ORIGINAL RESEARCH

Age and growth of the red flounder *Paralichthys orbignyanus* (Teleostei: Pleuronectiformes) in southern Brazil

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ABSTRACT. The red flounder *Paralichthys orbignyanus* is a large pleuronectiform fish endemic in coastal waters, coastal lagoons and estuaries in the southwestern Atlantic. Although less abundant than other *Paralichthys* spp., its high price makes it a valuable resource for small-scale fishers that have been intensely fished in the last decades. To study its growth and lifespan in southern Brazil, we examined thin otolith sections collected for age determinations of both young-of-the-year (YOY) and older fishes. Opaque bands form mainly in spring and summer, coincident with the reproductive season. Larger and older males reached 601 mm and eight years, while females reached 985 mm and 11 years. The assumed daily microincrements counts ranged from 127 to 196 for YOY of 135 to 184 mm TL. The common weight-length equation for grouped sexes was TW_{QO} = 0.000015TL^{2.93} (mm, g). The von Bertalanffy growth equations were: $TL_Q = 1,076(1-e^{-0.15 (t+0.78)})$; $TL_{O} = 652(1-e^{-0.28 (t+0.48)})$; and $TL_{QO} = 839(1-e^{-0.20 (t+0.67)})$. Therefore, *P. orbignyanus* is a fast-growing and relatively short-living species for which females attain larger length and older ages than males, characteristics that have to be taken into account for its stock assessment and management.

Key words: Fisheries, management, microincrements, population dynamics, southwestern Atlantic.

Edad y crecimiento del lenguado *Paralichthys orbignyanus* (Teleostei: Pleuronectiformes) en el sur de Brasil



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This work is licensed under a Creative Commons Attribution-NonCommercial-ShareAlike 4.0 International License **RESUMEN.** El lenguado *Paralichthys orbignyanus* es un pez pleuronectiforme de gran tamaño, endémico de aguas costeras, lagunas costeras y estuarios del Atlántico Sudoccidental. Aunque menos abundante que otros *Paralichthys* spp., su alto precio lo convierte en un recurso valioso para los pescadores artesanales que los han pescado intensamente en las últimas décadas. Para estudiar su crecimiento y edad en el sur de Brasil, examinamos secciones delgadas de otolitos para realizar determinaciones de edades tanto de juveniles menores a un año como de peces más viejos. Las bandas opacas se forman principalmente en primavera y verano, coincidiendo con la época reproductiva. Los machos más grandes y mayores alcanzaron los 601 mm y los ocho años de edad, mientras que las hembras alcanzaron los 985 mm y los 11 años. Los recuentos de microincrementos diarios asumidos oscilaron entre 127 y 196 para los juveniles de 135 a 184 mm TL. La ecuación peso-longitud para sexos agrupados fue $TW_{Q,d} = 0,000015TL^{2.93}$ (mm, g). Las ecuaciones de crecimiento de von Bertalanffy fueron: $TL_{Q} = 1.076(1-e^{-0.15 (t+0.78)})$; $TL_{d,d} = 652(1-e^{-0.28 (t+0.48)})$; y $TL_{Q,d,d} = 839$ $(1-e^{-0.20 (t+0.67)})$. Por lo tanto, *P. orbignyanus* es una especie de crecimiento rápido y vida relativamente corta, cuyas hembras alcanzan mayor longitud y edad que los machos, características que deben tenerse en cuenta para la evaluación y gestión de su población.

Palabras clave: Pesquerías, ordenación, microincrementos, dinámica de población, Atlántico Sudoccidental.

INTRODUCTION

The Brazilian or red flounder, *Paralichthys* orbignyanus (Valenciennes, 1839), is a medium to large-sized benthic pleuronectiform fish endemic to the Warm Temperate southwestern Atlantic biogeographic province (Spalding et al. 2007), with a continuous distribution between Rio de Janeiro State in Brazil (22° S) and the gulf of San Matías in Argentina (41° 30' S) (Cousseau and Perrotta 1998; Menezes et al. 2003). It is a euryhaline species that inhabit shallow coastal marine waters and estuarine environments (Chao et al. 1985; Haimovici et al. 1996; Rivera Prisco et al. 2001; Diaz de Astarloa 2002; Lopez Cazorla 2005).

