to about 0.30 (CAILLIET & GOLDMAN 2004; IVORY et al 2004; SULOWSKI et al. 2005) have been shown to be lower for larger sized species (FRISK et al. 2001). Additionally they usually take long to reach maturity. Both characteristics make these larger species especially susceptible to population declines. In 1998 e.g., CASEY and MYERS investigated the population status of one of the largest skates in the NW Atlantic (*Raja laevis*) and found it to be close to extinction.

Hence, to promote proper management of shark and ray fisheries, life history aspects (growth rate, length at maturity, total length, natural and fisheries mortality etc.) should be known at species or best at population level, for it has even been observed that different populations of the same species can exhibit great differences in these parameters (LUCIFORA 2003, FRISK 2004). Latitudinal changes in growth characteristics have been observed both in sharks (DRIGGERS et al. 2004, CARLSON et al. 2003) and rays (NEER & THOMPSON 2005).

Consequently, knowledge of population specific age-structure and growth rates etc. allows a better calculation of potential sustainable yield (HOENIG & GRUBER 1990) and prevents over-fishing. In the US age and growth laboratory manual WISCHNIOWSKI et al. (1998) state that "the ability to age fish is essential to the total understanding of fish population dynamics".

Counting growth increments (annuli) on otoliths, scales or other hard structures has been the most common method for ageing bony fish (WISHNIOWSKI et al. 1998). Due to the lack of otoliths and other skeletal hard parts though, ageing of elasmobranches has long been slowed down (CAILLIET et al. 1983). Although Ridgewood already observed concentric growth bands in the vertebral centra of cartilaginous fishes in 1921, it took some time until scientists came to using these bands regularly for the age determination of sharks and rays (CAILLIET et al. 1983). Only recently other structures have been investigated in the context of ageing e.g. thorns (GALLAGHER & NOLAN 1999), neural arches of vertebrae (MCFARLANE et al. 2002) and spines (MCFARLANE & BEAMISH 1987).

Crucial to every ageing study is the verification/validation of the ages obtained. Age estimates can only be used in growth models when it can be proven that band formation occurs annually (or periodically). CAILLIET (1990) describes age verification as the process of confirming an age estimate by comparison with other indeterminate methods. The most popularly used methods for age verification are: back calculation of lengths derived from measurements of calcified structures from larger individuals, size frequency-, centrum edge-, and marginal increment analysis, radiometric dating, laboratory growth studies (CAILLIET 1990) and last but not least bomb dating (for specimens born between 1955-1985 (CAMPANA 2002, WISCHNIOWSKI et al. 1998)). Annual band formation can also be proven by tag and recapture studies of known-age individuals and recapture studies with injecting markers (e.g. tetracycline) which incorporate into the calcified structures (GOLDMAN 2004). In spite of the importance of validating the periodicity of age rings there had been rather few studies which actually tried to validate band formation until 1990 (an overview is given in CAILLIET 1990). Nowadays validation is normally incorporated into the study, and for quite a few species of skates band formation has already been validated (GALLAGHER et al. 2004; GALLAGHER & NOLAN 1999; SULOWSKI et al 2003).

The von Bertalanffy growth function (VBGF) has been the most commonly used model for describing growth in fishes. Although criticism has been raised by some authors (CARLSON et al. 2005, references herein) and also other models have been applied (e.g. Gompertz), using the VBGF is probably the best way to compare parameters across and within species. Therefore this approach has been adopted for the present study too.

1.2 The Genus *Bathyraja* and Project ECORAYA

COUSSEAU & PERROTTA (2004) report 82 species of cartilaginous fishes for Argentinean waters. Out of these, 23 species are grouped under the synonym 'skates' – i.e. belonging to the family Rajidae. The taxonomy of this family has undergone great changes in the last 20 years (STEHMANN 1986; LAMILLA & SÁEZ 2003). Only in 2004 a new species (*Bathyraja cousseauae*) was described in Argentina, which is thought to be endemic to the SW Atlantic (DIAZ DE ASTARLOA et al. 2004).

The genus *Bathyraja* is the most diverse genus in the family Rajidae with 45 named species of three morphotypes occurring worldwide (STEHMANN 1986). Ten species of this genus are known to live in the southwest Atlantic, seven of which (probably plus one more – *B. cousseauae*) are endemic* to the Argentinean continental shelf and the southern part of the Chilean shelf (MENNI & STEHMANN 2000).

Table 1
Depth range and maximum total length (TL) found in literature. Data taken from AGNEW et al. (1999), COUSSEAU et al. (2000), Falkland Island Gov. (2002), LAPTIKHOVSKY et al. (2005), MENNI & STEHMANN (2000), SÁNCHEZ & MABRAGAÑA (2002), STEHMANN (1986)

Species	**Depth range (literature values)**	**TL_{max} (literature values)**
B. albomaculata (Norman, 1937)*	105-815m	99 cm
B. brachyurops (Fowler, 1910)*	25-600m	116 cm
B. cousseauae (n.sp. 2004)*	~180-500m	-
B. griseocauda (Norman, 1937)*	89-941m	157 cm
B. macloviana (Norman, 1937)*	82-505m	77 cm
B. magellanica (Steindachchner, 1903)*	50-400m	72 cm
B. meridionalis (Stehmann, 1987)	-	120 cm
B. multispinis (Norman, 1937)*	115-600m	131 cm
B. papilionifera (Stehmann, 1985)	660-1040m	>100 cm
B. scaphiops (Norman, 1937)*	115-600m	99 cm
Range total	**50-1040m**	**72-157 cm**

All members of the genus *Bathyraja* in Argentina are benthic deep water species, inhabiting the continental shelf (>50 m) and slope (see table 1). Up to now, little to nothing is known about the biology and ecology of all ten species.

Due to the increase in deep water shark and ray fisheries, the genus *Bathyraja* also experiences a growing fishing pressure in Argentina (DIAZ DE ASTARLOA et al. 2004). Around the Falkland Islands *B. griseocauda*, *B. brachyurops* and *B. albomaculata* are a dominant part of the skate catches, and for *B. griseocauda* declining biomasses have already been reported in this fishery (AGNEW et al. 2000).

In 2003 a project called ECORAYA was set up in Mar del Plata, Argentina to improve and update the state of knowledge of all ten *Bathyrajid* species of Argentina regarding their biology, ecology and taxonomy. This joint research project is conducted by the national fisheries research institute (INIDEP) and the Ichthyology Laboratory at the National University of Mar del Plata (UNMdP) on the **Argentinean side**, as well as the Centre for Tropical Marine Ecology (ZMT) in Bremen and the Ichthyological Research Laboratory (ICHTHYS) in Hamburg on the **German side**. It aims to work on important aspects (e.g. reproductive and feeding biology, age and growth, biodiversity etc.) of this genus in Southwest Atlantic waters. The contribution of the present work to this project is the study of bathyrajid age and growth.

1.3 Study site: Argentina

Argentina is a vast country, reaching from 22°S to the tip of South America at about 56°S. With a coastline of 4 989 km (CIA WORLD FACT BOOK 2006) facing entirely the Atlantic Ocean and an equally impressive continental shelf area (769 000 km^2) its waters host fishing resources of great importance to the country's economy (FAO country profile 2001). Almost half of the population (45%) is living within a hundred kilometres to the coast (EARTHTRENDS 2003).

The Argentinean continental shelf is one of the widest in the world, surrounding the Falkland Islands some 750 km east of the mainland (see fig.1A). At about 180m depth the shelf's edge is, for the most part, declining rapidly in a pronounced slope (CAPURRO 1981). The shelf is predominantly influenced by the Falkland/Malvinas current which is carrying cold, nutrient rich subantarctic water up north. Prevailing westerly winds produce upwellings of cold Antarctic waters along the edge of the continental shelf, which lower the surface temperature (NOAA 2003; GLORIOSO 2000). The Malvinas current meets the Brazil current at about 35-39°S (depending on the time of year) in the Brazil-Malvinas confluence. The southward flowing Brazil current brings warm, more saline subtropical water into north-Argentinean waters (see fig. 1B). Closer to the coast, the influence of tides and the freshwater discharge of large rivers like the Rio de la Plata (N-Argentina) and the Rio Negro (flowing through Viedma) create conditions which clearly distinguish these waters from the rest of the continental shelf. The Rio de la Plata carries between 19 000 and 26 000 $m^3\ s^{-1}$ which it receives from the second largest basin in South America. Its estuary is characterized by a permanent salt wedge and as a breeding ground for dozens of fish species (MIANZAN et al. 2001). During spring and summer, onshore winds force sediment rich fresh water down south along the Argentinean coast (GUERRERO et al. 1997).

Where different water masses meet, temperature and salinity values abruptly change. These so called 'fronts' are highly productive areas and sustain a significant fishery. As mentioned above, there are numerous fronts along the continental shelf of Argentina, including the polar-antarctic front, the subtropical front, a front which extends along the continental slope, and several coastal fronts (GUERRERO & PIOLA 1997). The whole Patagonian shelf LME is therefore considered a Class I, highly productive (>300 gC/m2-yr) ecosystem based on SeaWiFS global primary production estimates (NOAA 2003).

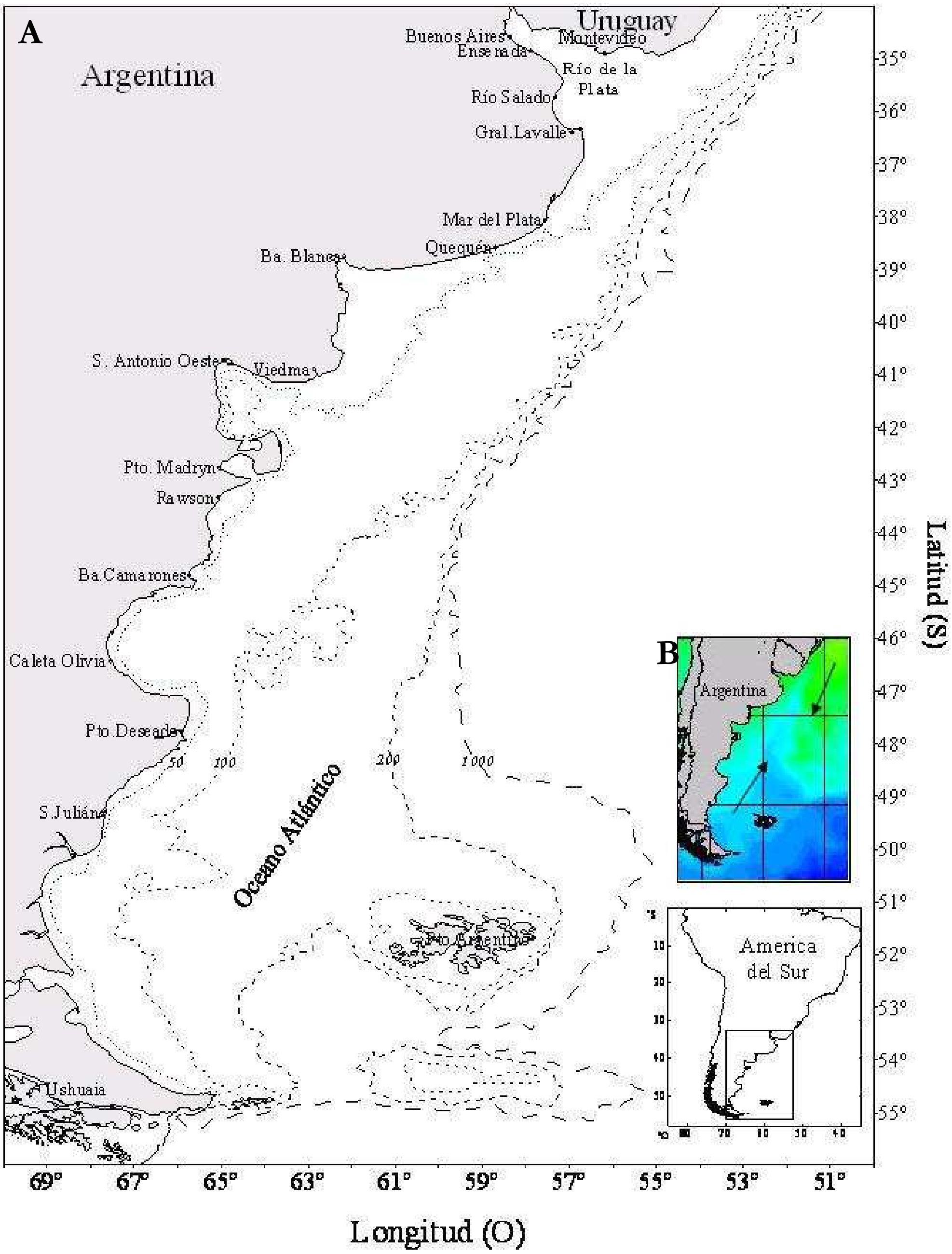


Figure 1 A: map of Argentina's coastal shelf showing depth contours down to 1000m,
B: general directions of the Malvinas (S→N) and Brazil (N→S) current with different SSTs

Scientists generally distinguish between the coastal/bonaerense district (distrito costero bonaerense) and the high seas district (here defined as 50 m depth and more, down to the continental edge at about 200m). Most species have ranges that roughly correspond to these borders.

Owing to these biogeographical characteristics, the fisheries sector is divided into two categories: the coastal fleet and the deep water fleet. In 1999 Argentinean fishery statistics reported 546 active, i.e. operating vessels (BEZZI et al. 2000).

Table 2
Composition of the argentine fishing fleet and its catches in 1999. Data from BEZZI et al. 2000. Species presenting more than 10% in the catches are shown.

	Vessel type	No	Landed catches	Predominant species
Coastal fleet	Coastal <18m	92	34.684 t	Argentine hake (*Merluccius hubbsi*), Striped weakfish (*Cynoscion striatus*)
	Coastal >18m	94	91.174 t	Arg. hake, Striped weakfish, Whitemouth croaker (*Micropogonias furnieri*), Argentine anchovy (*Engraulis anchoita*), Pink cusk-eel (*Genypterus blacodes)*
High seas fleet	Ice trawlers	109	188.623 t	Arg. hake, Arg. anchovy, Pink cusk-eel, Patagonien grenadier (*Macruronus magellanicus*)
	Freezing processing fleet	134	401.075 t	Arg. hake, Patagonian grenadier, Southern blue whiting (*Micromesistius australis)*, Argentine shortfin squid *(Ilex argentinus)*
	Longliners	10	6.558 t	Patagonian toothfish (*Dissostichus eleginoides*)
	Jiggers	107	290.835 t	Argentine shortfin squid *(Ilex argentinus)*
	Total	**546**	**1.012.949 t**	

The commercial coastal fleet is subdivided into two groups of vessels: boats <18m (rada o ría) and vessels with a length larger 18m. The high seas fleet mostly consists of trawlers, which are distinguished according to the type of processing on board. The traditional trawling fleet, i.e. ice trawlers work with refrigerated holds and provide the fish to factories on land. The freezing processing fleet on the other hand is equipped with the machinery to process the fishes on board. Other fleet types include Longliners and Jiggers (squid fishery) (COUSSEAU & PERROTTA 2004).

For long, sharks and rays which were caught as by-catch in Argentine hake or Whitemouth croaker (ground multispecies) fisheries were discarded at sea or used in the fish meal industry (MASSA et al. 2004b). A small fleet was landing condrichthyans since 1992, but the catch did not exceed 20 000 t annually. (MASSA & HOZBOR 2003). With the collapse of the hake fishery in 1994 fishers were forced to look for other exploitable species. Since then, and due also to the openings of new markets, landings of cartilaginous fishes greatly increased. In 2003, more than 31 600 t of elasmobranches were landed in Argentina, with the Narrownose smooth-hound shark (*Mustelus schmitti*) and Angel sharks (*Squatina* spp.) being the predominant species. Out of the 31 600 t, more than 17 000 t consisted of skates (rays of the family Rajidae). 9 450 t hereof were skates caught by the high seas fleet (MASSA et al. 2004a, see fig. 2 for the development of catches of skates in Argentina)

Both in commercial and artisanal fisheries, declared landings of skates have until recently been grouped under the general term 'rayas' (skates) and can therefore not be distinguished to species level (MASSA & HOZBOR 2003). This could have prevented the detection of population trends for single species (WAKEFORD et al 2004, DULVY et al. 2000). Therefore the INIDEP (Instituto Nacional de Investigación y Desarollo Pesquero) has been trying to promote the identification skills of fishermen and on-board observers to improve argentine fishing statistics, especially for rays. This program is ongoing and has already successfully conducted two courses for on-board observers and INIDEP staff respectively (pers. observation).

Figure 2: Development of declared landings of skates (family Rajidae) in Argentina (Falkland Islands not included). Data from MASSA et al. (2004b) and GARCIA DE LA ROSA et al. (2000)

The most important ports for skate landings in 1999 were Mar del Plata, Deseado and Madryn (GARCIA DE LA ROSA et al. 2000). Since 2000, one vessel - a longliner named "Sureste 501" is specifically landing skates. Its port of registry is Mar del Plata and it operates both near the coast (~50m) and along the 100m isocline, predominantly targeting *Dipturus chilensis*. Other species present in the catches in depths of ~50m are mostly *Sympterygia bonapartii* and *Atlantoraja castelnaui*, whereas in depths greater than 50m skates of the genus *Bathyraja* dominate in the bycatch (COLONELLO et al. 2002).

Around the Falkland Islands, a multi-species fishery is targeting skates since about 1989, when a Korean fleet entered the fishery (AGNEW et al. 1999). About eleven species of skates are caught, the most important being *Bathyraja griseocauda*, *B. albomaculata*, *B. brachyurops* and *Dipturus chilensis*. All other species, like *Amblyraja doellojuradoi*, *B. macloviana, B. scaphiops, B. multispinis, B. magellanica* and *Psammobatis spp.* constitute a rather minor part of the catch. Also mentioned in this latter group is one *Bathyraja. sp* (AGNEW et al. 1999) which most probably is the newly described *B. cousseauae (*Ana Massa *pers. com.).*

In conclusion it can be said that, during the last ten to twenty years, skates have become an economically important fish resource in Argentina (MASSA et al. 2001) and the lack of biological information on the species involved is therefore alarming. Up to now there is little to no data on population dynamics and growth parameters of *Bathyrajid* skates in Argentina. On top of this, there still exist methodological difficulties in the determination of age and growth in skates. This study therefore not only focuses on the estimation and interpretation of growth parameters, but also on the methodological part, investigating different processing techniques and comparing the outcome.

1.4 Study Objectives

General objectives

The general objectives of this study are to i) investigate different ageing methods for Argentinean *Bathyrajids* and ii) fit the length at age data obtained to the von Bertalanffy growth model. On basis of this growth model, the growth parameters will be estimated

Specific objectives

More specifically the objectives are i) to compare growth parameters between sexes (intra-specific) and between species and ii) to relate these growth parameters to biological or oceanographic conditions (total length, latitude etc.). iii) If possible, management necessities will be addressed.

2 Materials and Methods

Overview

2.1 Collection of samples

672 specimens of eight species of *Bathyraja* were caught during fourteen trips of the argentine research vessels Dr.E.Holmberg (INIDEP) and Cap.Oca Balda (INIDEP) between 2003 and 2005. Another 15 specimens came from a commercial longline fisher in November 2005. All specimens of *B. papilionifera* and *B. meridionalis* (20 and 13 individuals respectively) were captured in February 2004 by a research vessel of the Falkland Islands Fisheries Department. In total 720 specimens were therefore available for this study.

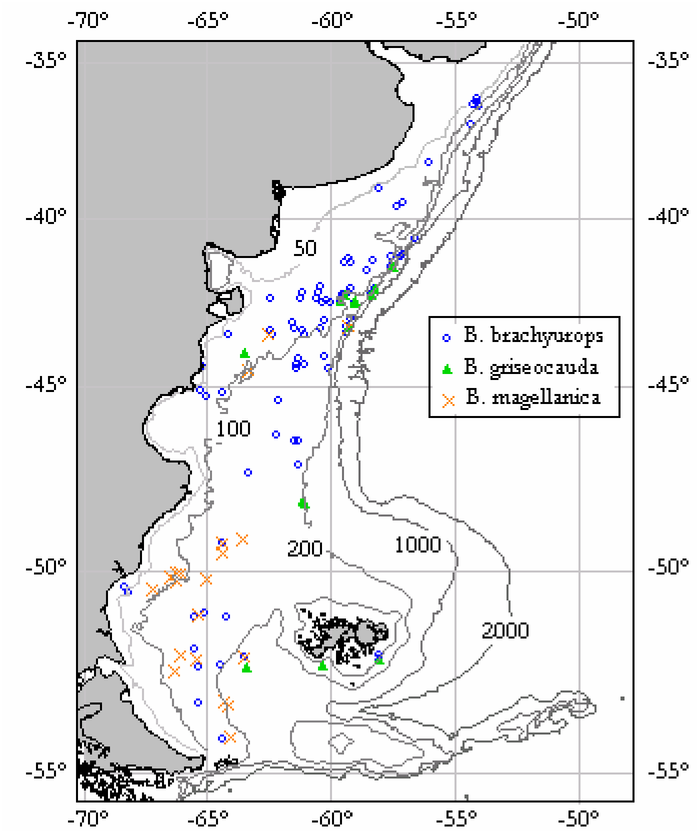


Figure 3: Catch map of *B. brachyurops, B. griseocauda* and *B.magellanica*

The argentine research vessels were operating with a bottom trawl, the duration of each trawl was about 30 min. Species were stored frozen and processed on land.

Length (TL) of each individual was measured to the nearest mm and sex was determined visually. For some samples, data for disc width (DW), maturity status and weight was also available.

For ageing, a part of the vertebral column consisting of approximately ten vertebrae was taken immediately from above the abdominal cavity. Thorns were either extracted from above the thoracic vertebral column or from the tail. Both was labelled and stored frozen in plastic bags.

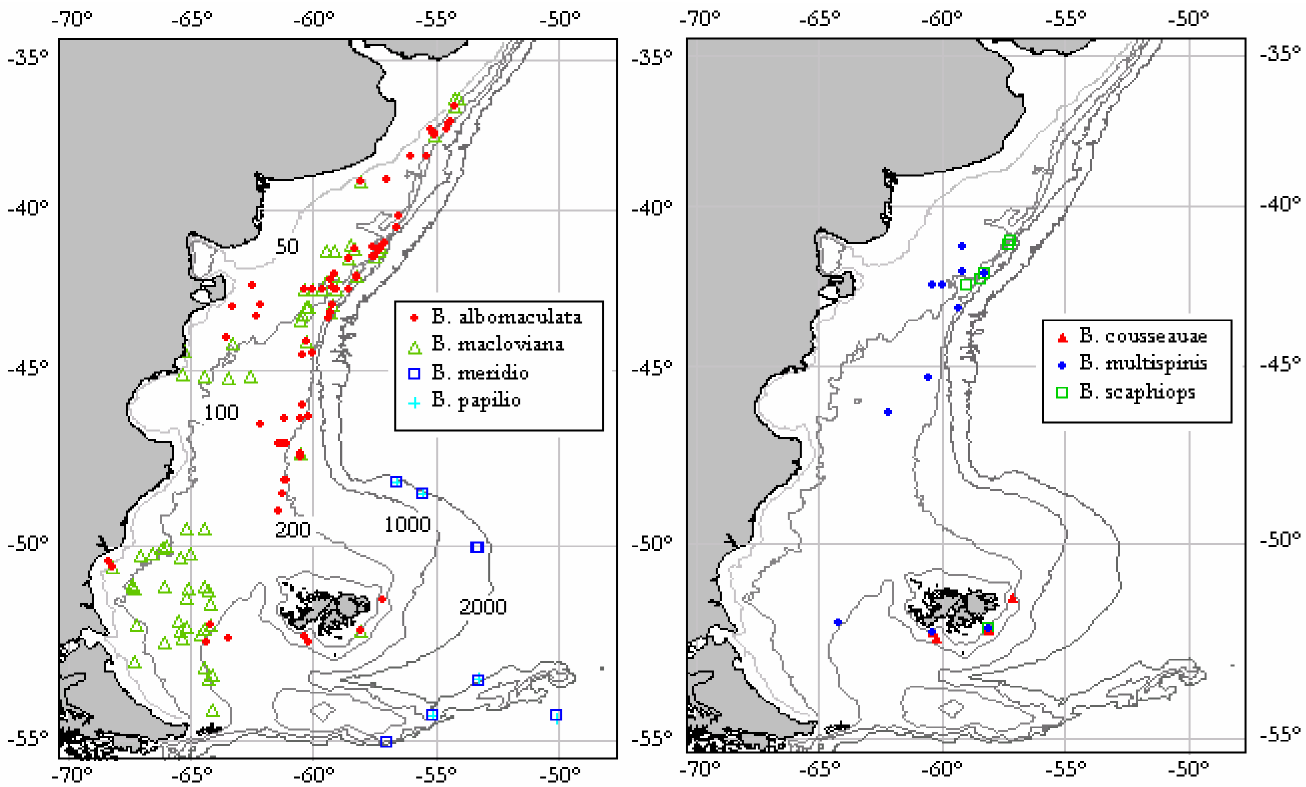


Figure 4: Catch maps **left**: of *B. albomaculata, B.macloviana, B.meridionalis* and *B.papilionifera*; **right:** of *B. cousseauae, B. multispinis, B. scaphiops*

Table 3
Depth range and maximum total length (TL) in samples with sample numbers

Species	TL range (cm) in samples		Depth range in samples	No. of samples
	Male	Female		
B. albomaculata	36.4 – 74.5	28.0- 77.5	66-399m	204
B. brachyurops	27.6 – 82.0	25.5 – 88.6	66-268m	193
B. cousseauae	51.1 – 108.2	52.2 – 113.9	209-344m	7
B. griseocauda	34.0 – 119.0	44.5 – 109.7	77-281m	40
B. macloviana	32.8 – 66.1	28.5 – 68.2	66-340m	158
B. magellanica	53.4 – 72.5	43.5 – 73.5	84-222m	63
B. meridionalis	121.2 – 128.3	95.2 – 146.1	930-2240m	13
B. multispinis	48.0 – 101.0	70.3 – 96.0	81-280m	13
B. papilionifera	76.8 - 129.5	76.8 – 132.5	930-1615m	20
B. scaphiops	43.0 – 74.5	43.5 – 82.8	121-209m	9

2.2 Preparation of hard parts

Cleaning

To remove flesh and connective tissue, vertebrae and if available thorns were put in a small flask with a 1% solution of 'Protex 6L enzyme' (pH 8-9). Protex 6L is a bacterial alkaline protease derived from a selected strain of *Bacilius licheniformis*.

In one step, 25 flasks with samples were thus filled up, and placed in a 65°C water bath. After about 1 ½ hours the flasks were checked and if necessary, the process was promoted by separating the vertebrae which still stuck together with a fine edged scalpel. The samples were then left another hour in the water bath before washing them under running tap water, pre-drying them and lastly putting them in labelled paper bags for storage.

Processing

Different methods to enhance visibility of growth rings (annuli) were tested on vertebrae and thorns respectively, which included cutting, staining, grinding and polishing.

Cutting: To obtain sagittal sections (see fig.5), the vertebrae were fixed in a plaque of epoxy resin which was left to dry for a day. One plaque consisted of three rows (1 to 3) with six columns (A to F), which allowed to choose 18 individual vertebrae for each plaque. The columns were then cut with a double bladed saw with spacers (thickness about 0.4-0.8 mm). A second plaque identical to the first one was prepared and processed in order to have two sections of the same individual.

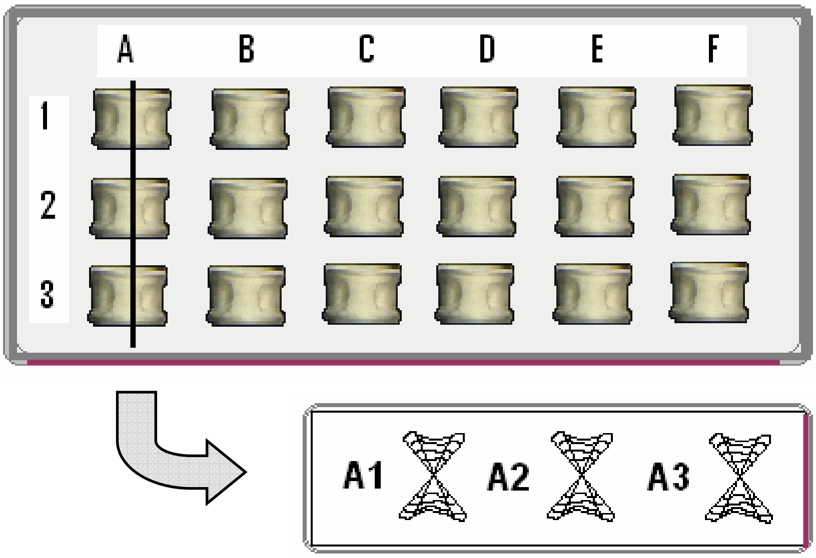


Figure 5: Schematic view of a plaque consisting of three rows and six columns. The black line on column A shows the direction of the cut and on the lower right side the resulting thin section of three vertebrae (sagittal cut) is illustrated

It was also tested if halved vertebrae were apt for ageing, so that during the testing period, for some samples vertebrae were only cut once through the longitudinal axis.

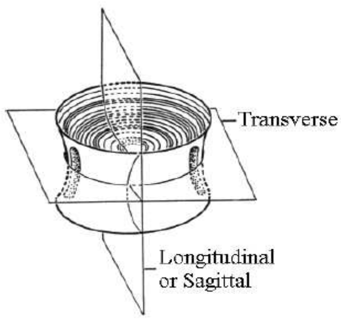


Figure 6. The two sectioning planes that can be used on vertebral centra. (Courtesy of G.M. Cailliet, Moss Landing Marine Laboratories.)

Staining: Sagittal sections as well as whole vertebrae were stained with alizarin red and crystal violet experimenting with different staining times (see table 4). Thorns were stained with silver nitrate and the readings compared to the ones for vertebrae of the same individual. A new method using potassium permanganate and ammonium hydroxide was also tested on the sagittal sections (for more information contact Dr Ernesto Christiansen in the Fisheries Research Institute INIDEP, Mar del Plata).

Table 4
Overview of stains used and the range of duration and concentration which was tested

Stain	Duration	Concentration	Hard structure
Alizarin Red	few min. to several hs.	Aqueous solution (saturated)	Vertebrae
Crystal violet	one minute to two hs.	0.005-0.01%	Vertebrae
Silver nitrate	30 to 40 min	1%	Thorns
Potassium permanganate	45 min to one hour	3%	Vertebrae

2.3 Reading of hard parts and validation of readings

Most authors (e.g. CAILLIET et al 1983; SCHWARTZ 1983) distinguish between rings and bands, the latter of which consist of a group of rings. In sagittal sections, bands with widely spaced rings appear as translucent and present areas of faster growth in summer whereas bands with tightly spaced rings are opaque and correspond to slower growth zones in winter. An annulus is usually defined as the winter band (GOLDMAN 2004). The easiest way to read a sagittal section is to follow the bands on the corpus calcareum into the intermedialia (see fig. 7). Bands have to be distinguished from checks, which are "opaque growth zones, denoting a slowing of growth that forms within the translucent zone" and which "do not form annually but reflect various environmental or physiological changes" (WISCHNIOWSKI et al 1998).

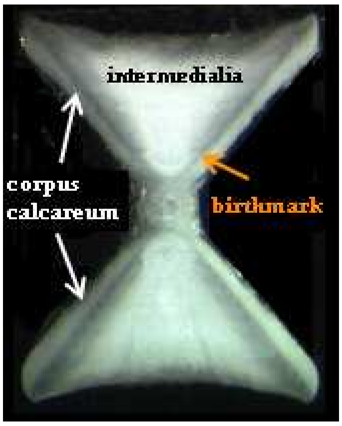


Figure 7: Sagittal section of a vertebra showing diffenent structures

Band counts were made independently by two readers without prior knowledge of TL or the age reading of the other reader. Due to lag of time of the second reader though, this procedure could only be maintained for *B brachyurops*. The first reader therefore made two independent reads in randomized, blind trials for the other species. If first and second read differed, the following procedures were initiated.

- If the reads differed by one year, a third (blind) read was made
- If the reads differed by two years, the mean of the reads was taken
- If the reads differed by three or more years, the sample was discarded

The birthmark, which can usually be discerned by an angle change along the intermedialia-corpus calcareum surface was defined as band 0 (e.g. GOLDMAN 2004).