Paralichthys orbignyanus was commercially fished in the Patos Lagoon and nearby coastal waters in southern Brazil, and used by the canning industry of the city of Rio Grande by the late XIX century (Odebrecht 2003). It is still fished by small-scale fishers in the region, mainly by double rig bottom trawlers but also with bottom gillnets (Haimovici and Mendonça 1996; Haimovici and Cardoso 2017). No reliable specific landing statistics are available for the red flounder, as it is rarely discriminated from other flounders (i.e. P. patagonicus and P. isosceles) in southern Brazil. However, reported landings of flounders by small scale fishers in Rio Grande, among which P. orbignyanus is dominant, decreased from a few hundred tons in the 1980s to less than 50 t in the 2000s (CEPERG 2012), suggesting its overfishing. This stock reduction perspective scenario was supported by long-term perceptions of red flounders catches by small-scale fishers in the Patos Lagoon (Thykjaer et al. 2019). In addition, there is an overall trend of overfishing of demersal fishes from the Patos Lagoon and the inner shelf along southern Brazil, among which the red flounder is not expected to be an exception (Haimovici and Cardoso 2017).

Some aspects of the life history of P. orbig-

nvanus in its natural environment have been studied in southern Brazil. The species has a long reproductive season between spring and summer since fully developed intraovarian oocytes and high gonadosomatic indices were observed between October and March (Carneiro 1995; Silveira et al. 1995; Robaldo 2003). Experimental studies showed that eggs only hatch at seawater salinities; therefore, their spawning is assumed to occur in coastal marine water, but the small pelagic larvae rapidly acquire the capacity to withstand low salinities, allowing them to colonize brackish waters (Sampaio et al. 2007). This capacity allows them to occupy nursery grounds in estuaries, coastal lagoons and brackish surf zone coastal waters, early on in life. In the Patos Lagoon estuary, juvenile red flounders feed mainly on polychaetes, preadults and adults feed mainly on small fish, brachyuran crabs, tanaidaceans, miscidacean, and small penaeid shrimp, while larger specimens feed both in the estuary and coastal waters mainly on small fishes and penaeid shrimp (Carneiro 1995).

Large size *P. orbignyanus* tolerance to low salinities and of high commercial value, led to studies of its potential for aquaculture in Brazil (Wasielesky et al. 1994; Sampaio and Bianchini 2002) and Argentina (Radonic et al. 2007). Its individual growth in the environment has been studied in the southern limit of its distribution, in the Bahia Blanca region in Argentina, based on age determinations on scales (Lopez Cazorla 2005) but not in southern Brazil, where the species is an important component of the estuarine and coastal shallow waters fish communities.

The lack of basic information on population dynamics of *P. orbignyanus* led to it being considered 'data deficient' in the IUCN Red List of Threatened Species (Riestra et al. 2020). In this study, the growth and longevity of *P. orbignyanus* in southern Brazil were estimated to contribute to filling this gap. For this purpose, ages were determined based on the interpretation of both microincrements in the otoliths of young-of-theyear and seasonal bands in the otoliths of subadults and adults. Otoliths grow along the life of fishes by the apposition of layers of proteins and salts that form layers of different optic densities both on a daily (microincrements) and seasonal (annuli) basis (Morales-Nin 2000; Green et al. 2009). The combined interpretation of bands formed in otoliths of juveniles and adults can contribute to the validation of the periodicity in the formation of the annuli (Cavole and Haimovici 2015; Cavole et al. 2018). Life-history parameters of age and growth obtained in this study are expected to be useful in future assessment models needed to define desirable states for appropriate fishery management.

MATERIALS AND METHODS

Sampling sites

Overall, otoliths of 224 specimens collected between 1989 and 2000 from small-scale gillnet fishing in the estuary of the Patos Lagoon and commercial bottom trawling and research surveys in coastal waters (< 25 m) along southern Brazil were examined (Figure 1).

Total weight (TW, g) and total length (TL, mm) measured from the tip of the snout to the midpoint of the caudal were recorded before the dis-



Figure 1. Estuarine and coastal regions along southern Brazil from where samples of Paralichthys orbignyanus were collected.

section of each specimen. Gonads from each fish were weighed (g) and examined visually for sex determination, and sagittae otoliths were extract-

ed and preserved dry for age determination.