Before using the age data obtained from the readings, precision of readings was measured. Percent of reader agreement (No. agreed/No. read) was calculated, as well as percent agreement ± one year, agreement ± two years and agreement ± three and more years (GOLDMAN 2004). Additionally Chang's Coefficient of Variation (CHANG 1982) was estimated using the following equation:

$$CV_j = 100 \times \frac{\sqrt{\sum_{i=1}^{R} (X_{ij} - X_j)^2}}{X_j}$$

Where X_{ij} is the *i*th age determination of the *j*th fish, X_j is the age of the *j*th fish and R is the number of times each fish was aged.

Also age bias plots were created by plotting the ideal-readings 45° line against the regression line of read one vs. read two (and Reader one vs. Reader two in *B. brachyurops* respectively). If the regression line parameters were within the confidence interval of the parameters (slope and intercept) of the ideal 45° line, then it was assumed that there was no bias in the readings and the data could be used to create growth models.

2.4 Age verification

Due to the relatively low amount of samples, length frequency analysis proved to be inefficient for age verification in this case. The method of choice therefore was a **centrum edge analysis**. Centrum edges were observed under magnification and it was tried to determine if the edge was translucent or opaque. Owing to the tight spacing of bands at the centrum edge, the author could not reliably decide on the nature of the edge, so that the analysis was eventually discarded and is therefore not mentioned further in this paper. Unfortunately no other methods could be administered so that verification of ages was not possible.

2.5 Data Interpretation

Growth parameters (L_∞, k, t_0) were derived by fitting length at age data to the **von Bertalanffy growth function (VBGF)** with the following equation:

$$L_t = L_\infty \cdot (1 - e^{(-k(t-t_0))}) \qquad \text{von Bertalanffy}$$

Where L_t = predicted length at age 't' , L_∞ = the asymptotic (max.) length, k = the growth co-efficient and t_0 = age or time when length theoretically equals cero.

The growth model parameters were estimated with Marquardt least-squares nonlinear regression. The model was implemented by using STATISTICA data analysis software system (STATISTICA version 6. StatSoft, Inc. 2001). As far as the sample number allowed, sexes were treated separately and were tested for differences using the Hotelling T^2 test (α=0.05).

Mean lengths at ages five to eight were compared via ANOVA (α=0.05) for the four most abundant species, namely *B. albomaculata, B. brachyurops, B. macloviana* and *B. magellanica.* The results were visualized using Box and Whiskers Plots for every age class.

Growth parameters were compared directly and via calculation of the growth performance index (ø') as by GAYANILO et al. (1992):

$$ø' = \log_{10}(k) + 2 \cdot \log_{10}(L_\infty)$$

Infinite length was plotted against the growth coefficient k to derive a possible relationship between these parameters.

A comparison of vertebral structure was also tried separating the species according to the degree of calcification of the vertebrae. This was done visually looking at all samples. Photos of whole and sectioned vertebrae were taken using a computer based camera system and the OTOLITOS Program of the Fisheries Research Institute INIDEP, Mar del Plata..

3 Results

Overview

3.1 Morphological comparison of vertebrae

When looking at the morphology of the vertebrae it becomes apparent that there are rather great differences in the structure and calcification between species. To simplify, vertebrae were here assigned to one of three groups, namely 'mineralized', 'intermediately mineralized' and ''sparsely mineralized'. In the first group, *B. albomaculata* (albo), *B.brachyrops* (bb), *B. macloviana* (maclo) and *B. magellanica* (magell) showed mineralized intermedialia and a therefore more or less rectangle-like shape of the vertebrae when viewed from above.

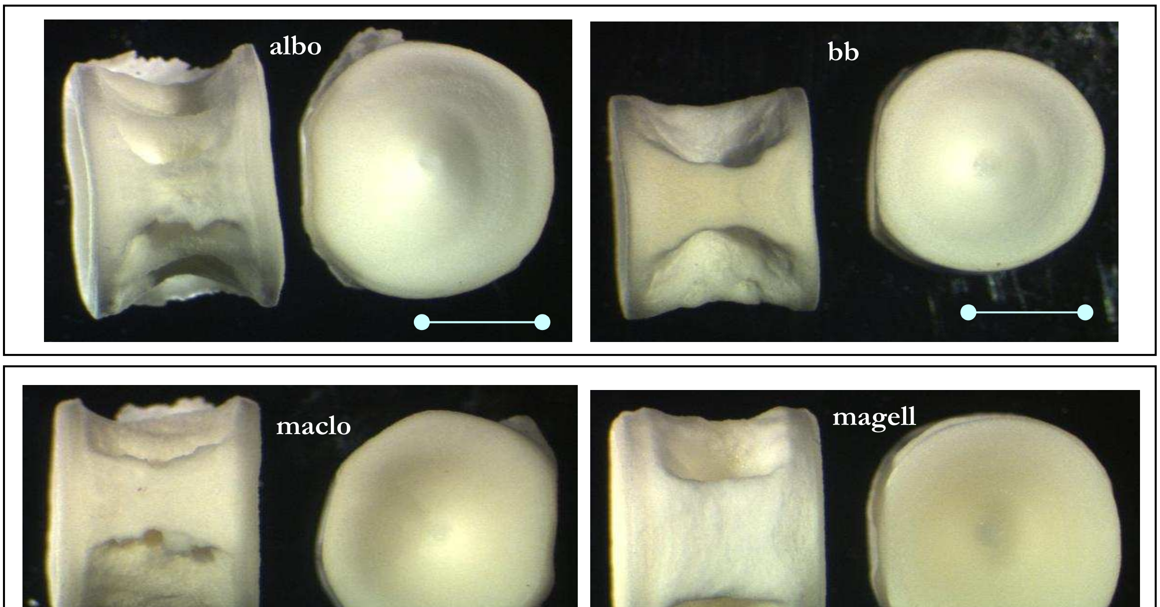


Figure 8. Vertebrae of *B. albomaculata* (albo)*, B.brachyrops* (bb), *B. macloviana* (maclo) and *B. magellanica* (magell) in dorsal (left) and front view (right), scale bar always 2cm

The second group consists of intermediately mineralized vertebrae which mostly have a whole through the focal point but still have moderately mineralized intermedialia. These characteristics were seen in vertebrae of *B. griseocauda* (griseo) and *B. multispinis* (multi).

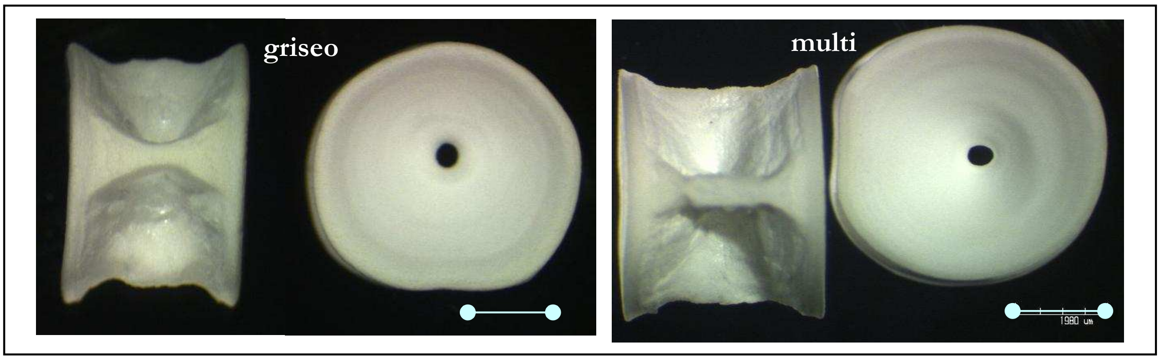


Figure 9. Vertebrae of *B. griseocauda* (griseo) and *B. multispinis* (multi), scale bar is 2cm

Group three contains poorly mineralized vertebrae with no real intermedialia visible. Sagittal sections were therefore hard to read or not readable at all. *B. cousseauae, B. meridionalis*, *B. papilionifera* and probably *B. scaphiops* were representatives of this group. For *B. scaphiops* too few vertebrae of too few individuals were available to make reliable conclusions.

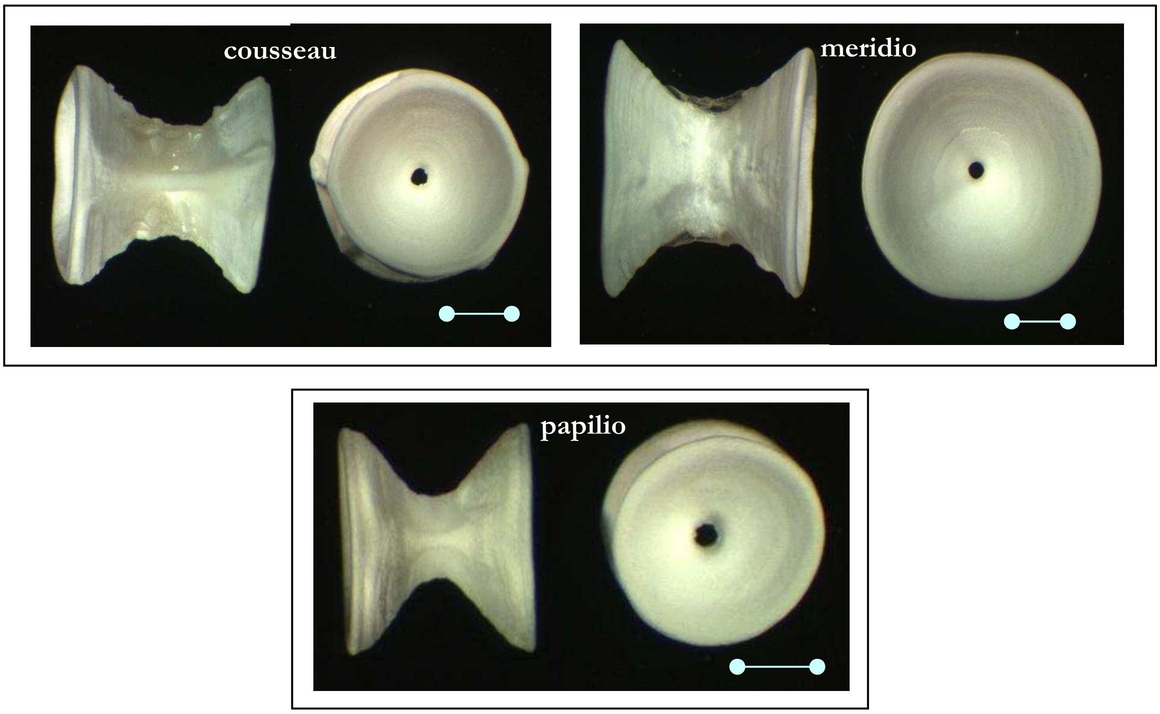


Figure 10. Vertebrae of *B. cousseauae* (cousseau)*, B: meridionalis* (meridio) and *B. papilionifera* (papilio), scale bar is 2cm

In general, vertebrae of small individuals differed sometimes from the ones of larger individuals of the same species. The above mentioned groups though were rather reliably based on common characteristics of a species within its size range.

3.2 Reader precision/bias

As already mentioned in the Material & Methods part, a second reader was only available for *B. brachyurops*. Therefore the 'between reader' precision could be estimated for this species, whereas in all other species 'within reader' precision was calculated. For the other five species reader precision was not estimated due to the low number of readings. As can be seen in table 5, precision of readings varied between species. In *B. albomaculata* ten individuals (4.9%) had to be discarded due to a reading difference of three or more years. This was slightly lower in *B. brachyurops* (4.1%) and *B. macloviana* (3.2%).

Table 5

Statistics of age readings. For *B. brachyurops* this refers to two different readers (between reader statistics), for the other four species it refers to within reader statistics. Total sample number as well as numbers discarded due to reader difference of three or more years are given.

Species	n (and n discarded)	Percent agreement of first and second read (reader*)				Chang's coefficient of variation
		Agreed (0)	±1	±2	±3	
B. albomaculata	204 (10)	56%	24%	15%	5%	7.9%
*B. brachyurops**	193 (8)	54%	30%	12%	4%	9.2%
B. griseocauda	40	55%	40%	5%	0%	9.8%
B. macloviana	158 (5)	71%	23%	3%	3%	7.5%
B. magellanica	63	70%	25%	5%	0%	8.1%

Age bias plots showed slight differences in first and second reading for all species (see 11 to 15), but only for *B. albomaculata* intercept and slope varied significantly from cero and one respectively (i.e. numbers were not in the range of the confidence interval). This means that there was a systematic error in these readings and the growth parameters should be seen as an estimate.

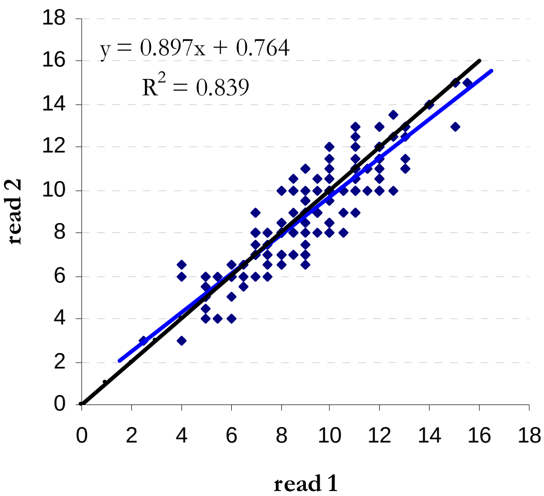


Figure 11: Age bias plot for *B. albomaculata*

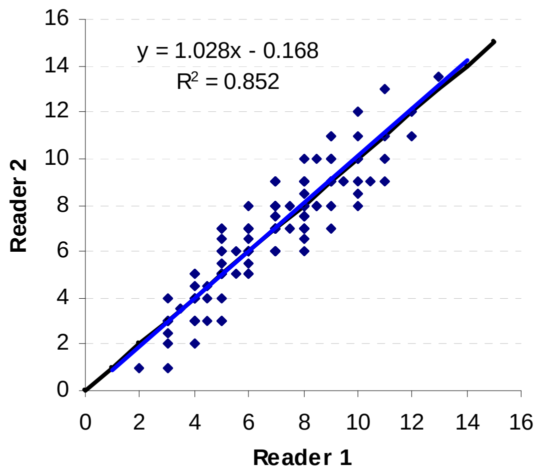


Figure 12: Age bias plot for *B. brachyurops*

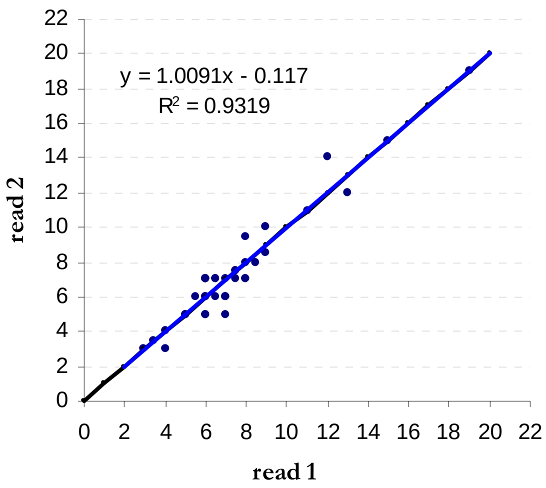


Figure 13: Age bias plot for *B. griseocauda*

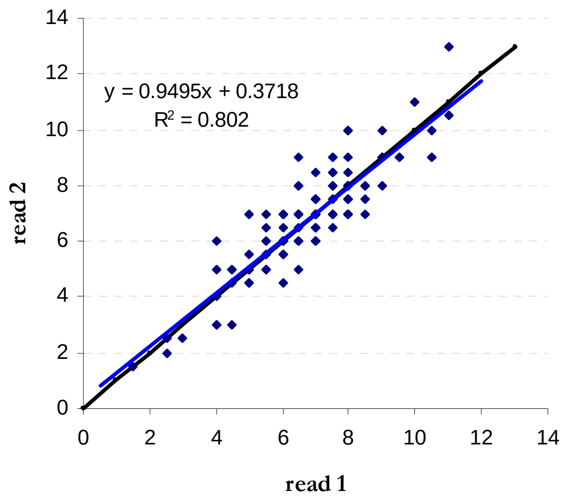


Figure 14: Age bias plot for *B. macloviana*

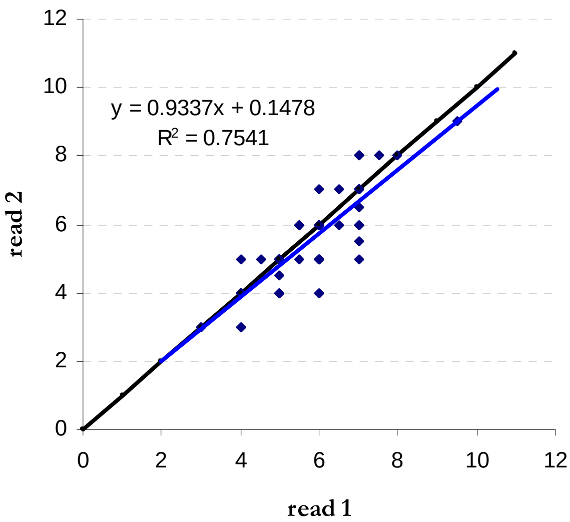


Figure 15: Age bias plot for *B. magellanica*

Fig. 11-15: Age bias plots showing the difference of the ideal 45° line (black) to the actual readings (blue). Regression equation and correlation coefficient are given for each species.