Age determinations

Thin transverse sections (0.20-0.30 mm) of right sagittal otoliths were cut through the nucleus and embedded in polyester resin using a lowspeed rotary saw (Buehler-Isomet). All sections were fixed on glass slides with xylol (dimethylbenzene) base mounting media (ENTELAN Merck®). Sections were examined with transmitted light under a stereoscopic microscope (× 10). Digital images of otolith sections (Figure 2) were obtained using a stereoscopic microscope at × 10 objective power on a camera with 2048 × 1536 pixels. Distances between the otolith core and the end of opaque bands assumed *a priori* as annuli (annual bands), were measured with the free software ImageJ 1.47 (www.imagej.nih.gov).

On the transverse sections, alternate opaque and translucent bands were counted independently by two readers. If counts differed, otoliths were read again by both readers and discarded from further analyses if the difference persisted. The periodicity of the formation of opaque and translucent bands on the edge of otoliths were evaluated by counting monthly opaque and translucent edges. Microincrements counted in the transverse sections of sagitta otoliths of four young-of-the-year measuring 135 and 184 were used to fit the von Bertalanffy growth curve along the first year of life with the annulus observed for older fishes. Otoliths were prepared and polished following the method described by Cavole and Haimovici (2015). Microincrements were counted between the otolith core and the outer edge of the otolith along the ventral axis (Figure 3).

Back calculations

To back-calculate the total length at each age, the procedure proposed by Campana (1990) was followed, which assumes a linear relationship between the fish length (L) and the radius of the otolith length (R) with a fixed intercept (biological intercept) for all analyzed individuals. This procedure assumes that the greatest variation between R and L of individual fishes occurs in the slope of the relationship and not in the hypothetical value of the radius for fishes at zero length, as shown in several experiments of controlled or manipulated individual fish growth (Vigliola and Meekan 2009).



Figure 2. Thin transverse section of a six years old and 750 mm female *Paralichthys orbignyanus* from southern Brazil examined with transmitted light. Black letters indicate the nucleus (N), the end of each opaque band (Ri) and the border (Rt).



Figure 3. Thin transverse section of a 153 mm juvenile *Paralichthys orbignyanus* from southern Brazil with 137 microincrements. White circles indicate some of the microincrements counted from the core. Scale black bar is 0.1 mm.

A radius of 0.0789 mm (R_0) measured on a sectioned otolith from a juvenile 135 mm total length (TL_0) was considered as the biological intercept. Back-calculated lengths were obtained according to the following equation:

$$TL_i = TL_c + (R_i - R_0). (TL_c - TL_0) (R_c - R_0) - 1$$

where TL_i is the back-calculated length-at-age *i*; TL_c is the total length of the fish at the time of capture; R_i is the radius of the otolith at a given age *i*; and R_c is the total inner radius of the otolith at the time of capture.

Growth analyses

Growth in length was described by the von Bertalanffy growth model (VBGM) from backcalculated mean lengths-at-age for each sex as follows:

$$TL = (L_{\infty} \ 1 - e^{-k(t-t_0)})$$

where *TL* is the total length-at-age *t* of the fish from the tip of the snout to the end of the upper limb of the tail in a normal position; L_{∞} is the asymptotic length; *k* is the growth coefficient, which represents the rate at which the fish length approaches L_{∞} ; and t_0 is the theoretical age at which the fish would have a length of zero. The fit of the model to the data was performed with a Bayesian approach (Kinas and Andrade 2010). Age-length data were assumed to follow a lognormal distribution: $y_i = \log N(\mu_i, \sigma^2)$ where y_i is the length distribution, μ_i is the mean length for each age class *i*, and variance σ^2 . A logarithmic version of the VBGM was used for computational convenience as follows:

$$\mu_i = log(L_{\infty}) + log(1^{-k(i-t_0)})$$

Seed values for each parameter were constructed from a non-informative prior with wide distribution intervals. The probability of *log k* was considered to follow a normal distribution with a mean of zero and variance equal to 0.001 and restricted to the interval of -5 and 5. The probability of *log L*_∞ was considered to follow a normal distribution with a mean equal to the logarithm of the observed maximum *L* and a variance of 0.001. The probability of t₀ was considered to follow a uniform distribution with a minimum equal to -3 and a maximum equal to zero. The probability of σ was considered to follow a uniform distribution with a minimum equal to zero and a maximum equal to five.