3.3 Methods of choice

In different species, different methods of treating the vertebrae proved best (see table 6). The alizarin red (AR) method was discarded after the first few trials since it was quickly found that the results are not satisfactory. Only few thorns were tested (n=30) due to lack of time. Results proved promising in *B. brachyurops* and *B. griseocauda* showing full or close (±1) agreement to the vertebral reads in 62%. Thorns of *B. macloviana* and *P. papilionifera* though were mostly difficult to read or not at all. The general problem was, that some thorn samples were taken from above the abdominal cavity whereas others were taken from the tail, where thorns are generally larger and not as worn out. This information was not noted down. Thorn samples were therefore not consistent and it couldn't be determined if excision site (on tail or on disc) is influencing readability or if physiological factors play a role.

Table 6

Overview of methods tested on the species (X). Respective methods which worked best are put in bold (**X**). <u>**X**</u> means this method has been used for age parameter calculation. All methods were tried on sagittal sections of vertebrae, exception are thorns and methods on whole vertebrae (*). AR=alizarine red, CV= crystal violet, PP=new method with potassium permanganate, SN= silver nitrate.

Species	**Vertebral sections (*whole)**				**Thorns**
	no stain	**AR**	**CV**	**PP**	**SN**
B. albomaculata	<u>**X**</u>		X	X	
B. brachyurops	X	X	<u>**X**</u>	X	X
B. cousseauae	X		X	X	
B. griseocauda	<u>**X**</u>			**X**	X
B. macloviana	**X**	X	<u>**X**</u>		X
B. magellanica	X		**X**	<u>**X**</u>	
B. meridionalis	X		X	<u>**X**</u>*	
B. multispinis	<u>X</u>		X	X	
B. papilionifera	X		X	<u>**X**</u>*	X
B. scaphiops	<u>X</u>		X	X	

For vertebral sections of ***B. albomaculata,*** crystal violet (CV) and potassium permanganate (PP) staining was both satisfactory, though in the end these methods were only applied for crosschecking the readings of unstained sections, when these were hard to read (reason for poor readability of some samples not known).

In ***B. brachyurops*** it was found that sagittal sections of vertebrae stained with crystal violet rendered the best results, although readability also varied between individuals. Some individuals could be read without staining, but it was observed that the risk of counting checks (definition see Materials&Methods) was high when not staining the sections.

Individuals of ***B. macloviana*** could be read both without staining and with CV stain. Comparison of 89 readings with both methods showed close agreement of readings (>70%) and no bias as to counting higher or lower ages (see fig. 16 left).

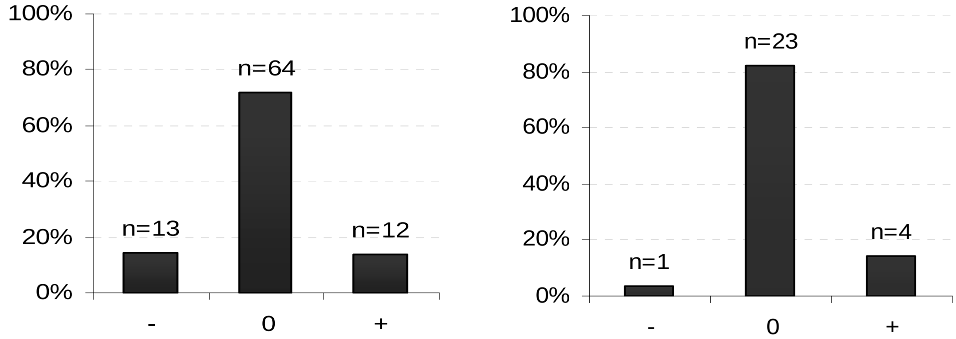


Figure 16. left: comparison of readings of unstained to stained (CV) sections of *B.macloviana*; **right**: comparison of readings of unstained to stained (PP) sections of *B.griseocauda* .'0' is full reading agreement, '-' means readings were lower (≥1) in unstained sections, '+' means readings were (≥1) higher in unstained sections

In ***B. griseocauda*** unstained and stained (PP) sections could both be read rather well, though when comparing the readings of 28 individuals slight bias of reading older ages in unstained sections was visible (see fig. 16 right).

B. magellanica. For this species staining with CV and with PP rendered equally good results. Banding pattern differed considerably from all other species though (annuli were broader spaced, see pictures in the appendix). A comparison of readings with different stains showed close agreement (fig. 17 left). When comparing stained (CV+PP) to unstained sections though, a bias to higher ages for readings of unstained sections was apparent (see fig 17 right).

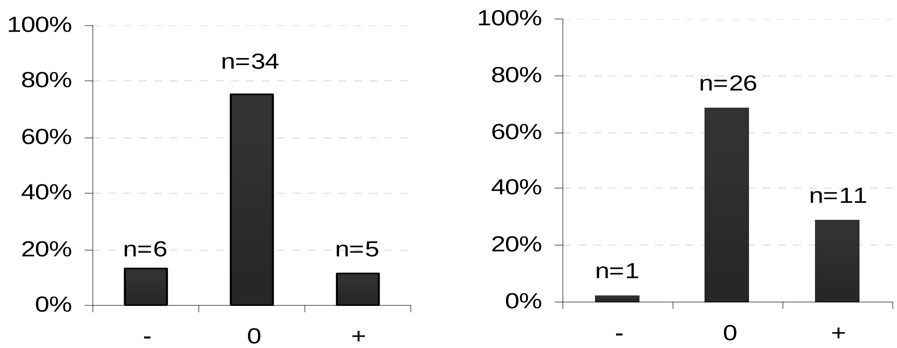


Figure 17. *B.magellanica.* left: comparison of readings of PP to CV stain. **right**: comparison of readings of unstained to stained sections (CV+PP). '0' is full reading agreement, '-' means readings were lower (≥1) in PP stained sections (left) and unstained sections (right)), '+' means readings were higher (≥1) in the PP stained (left) and unstained (right) sections)

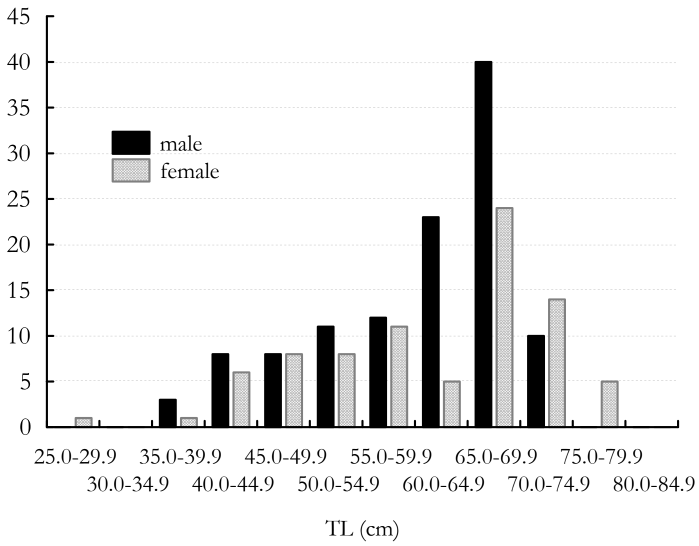
B. cousseauae, B. scaphiops, B. multispinis, B. papilionifera and ***B. meridionalis*** were found to be more difficult to age, due to a lack of calcification in the intermedialia. Sagittal sections were therefore hard to read, but in the first three species a (preliminary) reading was possible. With the last two species (***B. papilionifera*** and ***B. meridionalis***) a different method was tested, which has successfully been used on vertebrae of *Mustelus schmitti* in Argentina (Natalia Hozbor pers. com.) namely a modification of the PP stain on whole (or halved) vertebrae. The ages obtained are to be taken as a first approach for age readings of these species, but an underestimation of ages is to be expected due to low resolution of bands along the edge.

3.4 Growth curves and parameters

As far as sample number allowed, in the following the **catch** composition and distribution were described for every species, and a comparison of **mean length at ages five to eight** for individuals north and south of 45°S was made (to detect intraspecific latitudinal changes in total lengths). Furthermore, **growth parameters** as well as maximum estimated age (**T_{max}**) and **birth-length** are presented.

Bathyraja albomaculata

Samples consisted more of males than females, though most of the bigger individuals were females. Small sizes were generally underrepresented. Noticeable was the high number of males in size class 65-69.9cm (fig. 18). Sexes had to be combined for the estimation of growth parameters because of the lack of small sized individuals in both, males and females, and also because of the above mentioned doubts in reading consistency (see page 19).



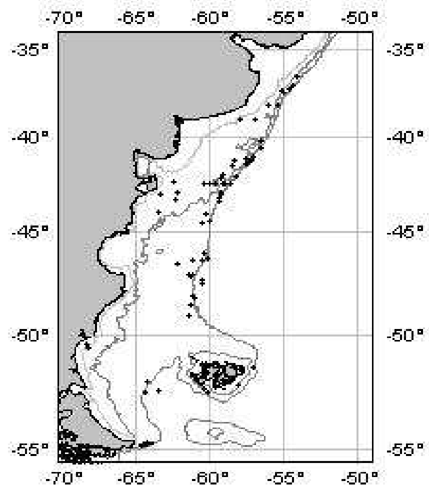


Figure 18. left: Length frequency of samples of *B.albomaculata*, n(male)=116, n(female)=83, five of unknown sex not shown; right: distribution of catches with depth contours of 50m, 100m and 200m shown.

Catches of *B. albomaculata* showed an overall more northerly distribution, over 70% of the individuals have been caught north of 45°S. Only about 20% were found in depths of less than 100m, the rest was mostly distributed along the shelf edge (fig. 18 right). **Mean length at ages five to eight** for individuals north and south of 45°S respectively were compared using an ANOVA (α=0.05), but no significant differences could be found in any of the age classes.

The **von Bertalanffy parameters** derived by the combined sexes growth curve were: L_∞ = 89.3cm, k = 0.128 and t_0 = -0.44. The maximum estimated age (**T_{max}**) was 13 years for males and 15 years for females. According to the combined von Bertalanffy growth curve the **birth-length** would be 5.0cm.

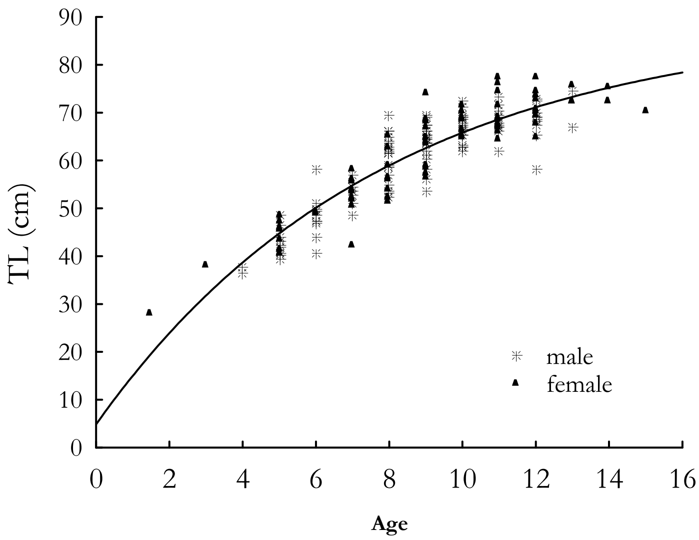
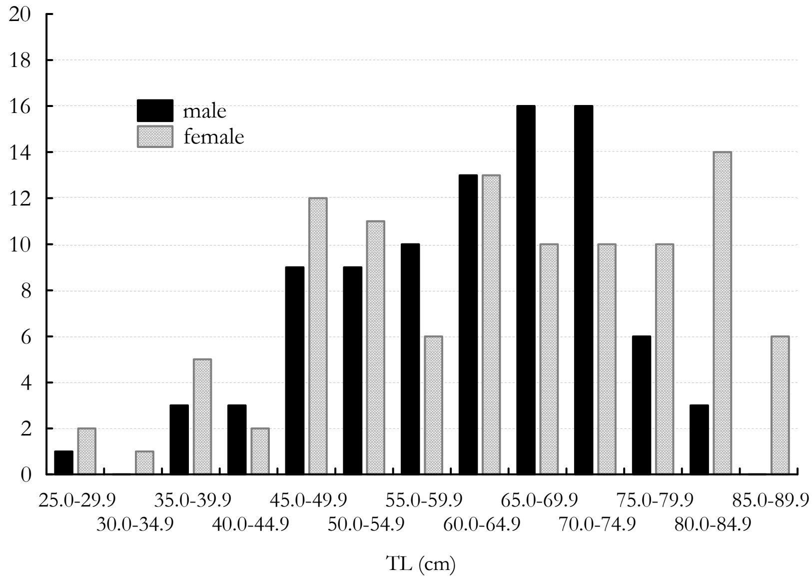


Figure 19. Von Bertalanffy growth curve for *B. albomaculata*. Sexes combined. Y-axis shows TL in cm, X-axis the rings counts (age)

Bathyraja brachyurops

Samples of *B. brachyurops* were available in a wide length range, though as in *B. albomaculata*, small individuals were rather underrepresented and the largest individuals were predominantly females.



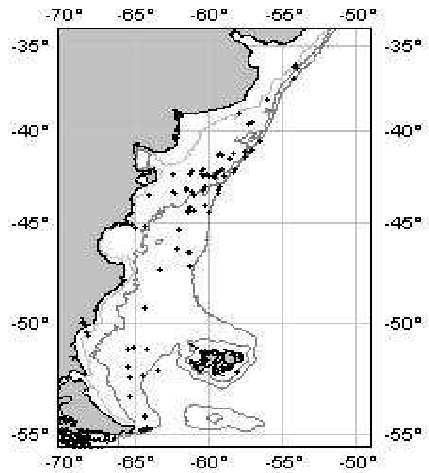


Figure 20: left: Length frequency of samples of *B.brachyurops*, n(male)=89, n(female)=102, two of unknown sex not shown. Notice different scale than fig.18!. **right**: distribution of catches with depth contours of 50m, 100m and 200m

About 80% of the *B. brachyurops* in this study were caught north of 45°S. A little more than half of the **catches** (55%) were from below 100m depth, which suggests a wide distribution along the continental shelf with no evident clustering along the continental edge. No differences of **mean length at ages five to eight** for individuals north and south of 45°S respectively could be identified.

Von Bertalanffy growth parameters were derived for both sexes separately but also for combined sexes. For males: L_∞ = 114.7cm, k = 0.094, t_0 = -1.63, for females: L_∞ = 107.4cm, k = 0.128, t_0 = 0.52, Sexes combined: L_∞ = 116.9cm, k = 0.099, t_0 = -1.19. A comparison of growth parameters between sexes showed no significant difference. Estimated T_{max} was 12 ys for males and 13 ys for females. **Birth-length** for males was calculated (taking the respective VBGF) to be 15.6cm for males, 7.0cm for females and 13.1cm for both sexes.

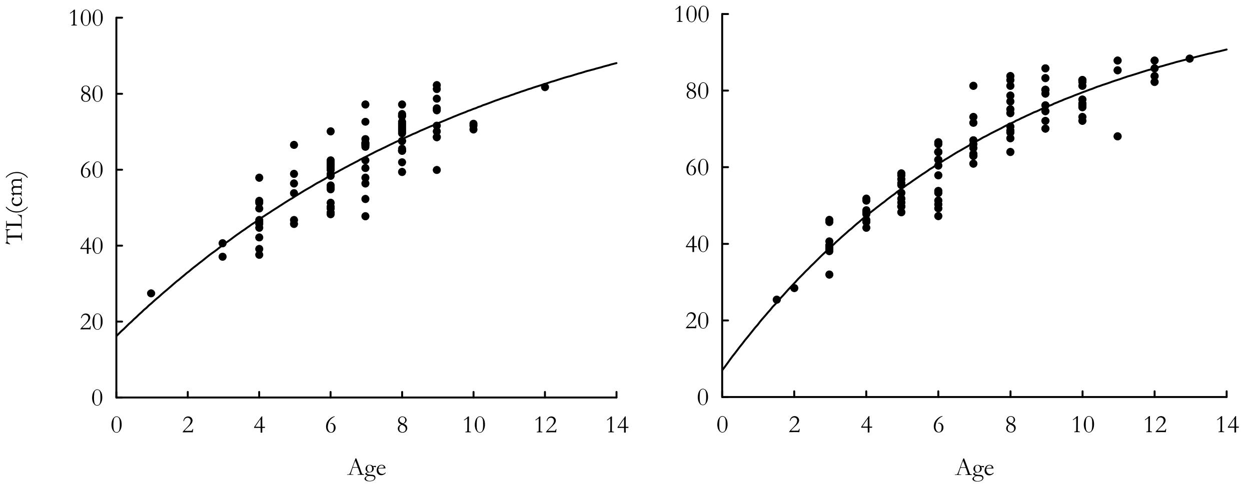


Figure 21. Von Bertalanffy growth curve for male (left) and female (right) *B.brachyurops*. Y-axis shows total length in cm, x-axis the ring counts (age).

Bathyraja griseocauda

Only 40 individuals of *B. griseocauda* could be investigated, but at least some individuals from both ends of the length range were available. Sexes combined for the estimation of growth parameters though, due to the low sample size.

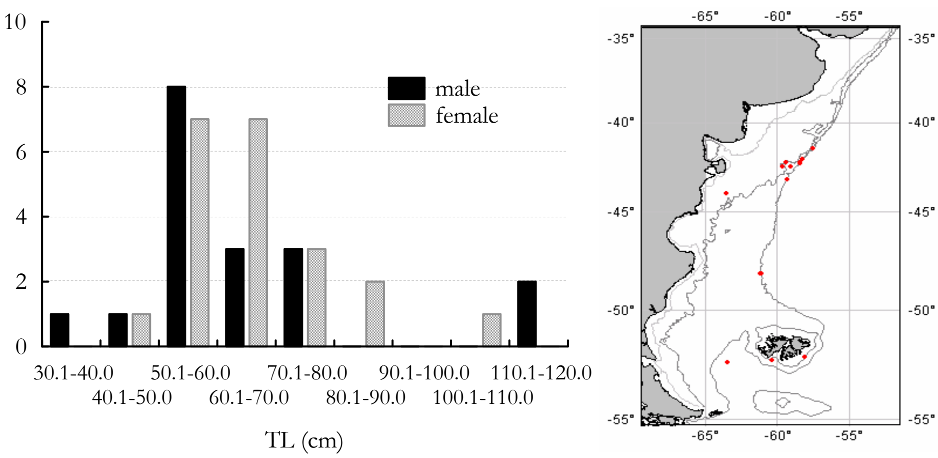


Figure 22. left: Length (cm) frequency of samples of *B.griseocauda*, n(male)=18, n(female)=21, one of unknown sex not shown. Notice different scale. **right**: distribution of catches with depth contours of 50m, 100m and 200m, points are drawn in red for better visibility

B. griseocauda was mostly **caught** north of 45°S, only about 18% of the samples came from the southern part of the continental shelf. Six out of the 40 specimens (15%) were found in depths of less than 100m, the rest was seemingly clustering along the shelf's edge. Differences in **mean length at ages five to eight** couldn't be compared due to the low sample number south of 45°S.

Growth appears to be rather uniform, with no pronounced change in the slope of the von Bertalanffy growth curve (fig. 23). **Growth parameters** for combined sexes were: $L_\infty = 169.9$cm, $k = 0.064$, $t_0 = -0.61$.

The largest individual, a 119 cm large male, was also estimated to be the oldest (**T_{max}** = 19 years). The **birth-length** was 6.1cm according to the von Bertalanffy growth curve.

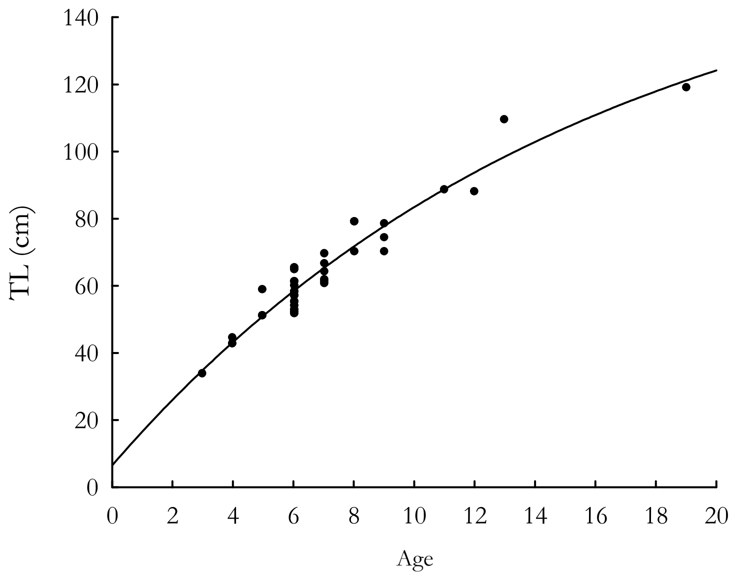


Figure 23. Von Bertalanffy growth curve for *B.griseocauda,* sexes combined

Bathyraja macloviana

In total 158 individuals of *B. macloviana* were processed. Few of the small sized ones were available though, and larger individuals were, as with most other species, predominantly females. The depth distribution showed a slight increase of **catches** in deeper waters. 62% of the specimens were caught in depth of more than 100m, but there was no evident accumulation of catches along the continental slope.

Growth parameters were calculated for males and females separately, as well as for combined sexes. Male: $L_\infty = 71.1$cm, $k = 0.235$, $t_0 = -0.38$, female: $L_\infty = 77.0$cm, $k = 0.176$, $t_0 = -0.97$, combined sexes: $L_\infty = 74.7$cm, $k = 0.194$, $t_0 = -0.79$. The Hotelling T^2 Test revealed no significant difference between sexes. As far as the latitudinal distribution is concerned, the catches seemed to be partitioned into a northern and southern population. Half of the specimens were caught north of 45°S and half of them south of this latitude. It was therefore also tested if there is a difference in growth parameters when samples are divided into a theoretical northern (north of 45°S) and southern (south of 45°S) population (see fig. 24 right). But parameters proved to be in the range (mean ± SE, see table 7) of the ones for combined sexes, meaning that there was no obvious latitudinal change of growth parameters (i.e. also for **mean length at ages five to eight**) in this species.

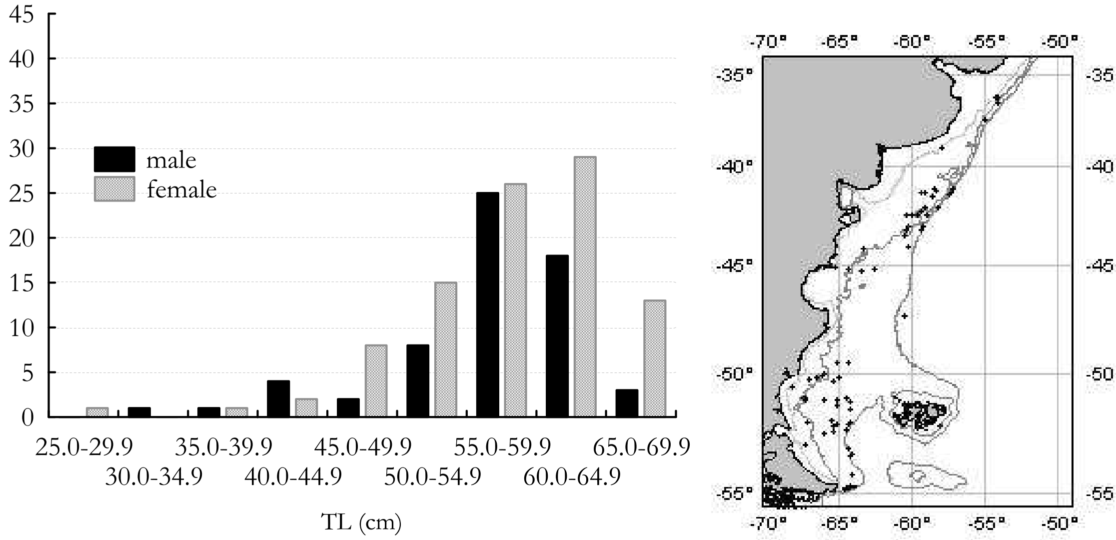


Figure 24. left: Length (cm) frequency of samples of *B.macloviana*, n(male)=62, n(female)=95, one of unknown sex not shown. Scale as in fig.18. **right**: distribution of catches with depth contours of 50m, 100m and 200m

Maximum estimated age (**T_{max}**) was 11 years for males, and 12 years for females. According to the respective von Bertalanffy growth curve the **birth-length** was calculated to be 6.2cm for males, 12.3cm for females and 10.4cm for the combined sexes.

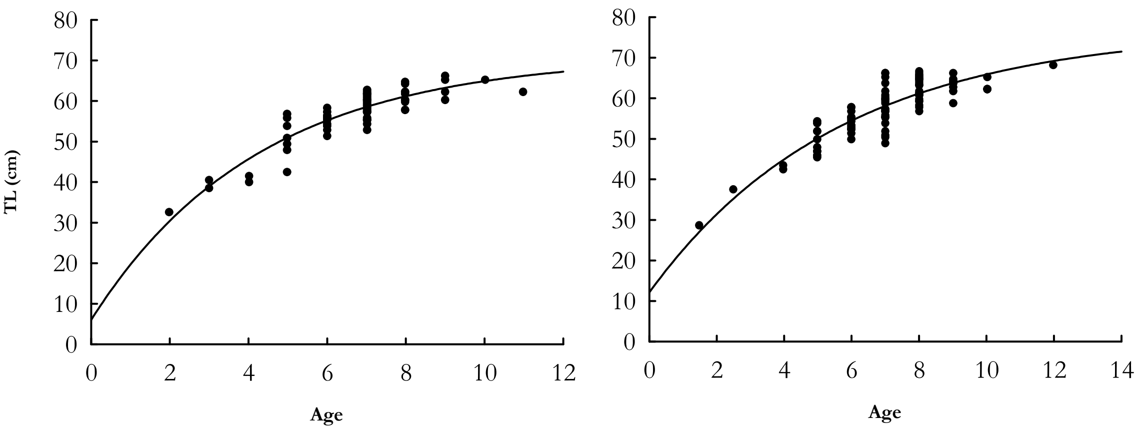
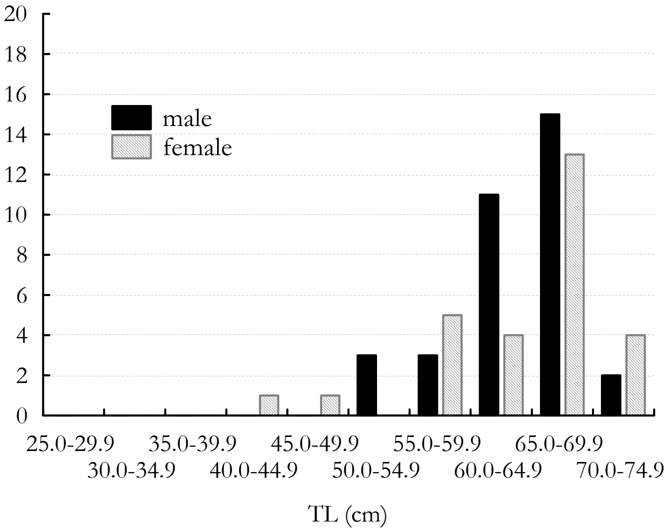


Figure 25. Von Bertalanffy growth curve for male (left) and female (right) *B.macloviana*. Y-axis shows total length in cm, x-axis the ring counts (age).

Bathyraja magellanica

In *B. magellanica* especially small sized individuals were completely missing. Larger specimens weren't predominantly females as in the other species and for the intermediate size class males were more abundant in the **catches**. *B. magellanica* was predominantly caught in the southern part of the Argentinean shelf (92%). Depth distribution was relatively homogeneous with 46% occurring in depth of less than 100m.



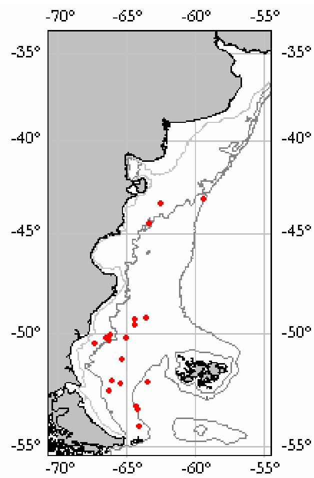


Figure 26. left: Length (cm) frequency of the samples of *B.magellanica*, n(male)=34, n(fem)=28, one of un-known sex not shown. Scale as in fig.20. **right** figure shows distribution of catches with depth contours of 50m, 100m and 200m

For the estimation of **growth parameters** sexes were combined due to the low samples size especially for small individuals. What's more, an additional data point namely the birth-length had to be derived by back-calculation of sizes at ring '0' (taking ring measurements of vertebral sections) using the quadratic-modified Dahl-Lea formula. **Birth-length** was estimated to be around 10cm (10.1cm, mean of n=7), this data point was added to the growth curve. Compared to the other species, the growth coefficient k was highest in *B. magellanica* with k = 0.357. Growth of young ones seems to be rather fast, flattening out at the age of four already (fig.27). L_∞ was estimated to be 74.7cm and t_0 =-0.37. Maximum age (**T_{max}**) was read to be nine years for a female with a total length of 73.5cm, which was also the largest individual in the catches.

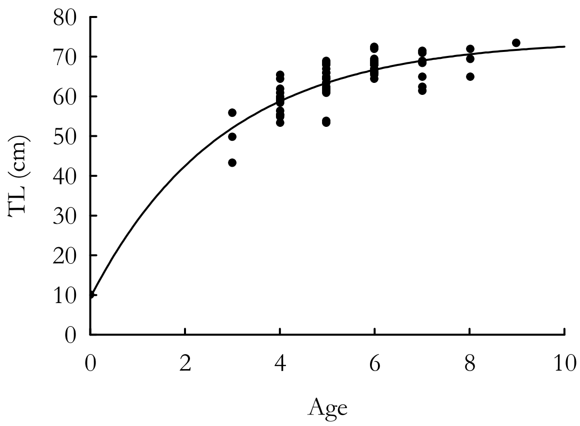


Figure 27. Von Bertalanffy growth curve for *B.magellanica*

Bathyraja spp.

For the other five species of *Bathyraja* only few samples were available. Compared to their possible maximum lengths there were mostly small individuals in *B. cousseauae* and *B. multispinis* and mostly large individuals in *B. papilionifera* and *B. meridionalis* (see fig. 28). The length range of *B. scaphiops* was, despite the low numbers, fairly representative. Only for *B multispinis* a preliminary growth curve was drawn, for the other species the available age at length data is shown in a scatter plot (fig 30-34). For an overview of catch locations please refer to fig.4.