Posterior distributions of parameters were obtained through the stochastic process of Monte Carlo Markov chains (MCMC), which provides an easy and clear way to compare the resulting parameters by analyzing the overlap between posterior probability distributions. In a single chain, 31,000 iterations were generated with a burn-in of the first 10,000 values and removal of one of the two remaining values, resulting in a final sample with 10,500 values in the posterior distribution of each parameter (Kinas and Andrade 2010). These analyses were performed using the OpenBUGS package and the libraries R2 WinBUGS (Sturtz et al. 2005) and BRugs (Thomas et al. 2006). All statistical analyses were performed in R software (R Core Team 2022) version 4.2.1.

Weight-length relationship

The relationship between weight and length was described by the potential model ($TW \alpha = TL^b$). Data were transformed into decimal logarithms for comparisons and linear regression models were compared between sexes through covariance analysis ($\alpha = 0.05$) (Zar 1984). The asymptotic weight (W_{∞}) was estimated by transforming length by age data to weight-by-age data, based on potential weight-length equations.

RESULTS

Otoliths of 224 specimens between 266 to 985 mm TL were examined by two independent readers (MH, EK) for alternate opaque and translucent bands. The thickness, curvature, height of the crista, and optic density of otoliths were variable, resulting in considerable differences in the visualization of the width of opaque bands. However, the two readers counted the same number of opaque bands in the otoliths of 171 specimens (76.3%). In a second joint reading, an agreement was reached for other 30 otoliths that differed only in one opaque band. An inconsistent pattern of opaque bands or higher count differences was observed for 23 otoliths (10.3%). Overall, ages were attributed to 89.7% of specimens, 70 males and 131 females.

Validation of age determinations

Opaque edges in sectioned otoliths occur yearround, with their relative frequency increasing sharply from 29% in September to 83% in October and 92% in December and gradually decreasing to 14% in May (Figure 4). Although confidence intervals among many months overlapped, the percentage of opaque bands between October and March was significantly higher than between April and September ($\chi 2$ (1; N = 224) = 42.7, p < 0.001), giving support to the hypothesis that each year one opaque was primarily formed in spring and summer, and a translucid band mostly in autumn and winter.

Ages were assigned to each fish according to the number of opaque bands (annuli) on otoliths. The midpoint of the period with higher proportions of opaque bands in the edge of sections of otoliths was between December and January. It was also approximately the midpoint of the period in which higher gonadosomatic indices (Carneiro 1995; Robaldo 2003) and hydrated oocytes were observed in ovaries (Silveira et al. 1995). Therefore, 1st January was considered the mean birthday date of all fishes and used to calculate the age in fractions of years, in which the number of opaque bands corresponded to the number of completed years of life.

Age-length relationships

The older male attained eight years old and measured 575 mm, while the older female had 11



Figure 4. Monthly percentages of opaque bands in the edge of transverse sections of otoliths of *Paralichthys orbignyanus* from southern Brazil. Sampled numbers are between brackets and vertical bars represent 95% of confidential intervals.

years and measured 830 mm. The larger sampled male measured 601 mm and was seven years old, while the larger female measured 985 mm and was eight years old. Total length at capture and back-calculated length at all ages of females were larger than those of males, with differences in the total length increasing from 8% at age one to 143% at age eight (Table 1).

The number of microincrements in sectioned otoliths of four young-of-the-year specimens measuring 135, 153, 168, and 184 mm (L) were 127, 153, 168, and 196, respectively. Microincrements were considered *a priori* daily due to their well-marked appearance and for presenting a concentric pattern from the focus to the edge of otoliths sections (Figure 3). Thus, microincrements counts, transformed in fractions of years, were used for estimations of von Bertalanffy growth curve, helping to fit the length-at-age in the beginning curve.

Growth analyses

Individual back-calculated length-at-age for each sex and microincrements readings of the four unsexed young-of-the-year were used to calculate the von Bertalanffy's growth parameters. Credibility intervals for both L_{∞} and k for males and females did not overlap, showing a significant difference between sexes. Values of t_0 did not differ significantly between sexes and showed a reasonable adjustment at early ages, with absolute values lower than one year (Table 2).