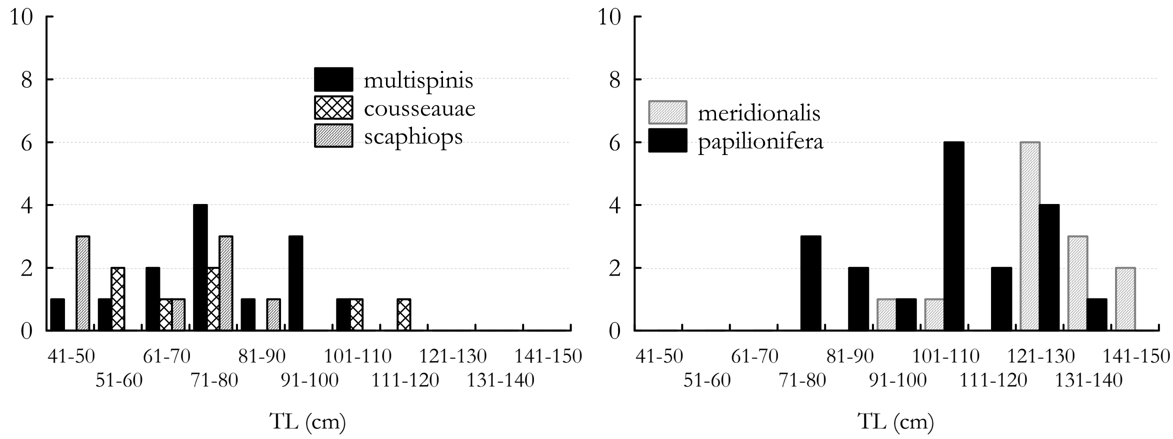


Figure 28. Length frequencies of *B. cousseauae* (n=7), *B. meridionalis* (n=13), *B. multispinis* (n=13), *B. papilionifera* (n=20, plus one of unknown size) and *B. scaphiops* (n=9), sexes combined. Scales as in fig. 22.

All thirteen individuals of ***B. multispinis*** could be aged (fig. 29). The biggest specimen (101.0cm) was also estimated to be the oldest ($\mathbf{T_{max}}$=14 ys). Nevertheless, young specimens as well as old ones were scarce, and additional data will probably change the appearance of the curve. Sample number was too low to compare **mean lengths at ages five to eight**.

The preliminary **VBGF** (both sexes) was: $L_t = 145.5*(1-e^{-0.073*(t+2.41)})$. Taking this growth function, the **birth-length** was calculated to be 22.6cm.

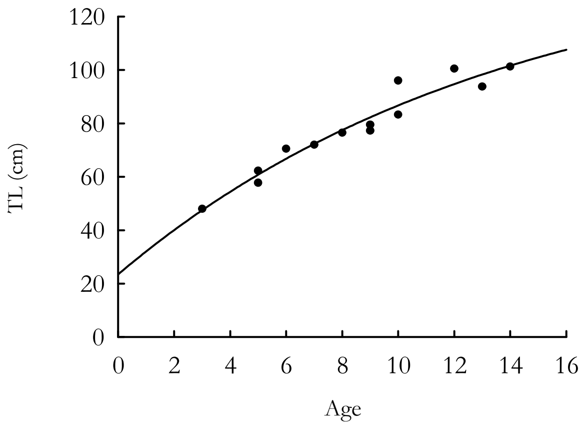


Figure 29. Preliminary von Bertalanffy growth curve for *B.multispinis,* sexes combined

Only four of the seven individuals of **B. cousseauae** could be aged. Reading was difficult due to little calcification of the intermedialia and tightly spaced rings. Data points seem not to be consistent (fig. 30), therefore ages are most probably no more than an approximation. T_{max} was 15 years for a 108.2cm large male.

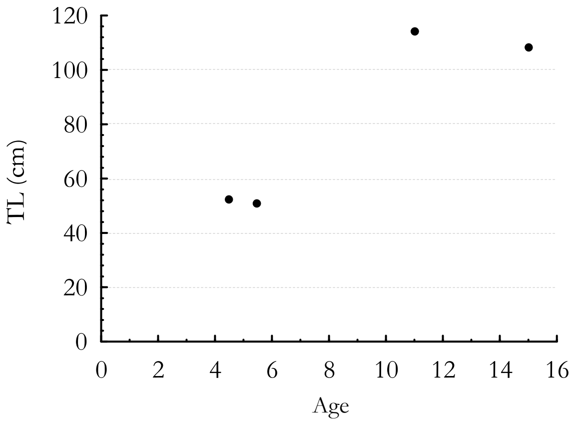


Figure 30. Lenght at age data for *B. cousseauae*

For ***B. meridionalis***, only large sized specimens (10 out of 13 available) were aged, hence no information on young individuals can be presented (fig. 31). Ages could have been underestimated due to the tight spacing of rings along the edge of the vertebrae. Especially the age (12 ys) of the largest specimen (146.1cm) might have been misinterpreted. Also, more age data of smaller specimens is necessary to be able to create a von Bertalanffy growth curve.

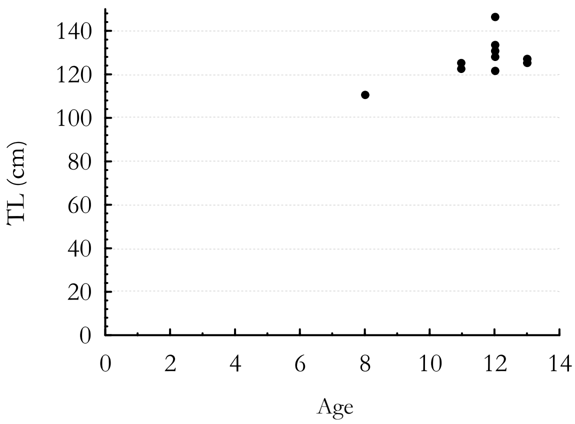


Figure 31. Length at age data for *B. meridionalis*

Length at age data for ***B. papilionifera*** has been obtained from 16 out of the 20 specimens available. As with *B. meridionalis*, only larger specimens were caught, thus there is no information on younger individuals. Data points seem rather scattered so ages are to be taken with reservation. Especially larger specimens (>120 cm) could have been under-aged, due to tight spacing of rings along the edge of the vertebrae. The specimen estimated to be the oldest (16 ys) had a total length of less than 120 cm.

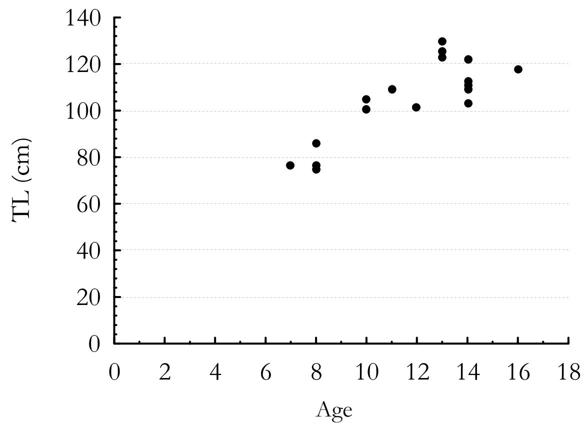


Figure 32. Length at age data for *B. papilionifera*

Six out of nine specimens of ***B. scaphiops*** could reliably be aged. Data points seem rather consistent, but due to the low sample number no conclusions can be drawn from this. The oldest specimen aged was a 74.5cm large male which was estimated to be nine years old in both, read one and two.

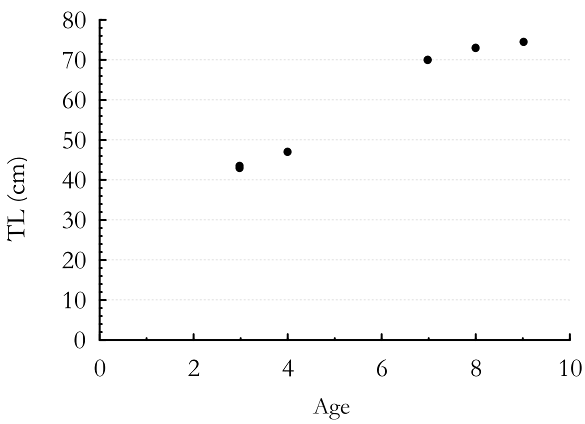


Figure 33. Length at age data for *B. scaphiops*

3.5 Comparison of species

Comparison of growth parameters/performance

Growth parameters of skates of the genus *Bathyraja* differed considerably. Generally it was found that species with a larger maximum length have lower growth rates k (see table 7). Growth performance values were all in the same range, as should be expected for related species, but still there was variation between species. In *B. magellanica*, which also had the highest k-value, growth performance was found to be highest. Nonetheless, the second highest growth performance was calculated for *B. griseocauda*, which had the lowest k-value of all species investigated. Interestingly the two species with a quite similar infinite length, namely *B. macloviana* and *B. magellanica* seemed to differ greatly in their growth rate and therefore also in their growth performance.

Table 7
Overview of growth parameters (including standard error) derived from the von Bertalanffy growth model. Also growth performance indices $ø' = \log_{10}(k) + 2 \cdot \log_{10}(L_\infty)$ and sample numbers (n) are given.

Species	**L_∞** (cm)	**k**	**t_0**	**r^2**	**ø'**	**N**
B. albomaculata						
Both sexes	89.3 (±4.9)	0.128 (±0.020)	-0.44 (±0.48)	0.84	3.016	203
B. brachyurops						
Both sexes	116.9 (±13.4)	0.099 (±0.024)	-1.19 (±0.53)	0.82	3.136	193
B. griseocauda						
Both sexes	169.9 (±27.1)	0.064 (±0.019)	-0.61 (±0.70)	0.93	3.239	40
B. macloviana						
Both sexes	74.7 (±3.3)	0.194 (±0.031)	-0.79 (±0.44)	0.78	3.025	158
B. magellanica						
Both sexes	74.3 (±2.1)	0.357 (±0.039)	-0.37 (±0.18)	0.84	3.298	63
B. multispinis						
Both sexes	145.5 (±46.1)	0.073 (±0.050)	-2.41 (±1.09)	0.94	3.171	13

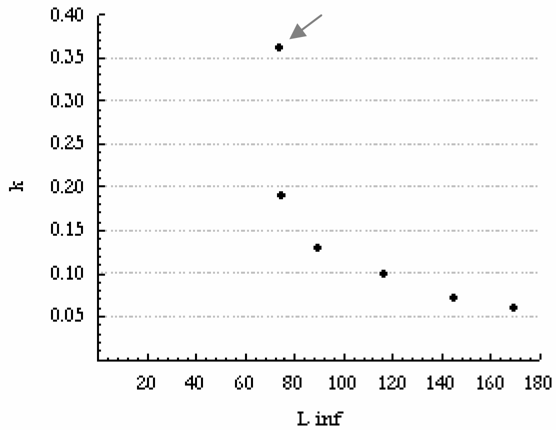


Figure 34. Relationship between growth rate (k) and infinite length (L_{inf}) in cm for the species investigated. Arrow indicates position of *B. magellanica*

It was found that growth rate and infinite length were related in the *Bathyrajids* investigated. K increases with decreasing maximum length. Only *B. magellanica* was an exception with a much higher k than would be expected with the calculated L_∞. When excluding *B. magellanica* the relation of ln(k) to ln(L_∞) can be described by a linear fit:

$$\ln(k)=4.1855-1.3683*\ln(L_\infty) \qquad (r^2=0.99)$$

Taking this fit and the maximum observed lengths (obs) in this study as well as the ones found in literature (lit) (AGNEW et al. 2000 and STEHMANN 1985, GALLAGHER 2001) the following k-values result for the other *Bathyrajid* species:

B. meridionalis: $L_{max\ (obs)}$ = 146.1cm; $L_{max\ (lit)}$ = 120cm; → k ~ 0.072

B. papilionifera: $L_{max\ (obs)}$ = 132.5cm; $L_{max\ (lit)}$ = >100cm; → k ~ 0.082

B. scaphiops: $L_{max\ (obs)}$ = 82.8cm; $L_{max\ (lit)}$ = 114cm; → k ~ 0.101

B. cousseauae $L_{max\ (obs)}$ = 113.9cm; $L_{max\ (lit)}$ = ~120cm; → k ~ 0.094

These values are of course to be taken with care, and only given to provide some first rough estimate of the growth potential of these species.

Comparison of total length at age five to eight

Length at age five to eight was compared for *B. albomaculata* (albo), *B. brachyurops* (bb), *B. macloviana* (maclo) and *B. magellanica* (magell) using ANOVA and a Post-hoc Test (Scheffés) (α=0.05). A Whisker graph was drawn to visualize the results. Unfortunately not enough data was available on the other age classes and species respectively.

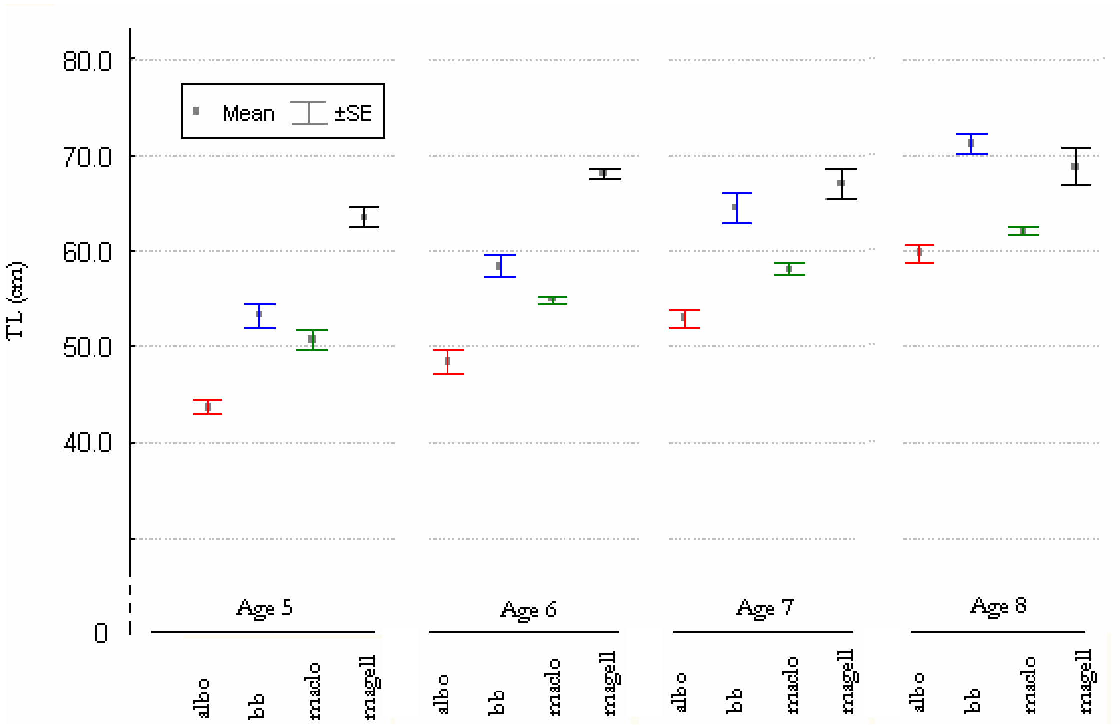


Figure 35. Comparison of mean lengths at ages five to eight for the four species best represented in this study. Species are colour coded: *B. albomaculata* (albo) in red, *B. brachyurops* (bb) in blue, *B. macloviana* (maclo) in green, and *B. magellanica* (magell) in black.

Sample numbers available for this analysis were the following: *B. albomaculata* n_5=17, n_6=12, n_7=15, n_8=30; *B. brachyurops* n_5=19, n_6=30, n_7=26, n_8=31, *B. macloviana* n_5=17, n_6=27, n_7=46, n_8=36, and *B. magellanica* n_5=17, n_6=18, n_7=7, n_8=3.

At the age of five, both, *B. albomaculata* and *B. brachyurops* had attained around 45% of their calculated L_{∞}. *B. macloviana* already had grown to almost 70%, and *B. magellanica* even to around 85% of its infinite length. In *B. magellanica* mean length at age seven (66.9cm) was lower than mean length at age six (67.9cm), which might be due to the low number of samples available for age group seven (n=7). Assuming that the birth-length is not differing much in the four species presented here, *B. albomaculata* grew slower in the first five years than the other species whereas *B. magellanica* was growing fastest. *B. brachyurops* was found to be intermediate at the age of five but continued growing steadily during the next three years while growth of *B. magellanica* slowed down already at the age of six.

Differences in mean length between *B. brachyurops* and *B. macloviana* became significant at the age of six (α=0.05). On the other hand, the difference between *B. brachyurops* and *B. magellanica* during the age of five and six years became non-significant at the age of seven (α=0.05).

4 Discussion

The results clearly show that life history parameters of skates of the genus *Bathyraja* vary quite a lot between species. Also methods to improve readability of rings on sagittal sections of vertebrae were differing from one species to the other. The crystal violet stain proved best for *B. brachyurops*, *B. macloviana* and also *B. magellanica*, whereas in *B. albomaculata* and *B. griseocauda* no stain was necessary at all. For the species with the least mineralized vertebrae, i.e. *B. meridionalis* and *B. papilionifera* (maybe including *B. cousseauae*) sagittal sections were not possible to read, thus another method using a potassium permanganate stain on whole vertebrae had to be applied. Generally, the rings on the outer edges of the vertebrae were hard to discern, therefore readings of older aged individuals might be underestimates. Reading agreement was good for all investigated species and the estimated coefficient of variation as by CHANG (1982) lied in the range of other ageing studies (see e.g. GALLAGHER et al 2004; IVORY et al 2004).