Although a large variability of the length-atage was observed for both sexes, a good overall fitting was observed between the length-at-age observed in the catch and the growth curve estimated for the back-calculated length-at-age (Figure 5). Males grew much smaller than females, reaching only 57% of females' L_{∞} . In contrast, the intrinsic growth rate k was significantly larger for males (k = 0.40), and more than twice that for females (k = 0.18). The difference occurs because of the rapid decrease in growth of males after age 3 (Figure 5; Table 1). The total length-at-age of the four unsexed young-of-the-year forced curves to relatively low t_0 values, indicating that both male and female estimated growth curves fit well at all ages (Figure 5).

Males									
Age	n	1	2	3	4	5	6	7	8
1	15	266							
2	26	264	378						
3	17	251	366	465					
4	5	230	348	443	500				
5	2	239	357	453	505	540			
6	1	270	400	474	520	546	575		
7	3	259	377	451	514	561	597	625	
8	1	258	366	441	472	509	535	554	575
Mean TL back-calculated	70	255	370	455	502	539	569	589	575
Mean TL in the catch	314	394	477	500	540	575	548	575	
Females									
Age	n	1	2	3	4	5	6	7	8 >
1	9	286							
2	44	276	400						
3	43	248	391	499					
4	15	277	402	507	583				
5	13	250	393	519	621	688			
6	4	271	389	503	628	701	746		
8 >	3	321	453	534	610	676	730	781	824
Mean TL back-calculated	131	276	405	512	610	688	738	781	824
Mean TL in the catch	335	428	515	607	691	746		808	

Table 1. Observed mean total length (TL, mm) at capture and back-calculated mean TL at age of males and females red flounders *Paralichthys orbignyanus*, fished in southern Brazil between 1989 and 2000. n = number of sampled individuals.

Weight-length relationships

Total weight (g)-total length (mm) relationships for 190 fishes between 230 to 865 mm did not differ between sexes (F = 1.04; p = 0.31). The relationship for pooled sexes including unsexed juveniles was W = 0.000015 TL^{2.930}, R² = 0.99. The 95% confidence limits for the slope coefficient was 2.895-2.996, therefore, for this set of data, the growth relationship between length and weight cannot be considered straightforward isometric. Weight-transformed growth curves show that males attained 36.7% of females' weight at age eight and that absolute yearly growth was 447 g between ages tree and four for males and 932 g between ages seven and eight for females (Figure 6).

southern Brazil.

		Males	Females	Both sexes
L_{∞}	Lower Cr.I	590.5	1,045.1	845.8
	Mean	612.1	1,082.7	902.8
	Upper Cr.I	638.8	1,122.7	986.0
k	Lower Cr.I	0.34	0.17	0.16
	Mean	0.40	0.18	0.21
	Upper Cr.I	0.47	0.20	0.24
t_0	Lower Cr.I	-0.57	-0.69	-1.11
	Mean	-0.35	-0.61	-0.79
	Upper Cr.I	-0.17	-0.54	-0.55

Table 2. Von Bertalanffy's growth parameters and their respective credibility interval (Cr.I, $\alpha = 0.025$) for the back-calculated mean total length (mm) at age of males, females and both sexes of the red flounders *Paralichthys orbignyanus*, from



Figure 5. Von Bertalanffy's growth curves for mean back-calculated total length-at-age of females (A) and males (B) *Paralichthys orbignyanus* in southern Brazil. Full circles indicate the individual total length-at-age observed at capture. Triangles indicate the four young-of-the-year for which microincrements were counted. The continuous line indicates the regression line. The dashed line indicates the credibility interval ($\alpha = 0.05$).

DISCUSSION

Understanding the life history strategy of the red flounder *Paralichthys orbignyanus* in southern Brazil is essential to support its management, especially the growth parameters that form part of most fisheries assessment methods, influencing population dynamics through its effects on lifetime patterns of biomass production, natural and fishing mortality, and reproductive output (Francis 2015; Lorenzen 2016).

Results from the present study indicate that P.