Discussion of methods

This study tried out different methods, which already had been used in other studies (e.g. GALLAGHER & NOLAN 1999), to increase visibility of growth rings, namely alizarin red, crystal violet and silver nitrate. Although alizarin red (AR) had been used successfully on shark and ray vertebrae (CRUZ-MARTINEZ et al. 2004, COELHO & ERZINI 2002, LESSA & SANTANA 1998), it was not improving banding pattern in the *Bathyrajids* observed here. There is still not much known about the histological background of band deposition and the chemical structure of vertebrae (GERLSLEICHTER 1998). But due to the staining properties of AR, namely to attach to the calcified rings in vertebral sections (PUCHTLER et al. 1969), it might be hypothesized that vertebrae of deep water elasmobranchs exhibit too little calcification, due to a calcium poor habitat (CAILLIET 1990) to be stained properly by AR. This would also explain why crystal violet (CV), which stains the protein rich parts in thin sections (LIGHTNING 2000), enhanced visibility of banding pattern in the species investigated here.

Although *B. albomaculata* could be read without staining, the age bias plot showed that in the second reading bands had been systematically over- and undercounted in younger and older individuals respectively. The underestimation of older specimens can probably be attributed to the fact that after becoming more experienced, the reader was trying to distinguish better between bands and checks (definition see page 14), and was therefore reading (too) conservatively.

Apart from methods used by previous studies, a new method using potassium permanganate (PP) was applied on the vertebrae. The results proved promising, and in *B. magellanica* and *B. griseocauda* agreement of readings comparing CV to PP and no stain to PP (fig. 16 and 17) respectively was around 80%. Although still not further investigated, it seems that this stain attaches to the same regions as does crystal violet, and is therefore apt for ageing deepwater elasmobranches.

For species with a reduced amount of calcification like *B. meridionalis, B. papilionifera* and probably *B. cousseauae*, the PP stain applied on whole vertebrae also rendered satisfactory results. But further research needs to be conducted in this area because resolution of bands along the edge of the vertebrae remains poor. The morphological structure of vertebrae was obviously a useful indicator of good or bad readability (see fig. 8 to 10). Poorly mineralized vertebrae with no real intermedialia were a lot harder to read and reliability of counts was insufficient. On the other hand, the well mineralized vertebrae were all rather easy to read, either with or without stain. Although it is reasonable to believe that poorly mineralized vertebrae result from a mineral (calcium) poor habitat (CAILLIET 1990), it doesn't explain the obvious difference in mineral content of e.g. *B. macloviana* and *B. griseocauda*, which were both caught in depths of around 70-300m (see table 3). Maybe the physiology of species which can occur in depth of more than 500m (e.g. *B. griseocauda*, *B. meridionalis* and *B. papilionifera,* see table 3) is somehow different to the one of species living in shallower waters. They might also exhibit migrations during their ontogenetic development which are absent in the other species. Food differences can be excluded as a possible reason though, because all of them feed on roughly the same taxonomic groups (amphipods, polychaetes, crustaceans, fishes) as can be seen in BRICKLE et al. (2003) and MABRAGAÑA et al. (2005). The reasons for the obvious differences in mineral content of the vertebrae remain a matter of debate.

Also it occurred sometimes that sagittal sections did not take up the stain and/or were not readable at all because of a rather blurry or not discriminable banding pattern. This feature was always consistent in all vertebrae of the same individual and is probably of physiological cause, for example mineral deficiency due to illness or stress (OFFICER et al. 1995).

Another abnormality found in some (large) individuals of *B. brachyurops* was an excessive accretion of minerals (calcified cartilage?) on the ventral side of the vertebrae. Maybe this was just a sign of old age, but it must have impeded the flexibility of the vertebral column (see pictures in appendix).

In general, vertebrae from above the abdominal cavity were easier to read (because of the bigger size) than vertebrae taken from the tail. Unfortunately, only these latter ones were available for some samples, which might have led to an underestimation of ages in these individuals (OFFICER et al. 1996).

There was unfortunately too little time to look at all thorns available in this study. The few ones investigated confirm works done by GALLAGHER (2000), GALLAGHER & NOLAN (2005) and BAUMGARTNER et al. (2005), who compared thorn readings to those done on vertebrae and found no significant difference in the readings. It should be considered though, that oftentimes thorns of older individuals are attrited or totally missing and that they might not be reliably readable in all of the *Bathyrajid* species. What's more, SERRA-PEREIRA et al. (2005) observed differences in readability of thorns from different regions of the tail.
Nonetheless thorns should be seen as a useful tool for cross-checking age readings of vertebrae. They could even (partly) act as a substitute for vertebral ageing, for they can be "removed with minimal damage […] and without alteration of their *['their' relates to rays]* commercial value" (SERRA-PERREIRA et al. 2005).

Validation of annual band deposition

Annual deposition of bands could not be proven by this study. Centrum edges were not clearly distinguishable into opaque and translucent stages, and the assumption of annual formation of bands could therefore not be tested. However, previous studies conducted on *B. brachyurops, B. albomaculata, B. griseocauda* and *B. scaphiops* (GALLAGHER 2000, HENDERSON et al. 2004) could provide evidence of annual band deposition with opaque bands being formed in Austral winter and translucent bands being formed in Austral summer. Annual band deposition was therefore assumed to hold true for all investigated species of *Bathyraja*. Future research should be conducted on verification/validation of band formation to make sure that this conclusion was not misleading (see also discussion on *B. magellanica*).

Growth parameters

Up to date, there are only few studies which worked on life history aspects of *Bathyrajids* in the south-western Atlantic. Two of them, namely GALLAGHER 2000 and HENDERSON et al. 2004 present data on growth parameters (L_∞, k, t_0) and maximum lengths (L_{max}) and ages (T_{max}) for *B. albomaculata, B. brachyurops, B. griseocauda* and *B. scaphiops.* The information provided by these studies is compared to the estimations done by the present study in table 8.
As can be seen, for ***B. brachyurops*** L_∞ was calculated to be larger and k estimated to be lower by GALLAGHER (2000). The size range in his study was larger though, with a L_{max} of 115cm, which is 26cm larger than the L_{max} in the present study. This most likely also explains the higher T_{max} in GALLAGHER'S study. There are two possible explanations for the larger total length (TL) found in GALLAGHER'S samples. Firstly the specimens in his study were caught within the Falkland Islands'

Interim Conservation zone (FICZ) between 1994 and 1996, which was shortly after skate fishery was being commercialized in the south-western Atlantic (AGNEW et al. 1999). It is possible that after years of intensive fishing, the larger individuals became fished out, so that in 2003, when sampling for the present study was initialized, individuals with a TL >100cm already were scarce. On the other hand it could be hypothesized that latitudinal factors also play a role. Samples for this study predominantly were caught in the northern part of the Argentinean continental shelf, whereas all of GALLAGHER'S samples were taken in the FICZ, which lies at the southern end of the shelf. An increase in total length with increasing latitudes has already been postulated to exist e.g. for the cownose ray, *Rhinoptera bonasus* (NEER & THOMPSON 2005). A combination of both factors might be the most probable explanation, though.

For ***B. albomaculata*** the same observation regarding L_∞ (for females) and k (both sexes) holds true when comparing the present to GALLAGHER'S study, but maximum observed lengths coincide rather well. Interestingly, HENDERSON et al. (2004) mention specimens with a disc width (DW) of up to 73cm, which would mean a TL of around 104cm (taken the TL/DW relationship for samples in this study, i.e. TL(cm)=1.402*DW+1.391; r^2=0.97). This means he investigated individuals which were more than 25cm larger than those caught during both, GALLAGHER'S and the present study. It sounds rather improbable that either of the above mentioned factors, namely fishing and latitudinal changes would explain a difference in TL as big as this. Also, HENDERSON'S samples were taken in 2001 i.e. long after the skate fishery was introduced. Large individuals were all caught in depths of 101-300m in his study, but this depth range was also covered by the present study so that depth related differences in TL can be excluded as well. The only explanation could be, that individuals this large are very rare and are only caught seldom, so that the bigger the sample size, the more probable it becomes to catch at least some of the large specimen. Sample size of HENDERSON et al 2004 was about twice the size of this study (HENDERSON n=430, this study n=204, GALLAGHER n=52). Additionally, all of HENDERSON'S samples were from the FICZ, where *Bathyrajid* species seem to have reached generally larger sizes (see *B. brachyurops*, also lengths mentioned in AGNEW et al. 2000). Although GALLAGHER (2000) as well as the present study disposed of samples from this zone as well, sample sizes seemed to have been too small (this study n=8, GALLAGHER n=52) to catch one of the rarely large specimen.

Another species investigated by GALLAGHER (2000) was ***B. griseocauda***. As with *B. brachyurops* he was able to work with a wider size range than was available for this study, but as he himself states, his values for L_∞ show "poor agreement with the maximum observed sizes" (GALLAGHER 2000). Although sample numbers were a lot higher in his study (n=141), growth parameters calculated in the present study (n=40) are probably more realistic when looking at L_∞, k and t_0. WAKEFORD et al. 2004 mention a maximum disc width of 130cm for *B. griseocauda* though, which would be a TL of even 178cm according to the TL/DW relationship calculated in the present work

(TL(cm)=1.362*DW+1.667, r^2=0.99). The samples for WAKEFORD et al 2004 were taken in 1993-2001 around the Falkland Islands.

The combination of sexes in this species was justified as GALLAGHER (2000) couldn't detect differences in growth of males and females. All in all the age counts seem to have been rather similar in both studies. For the age of 19 (T_{max} in this study), one can derive a TL of around 120cm in GALLAGHER'S growth curve which fits to the respective TL of the 19 year old individual in the present work (119cm).

Table 8

Overview of growth parameters of southwest Atlantic *Bathyrajids* with their maximum observed lengths and ages and sample numbers (n). For the study of HENDERSON et al. 2004 only disc width (DW) was given. This data was translated into total length using the relationship of TL to DW calculated in this study, namely: TL=1.396*DW+1.722

Species	Study	Sex	L_∞	K	t_0	L_{max} (cm)	T_{max}(ys)	N
B. brachyurops	GALLAGHER (2000)	Male	129.6	0.058	-2.15	100	18	198
		Female	130.0	0.060	-2.19	115	20	
	BAUMGARTNER et al. (2005)	Male					18	222
		Female					16	
	This study	Male	114.7	0.094	-1.63	82	12	193
		Female	107.4	0.128	-0.52	89	13	
B. albomaculata	GALLAGHER (2000)	Male	89.1	0.070	-3.20	72	15	52
		Female	111.2	0.048	-3.89	76	19	
	HENDERSON et al. (2004)	Both sexes	~96	0.08	-2.14	~104	17	430
	This study	Both sexes	89.3	0.128	-0.44	78	15	204
B. griseocauda	GALLAGHER (2000)	Male	219.7	0.033	-2.20	146	28	141
		Female	311.0	0.020	-3.03	161	31	
	BAUMGARTNER et al. (2005)	Male					20	172
		Female					29	
	This study	Both sexes	169.9	0.064	-0.61	119	19	40
B. scaphiops	GALLAGHER (2000)	Male	~81.4	0.138	-0.48	93	(16)	47
		Female	~119.6	0.063	-1.86	114	(18)	
	This study	Both sexes		0.101		83	(9)	9

Growth parameters for ***B. scaphiops*** couldn't be estimated due to the low sample size (n=9), with only six individuals reliably aged. The k-value derived by the relationship of k and L_∞ (fig. 34), namely 0.101, coincides rather well with the values calculated by GALLAGHER (2000) (k=0.14 for males and k=0.06 for females). He mentions in his study individuals with a TL of 114cm, but these were obviously not aged because they are not included in the respective von Bertalanffy growth curve. Therefore, maximum age in table 8 relates to specimens with a TL of around 75cm for males and around 85cm for females in GALLAGHER (2000). Maximum age in this study also wasn't determined for the largest specimen (TL=83cm). This individual was not aged due to reading difficulties, thus the oldest aged (male) specimen had a TL of 74.5cm and was determined to be nine years old. Still, reading differences between this and GALLAGHER'S study were quite big, as males with a TL of around 74cm were read to be 15 years according to GALLAGHER'S calculated growth function. More research is needed on this species to determine age at length accurately and maybe reading techniques should be worked over again, as banding pattern might have been misinterpreted.

Nothing has been published yet on age and growth of ***B. macloviana***. Therefore estimated growth parameters can't be compared to literature values. Due to the relatively high sample size (n=158) and rather good agreement of L_∞ with the observed maximum length, values are probably reliable and clearly underline the trend of higher growth coefficients in smaller sized species (FRISK et al. 2001). Although catches seemed to be visibly divided into a northern and southern population, there was no trend for differing growth characteristics. This observation was also made for feeding preferences in *B. macloviana* (MABRAGAÑA et al. 2005). The authors compared food items of stomachs of more northerly vs. more southerly caught specimen but didn't detect any significant differences. The diet of this species consists mostly of polychaetes (SCENNA et al. 2006) and shows no or only little regional or seasonal variation (MABRAGAÑA et al. 2005). The fact that no latitudinal change in growth parameters or total lengths could be found for *B. macloviana* contradicts the supposition of increasing body size with increasing latitudes. Furthermore, the oceanographic characteristics of the argentine continental shelf would suggest that the northern population is living in different salinity and temperature conditions compared to the southern population (being influenced by the Brazil and Malvinas current respectively) but neither of the two factors seems to have influenced the growth traits of the species. Nevertheless, AGNEW et al (2000) state that in the mixed species fisheries around the Falkland Islands on board observers measured specimens with a disc width of up to 58cm, which equals a total length of roughly 80cm (AGNEW et al. 2000 give an assumed TL of 77cm, but taking the relationship of TL to DW for *B. macloviana* in this study: TL(cm)=1.429*DW+2.465, r^2=0.97 the respective length would be 85cm). Two other studies conducted on *B. macloviana* (SCENNA et al 2006; MABRAGAÑA et al. 2005) investigated samples caught on the Argentinean continental shelf excluding the Falkland Islands. Both studies found TL similar to the ones in this study, namely around 66-68cm. It therefore seems as if total lengths of all *Bathyrajids* with wide distributions along the Argentinean continental shelf are (or were) generally larger growing around the Falklands.

As with *B. macloviana*, no studies on age and growth have been published yet for ***B. magellanica***. Because of the lack of individuals smaller than 40cm, the introduction of the supposed birthlength (BL) was necessary. This of course might falsify the parameter estimation because no first hand information on BL exist as of now. WAKEFORD et al. 2004 caught individuals as small as 9cm DW which would relate to a TL of 20cm (TL(cm)=1.276*DW+8.613, r^2=0.93). Morphological relation of disc width to total length might be different in small individuals though, therefore a BL of 10cm can't be precluded.

It nonetheless seems as if young specimens are growing unusually fast until the age of four when growth becomes slower. MENNI et al (2000) and OJEDA et al. (2000) state, that *B. magellanica* has a rather limited distribution compared to other south-west Atlantic *Bathyrajids* with a predominant occurrence in the southern ('magellanic') province. It was also reported from the north, but only rarely (this study) or in depth of around 600m (KREFFT 1968). CONOVER (1990) proposed, that a species which is exposed to shorter growth seasons (as occurring in higher latitudes) should have higher growth rates to compensate for the lack of growing-time. He was working on silversides (*Menidia menidia*), but this might also be applicable to skates. Generally, more information on the distribution of individuals <40cm is needed to be able to discuss the observed rapid change in growth rate with age.

Another interesting characteristic of *B. magellanica* was that its banding pattern in the vertebrae differed immensely from the pattern found in the other species of *Bathyraja*. Bands were broader spaced and were stained well with both the CV and the PP stain (see pictures in appendix). Vertebrae also seemed to be rather characteristic in *shape* (see fig.8).

The only life history parameter available for *B. magellanica* is the length at 50% maturity (L_{50}). AGNEW et al. (2000) give a value of 38cm disc width, which would be a TL of around 57cm after the TL/DW relationship calculated in this study (see above). That means that 50% of the population would already be mature at the age of three to four years (see fig. 27) which would be an indicator of a totally different life history strategy compared to the other species, i.e. fast growth until the attainment of maturity, whereupon energy is put almost exclusively into reproduction. *B. magellanica* could be expected to be rather fecund and have high resilience to fishing pressure if this assumption was true.

A totally different but rather simple explanation for the seemingly early maturity would be the misinterpretation of yearly bands. The obvious difference in banding pattern might indicate an irregular or non-yearly formation of bands. Before making any conclusions on the life history of *B. magellanica*, band formation should therefore be investigated further, e.g. through laboratory growth studies.

For the other four species (*B. cousseauae, B. meridionalis, B. multispinis*, *B. papilionifera*) only preliminary results could be presented here. Growth parameters calculated for ***B. multispinis*** appear to be rather realistic with the k value being typically low for a species of its size. Compared to the maximum observed length in this study (L_{max}=101.0cm) the L_∞ seems to be quite high (L_∞=145.5cm). AGNEW et al. (2000) mention a L_{max} of 98cm DW in their samples though, which would be a TL of around 144cm (taken the TL/DW relationship calculated in this study: TL(cm)=1.478*DW-0.408, r^2=0.99) i.e. almost exactly the value calculated for the infinite length in the present work. Still there is dire need for more length at age data to make reliable statements on the life history of *B. multispinis*

Only four individuals of ***B. cousseauae*** have been aged, so no conclusions can be drawn for this species. Its rather large maximum length (~120cm, AGNEW et al 2000) suggests a k value of less than 0.100 (see fig. 34), meaning that it is probably rather slow growing. The same holds true for ***B. meridionalis*** (L_{max}>130.0cm) and ***B. papilionifera*** (L_{max}>145.0cm), both of them being considered real deep water species (STEHMANN 1985, MENNI & STEHMANN 2000). Length at age data for the latter two species was pretty scattered and reflect the reading difficulties encountered in this study. More research is needed on ageing methods of these species with sparsely calcified vertebrae and also additional length at age data is required to get more specific clues regarding their life history traits.

Birth-length

Birth-lengths (BL) derived from the von Bertalanffy growth functions (VBGF) differed quite a lot. The values ranged between 5.0cm for *B. albomaculata* to 22.6cm for *B. multispinis*. A BL of around 10 to 15cm can be assumed for most of the *Bathyrajids* though, taking data of minimum DW in the samples of WAKEFORD et al. (2004) namely 8cm DW for *B. brachyurops* (TL~14.0cm), *B. griseocauda* (TL~12.6cm) and *B. macloviana* (TL~14.0cm) and a DW of 9cm for *B. multispinis* (TL~12.9cm). Also, HENDERSON et al. (2004) gives a minimal DW of 7cm for his samples of *B. albomaculata* (TL~11.5cm) and RUOCCO et al. 2006 found an egg case containing an embryo of *B. macloviana* with a TL of 6.8cm. In the northern hemisphere, EBERT (2005) found specimens of other *Bathyrajids* with total lengths of 16.2cm (*B. interrupta,* with an open umbilical scar and an internal yolk sac present), 17.0cm (*B. lindbergi*) and 15.1cm (*B. minispinosa*).

Taking this information, the BL calculated for *B. albomaculata* and *B. griseocauda* were probably too low, whereas the BL for *B. multispinis* was too high. For *B. brachyurops* and *B. macloviana* birth-lengths seem to be realistic for the combined sexes. It was therefore tested for the formerly mentioned three species what would happen to the growth parameters when a birth-length of 10cm is introduced. For *B. albomaculata* the parameters changed from L_∞= 89.3cm to 93.2cm, from k=0.128 to 0.112 and from t_0=-0.44 to -0.91 (r^2=0.87). For *B. griseocauda* the L_∞ went from 169.9cm to 180.8cm, the value for k didn't change much (from k=0.064 to 0.056) and t_0 went from -0.61 to -0.94 (r^2=0.95). The changes observed in *B. multispinis* were more dramatic namely from L_∞=145.5cm to 121.5cm, from k=0.073 to 0.117 and from t_0=-2.41 to -0.85 (r^2=0.97). The dramatic changes in the values of *B. multispinis* result most probably from the low sample size, but reflect the uncertainty of the curve parameters. Changes in *B. albomaculata* and *B. griseocauda* are not as big which indicates a rather good stability of the curve characteristics. Still, first hand information on birth length is dearly missing to be able to comment on the reliability of parameters for all species investigated here.

Comparison of species and management implications

According to their life history parameters, the *Bathyrajids* investigated in this study can be roughly divided into three groups. Group one containing large sized species with low k-values (<0.10) and late maturity (13 years and more), group two growing to intermediate size with k-values around 0.10-0.15 attaining maturity at around ten years of age, and group three, the rather small species with higher k-values (>0.15) and a comparably early maturity (after around 4 to 6 years).

The first group contains *B. griseocauda* and *B. multispinis,* and most probably also *B. cousseauae, B. meridionalis* and *B. papilionifera.* For *B. griseocauda* different L_{50} have been published, the range being from around 105cm to 120cm (AGNEW et al. 2000, GALLAGHER 2000). GALLAGHER even states, that according to his data, the age at 50% maturity for female *B. griseocauda* would be around 25 years! Translated into response to fishing pressure, the first group is most prone to population declines, a fact that has already been reported for *B. griseocauda, B. multispinis* and *B. cousseauae* (WAKEFORD et al. 2004). Especially in a multi-species fishery management measures should be sensitive to these less productive species (MUSICK et al. 2000). Species specific monitoring of population dynamics is a prerequisite in this fishery to be able to decide on soundly founded catch limits for all species involved (DULVY et al. 2000). Aggregated catch statistics tend to seem stable even if some species are already declining due to the compensation of catches by other, faster growing species (DULVY et al. 2000)

The second group consists of *B. brachyurops* and *B. albomaculata,* and possibly *B. scaphiops*. All of them attain maturity at around the age of 10 years according to GALLAGHER (2000) (*B. scaphiops* being more variable), and taken the L_{50} mentioned for *B. albomaculata* in RUOCCO et. al (2006) and HENDERSON et al. (2004) this would also hold true when applying this length to the age data of the present study. Even if growth rate is higher and the L_{50} lower in this group, vulnerability to overfishing might still be high and cautionary management is needed.

The last group comprises the two smallest species, namely *B. macloviana* and *B. magellanica.* Although rather different in their life history strategy (see discussion on *B. magellanica*), both of them seem to reach maturity relatively early, with an L_{50} at around 52-55cm for *B. macloviana* (SCENNA 2003, SÁNCHEZ et al 2002) and around 57cm for *B. magellanica* (AGNEW et al 2001, DW measures translated into TL with the equation mentioned earlier in this paper). Taking the length at age data of the present work, this would mean the attainment of maturity at the age of around 5-6 years and

4 years for these two species respectively. But as already mentioned, doubts exist as far as the yearly formation of bands (or the band reading respectively) in *B. magellanica* is concerned, therefore it would be premature to assume higher resilience to fishing pressure based on the results of this study.

As was shown, most of the species of *Bathyraja* investigated in the present work seem to be prone to population declines under high fishing pressure. It has to be taken into consideration that eight of the ten species are endemic to the Argentinean continental shelf and part of the Chilean shelf and that they already form part of a growing multi-species fishery in this area. Hence a precautionary management is of even greater importance to prevent over-fishing and work towards a sustainable use of these and other elasmobranchs in the southwest Atlantic.

5 Conclusion

Compared to other rajid species, the genus *Bathyraja* has been found to be quite difficult to age (GBURSKI 2004). Nevertheless this study achieved to derive growth parameters for six of the species (*B. albomaculata, B. brachyurops, B. griseocauda, B. macloviana, B. magellanica* and *B. multispinis*) and to make estimates on growth rate (k) for the other four (*B. cousseauae, B. meridionalis, B. papilionifera* and *B. scaphiops*). Different groups were identified showing slower or faster growth and attaining larger or smaller maximum sizes respectively. Areas for further research were identified, namely on the ageing methods of species with poorly mineralized vertebrae (*B. cousseauae, B. meridionalis, B. papilionifera*) and on band formation of *B. magellanica*.

It was found that all *Bathyrajids* caught (by other studies) around the Falkland Islands seemed to have attained a larger size than anywhere else on the Argentinean continental shelf (see sizes mentioned in AGNEW et al. 2000 and WAKEFORD et al. 2004). If this is owing to a greater productivity of the area or other reasons could not be determined by this study, and to the author's knowledge nothing has been published yet on this phenomena. Depth related differences could be excluded though, and also latitudinal changes seem improbable since total lengths of skates living in the same latitudes but closer to the Argentinean coast were the same as the ones found in the north of the Argentinean continental shelf. .

The supposition of variations in growth parameters in different regions (MASSA et al. 2004b) could be partly proven as far as TL was concerned (see paragraph above), but growth coefficients were found to be similar in the northern and southern distributional range of the species (e.g. in *B. macloviana*). Thus it can be said that for the *Bathyrajids* observed in the present work neither temperature nor other oceanographic factors seem to have influenced growth characteristics within a species along the continental shelf of Argentina (the Falkland Islands being a special case).

Based on the information gathered in this and former studies management considerations could be addressed, although for some species more life history data is needed to make soundly founded conclusions. In general it can be said that the study objectives were achieved.

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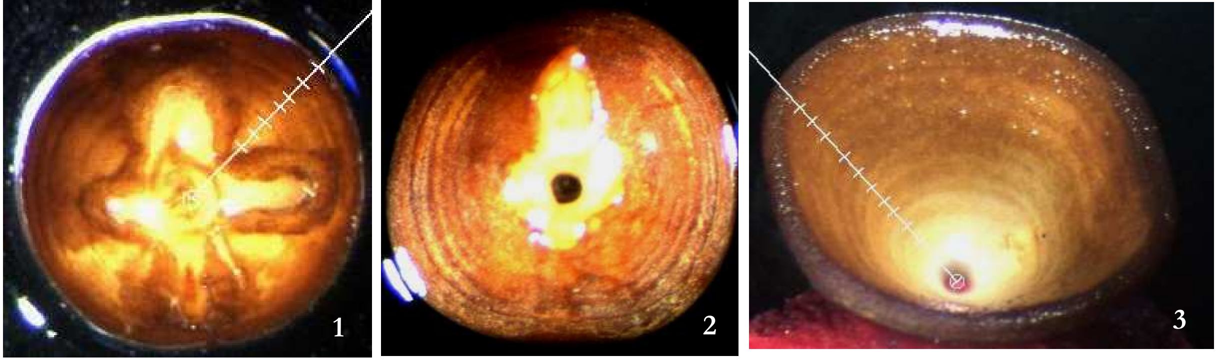
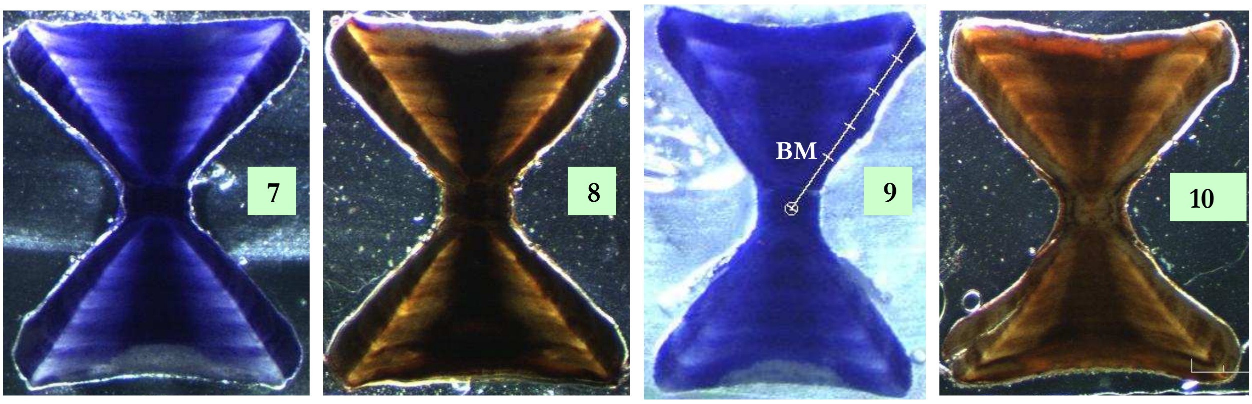
Appendix

Contains: Pictures, CD with raw data and pdf file

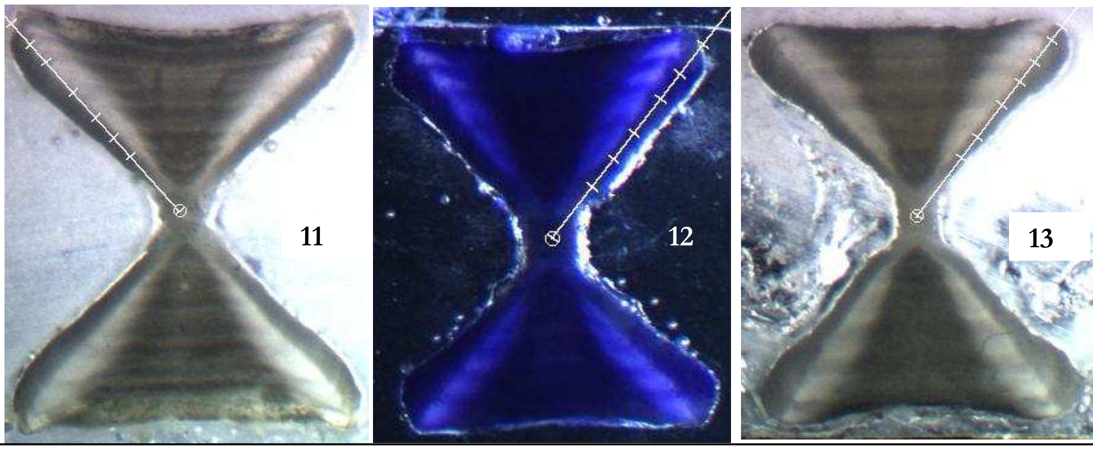


Halved vertebrae of *B. papilionifera* (1) and *B. meridionalis* (2,3) stained with Potassium permanganate

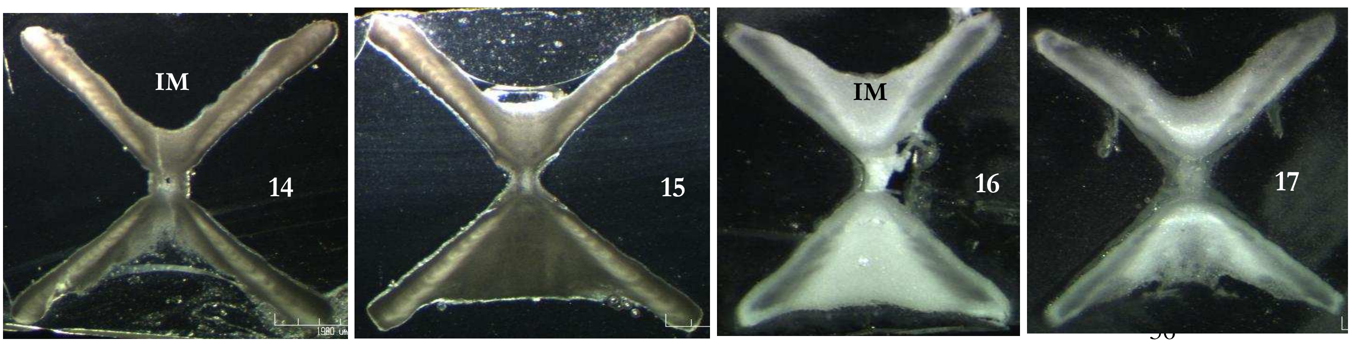
Whole vertebrae of *B. brachyurops*. Normal one (4), and one with overaccretion in dorsal (5) and ventral (6) view



Sagittal sections of centra of *B. magellanica* stained with crystal violet (blue) and Potassium permanganate (brown). Pictures 7 and 8 belong to the same individual (read to be 5ys old). Individuals 9 and 10 were read to be 4 ys old.



Sagittal sections of centra of *B. brachyurops* (11) and *B. macloviana* (12 CV stain, 13 no stain); not in scale



Sagittal sections of centra of *B. cousseauae* (14,15, under transmitted light) and *B. multispinis* (16,17, under reflected light), with low amount of calcification in the intermedialia (IM). Vertebrae not in scale!