Figure 6. Female (black) and male (grey) *Paralichthys orbignyanus*. A) Weight transformed von Bertalanffy's growth curves. B) Yearly increments in weight-at-age in southern Brazil.

orbignyanus is a fast-growing and relatively short-living species with females showing higher growth and attaining larger sizes and older ages than males. The Genus *Paralichthys* has 20 species widespread in warm to temperate waters on continental shelves of the world (Froese and Pauly 2022). Ages and growth of several commercially important species of this genus have been studied, such as *P. californucus* from the western US (Pattison and McAllister 1990; Mac-Nair et al. 2001; Barnes et al. 2015); *P. lethostigma* from the Gulf of Mexico and eastern USA (Fischer and Thompson 2004); *P. dentatus* from the eastern USA (Dery 1997); *P. olivaceus* from Japan (Atsuchi et al. 2004; Yoneda et al. 2007); *P.* *patagonicus* from southern Brazil (Araujo and Haimovici 2000) and Uruguay to Argentina (Riestra 2010); *P. isosceles* (Fabré and Cousseau 1990); and finally *P. orbignyanus* from Argentina (Lopez Cazorla 2005). Among these species most show the same growth pattern as *P. orbignyanus*; however, no consistent pattern was observed in the seasonality formation of opaque bands in otoliths, or annuli on scales, either between different species or even among different stocks of the same species. In the case of *P. orbignyanus* from southern Brazil, opaque bands in otoliths form mainly in spring and summer when gonads mature, and the species spawn (Silveira et al. 1995). This correspondence between spawning

season and opaque band formation was also observed for *P. patagonicus* in the same region (Araujo and Haimovici 2000). At higher latitudes (41° S), narrow growth bands in the edge of scales of *P. orbignyanus* were observed from autumn to spring, and only wide bands in summer (Lopez Cazorla 2005), suggesting a similar seasonal growth pattern as in southern Brazil. No differences in the weight-length relationship was either observed between sexes in both regions. A similar lack of difference of the weight-length relationship between sexes was observed for *P. lethostigma* (Fischer and Thompson 2004).

Juveniles of piscivorous fishes, as those of the genus Paralichthys, need to grow quickly to be able to prey on other species of the same year class in their common nursery grounds (Juanes and Conover 1994). Therefore, it is not surprising that P. orbignyanus is a fast-growing fish, with males attaining an average of 255 mm and females 276 mm TL in the first year of life. Despite that, at the age of eight, males attained only 57% of L_{∞} and 36% of the weight of females. Consistent with the scientific literature, from age three onwards, the greater size and weight of females compared to males are evident, a pattern that was also observed for the southern distributions of the species (Lopez Cazorla 2005), and other species of the genus in other oceans (MacNair et al. 2001; Yoneda et al. 2007). The larger size attained by females increases fecundity, while the earlier onset of maturity of males at a smaller size diverts energy from growth to reproduction and affects both the maximum size and longevity (Saborido-Rey and Kjesbu 2005).

Maximum ages recorded in otoliths in this study corresponded to eight years in males and eleven years in females, while the observed age in scales by Lopez Cazorla (2005) were six years in males and seven years in females. The correspondence between age readings of both apposition structures can be considered acceptable; however, age determination on scales can be less reliable for older fish because of the crowding of the rings at the scale border, as is the case of *P. dentatus* in the northwestern Atlantic (Sipe and Chittenden 2001) and *Pagus pagrus* in southern Brazil (Haimovici et al. 2020). Therefore, it is not unlikely that further studies of the growth of *P. orbignyanus* in Argentina, aged through their otoliths, produce larger annuli counts than those observed by Lopez Cazorla (2005).

The total length at which *P. orbignyanus* attains sexual maturity in southern Brazil has not been established with precision, but histological studies showed that sperm was present in testes of males under 300 mm and maturing oocytes in females larger than 385 m (Silveira et al. 1995). On our growth curves, these lengths correspond to ages under two for males and three for females. Fast growth and early onset of maturation are life history traits associated with increased natural mortality and shorter lifespans (Adams 1980).

Although less abundant than other Paralichthys species in the region, the high price and large size of P. orbignyanus makes it a valuable resource for small-scale fishers. The drastic decrease in recorded landings in the 2000s (CEPERG 2012) suggests overfishing in southern Brazil. Avoiding the catch of juveniles in their shallow estuarine waters and in their nursery grounds may result in relatively fast stock recovery and, consequently, the potential yield (Horwood et al. 1998). In addition, studies of the impact of illegal shrimp trawling in the estuary and beach nets along the coast are required, as large females are frequently found in shallow estuarine and coastal waters. Because of differences in growth between males and females, intense fishing exploitation can produce changes in the sex ratio that can negatively affect reproductive success by reducing the probability of encountering potential mates or by reducing fertilization success (Rowe and Hutchings 2003). Therefore, the management of this species has to take into account also the marked difference in growth between sexes.

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