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Long-term changes in the life history of the Jamaican weakfish, *Cynoscion jamaicensis* (Vaillant and Bocourt, 1883), in southern Brazil



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ABSTRACT

Overfishing has changed the life histories of commercially harvested marine fishes worldwide. The Jamaican weakfish, Cynoscion jamaicensis, which has been caught by trawl fisheries off southern Brazil since the 1950s, was sampled in two periods (1977-80 and 2016-17) to study its life history and changes in growth and sexual maturation and assess its spawning potential ratio. The annual formation of one opaque band on the otoliths was validated, and the oldest sampled fish was a 9-year-old male. Growth patterns did not differ between sexes. The von Bertalanffy growth parameter L_{∞} increased with time, and the growth curves were significantly different between periods. Fish of the same age classes were significantly larger, heavier and had higher allometric condition factors in the most recent period than those in the first period. Reproduction occurs seasonally from late spring to early autumn, and the length and age at first maturity decreased between periods. Based on the length distributions obtained in 2016-17, the spawning potential ratio was between 57 and 62%, suggesting a moderate decrease in the abundance of the species in the region. The changes in growth are likely due to densitydependent processes because of the intense fishing that decreased the abundance of the species and of its main competitors. The changes in maturation parameters are more difficult to explain since there are three possible drivers: density-dependent processes and increasing water temperatures for the changes in the age at first maturity and increasing water temperatures and genotypic responses to differential selection for the changes in the size at first maturity. Although C. jamaicensis can be considered a resilient species due to its life history characteristics, the intense biomass removal by fishing in southern Brazil has changed its population dynamics and reduced its spawning potential. © 2020 Published by Elsevier B.V.

1. Introduction

Overfishing has caused changes in the life histories of commercially harvested marine fishes worldwide (Audzijonyte et al., 2016; Law, 2000; Trippel, 1995). Many species are beginning to present faster life histories with earlier maturation (Jørgensen, 1990; Rijnsdorp, 1993) and increased growth (Audzijonyte et al., 2016). These changes may be a result of density-independent factors, such as temperature and other climate changes (Morrongiello and Thresher, 2015; Tresher et al., 2007); and density-dependent factors, such as biomass removal by fishing (Law, 2000; Trippel, 1995). Increased mortality caused by fishing, can influence the dynamics of sexual maturation and growth in the following ways: (1) by reducing population density, which increases food availability and relaxes the density-dependent effects responsible for the reduction in growth and the increase in

age at maturity, leading to an increase in growth and a decrease in age at maturity (Barot et al., 2004); and (2) through a biased removal towards individuals who mature at large sizes, which increases the proportion of genotypes associated with reproduction at small sizes and slow growth over the long term (Dieckmann and Heino, 2007; Jørgensen, 1990; Rijnsdorp, 1993). In other words, increased mortality in the age and size ranges at which the onset of maturation can occur favors early maturation (Olsen et al., 2004).

The Jamaican weakfish, *Cynoscion jamaicensis* (Vaillant and Bocourt, 1883), is a coastal marine sciaenid that inhabits sand-muddy bottoms from the Caribbean Sea in the North Atlantic to Argentinian waters in the southwestern Atlantic (Menezes and Figueiredo, 1980). This species is a component of the coastal bottom trawl and gillnet fisheries along southeastern (23° to 28°S) and southern Brazil (28° to 34°S), comprising one or two stocks. In these regions, intense fishing has reduced the abundance of demersal and benthic fish resources since the 1950s (Haimovici et al., 2006; Yesaki and Bager, 1975; Valentini et al., 1991; Haimovici and Cardoso, 2016). The Jamaican weakfish is

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one of the three main species in the landings of the bottom trawl fishery in southeastern Brazil (Castro et al., 2002; Valentini et al., 1991) and is also captured along the coast of southern Brazil. The Jamaican weakfish is a relatively small species that rarely exceeds 350 mm in total length (Castro et al., 2002; Haimovici, 1987) and feeds mainly on crustaceans and fishes (Martins, 2000; Rondineli et al., 2007). Former studies on the life history of the species, including the seasonality of its reproduction (Castro et al., 2002), length at first maturity (Carneiro, 2007; Vazzoler and Braga, 1983), aging (David, 1997; Santos, 1963), growth and mortality (Carneiro, 2007; Castro et al., 2002), were performed in southeastern Brazil. Carneiro (2007) concluded that the stock was overexploited by analyzing the exploitation rates from lengthbased catch curves. It is not known whether the C. jamaicensis that is fished along the coast of southeastern Brazil is a part of the stock or composes a different stock from that fished along the coast of southern Brazil. No studies on the life history and population dynamics of the C. jamaicensis stocks fished in southern Brazil have been performed until now.

The evaluation of the state of stock exploitation is a fundamental step in the development of any fisheries management strategy and depends on the data availability. For the Jamaican weakfish along the coast of southern Brazil, as for most fisheries across the globe, data availability is limited (Dowling et al., 2014). However, there are many models with varying requirements for data quantity and type (Newman et al., 2015). Among the available models, the model developed by Hordyk et al. (2015a,b) seems appropriate for the type of data generated in this study.

Data on the life history and size composition of the demersal fish stocks harvested along the coast of southern Brazil were collected in two periods (1977-1985, 2016-2017) as part of a long-term study on their population dynamics and the fishery (Haimovici, 1987; Haimovici and Cardoso, 2016). The intense fishing exploitation of demersal resources in southern Brazil has caused a decrease in abundance and changes in the life history of the mainly landed species (Cardoso and Haimovici, 2011, 2014; Haimovici and Ignácio, 2005; Haimovici et al., 2006; Miranda and Haimovici, 2007). Although not a target species, C. jamaicensis is part of the demersal fish community affected by fishing that, in addition to reducing its abundance, has resulted in changes in its life history. Thus, the objectives of this study were to validate the age determination of the species and assess possible changes in its growth and sexual maturity between two time periods. We also evaluated the exploitation state of the stock in southern Brazil by estimating the remaining spawning potential ratio (SPR).

2. Materials and methods

2.1. Sampling and data collection

Length composition and biological data of C. jamaicensis were collected from landings of the industrial trawl fishery in Rio Grande between 1977 and 1985 (Haimovici, 1987) and again during 2016 and 2017, as well as from bottom trawl surveys in the same region (Haimovici et al., 1996) between 1981 and 1983 (Fig. 1). For the length composition samples, between 100 and 400 specimens were randomly sampled from the catches. The total length (Lt) of each specimen was measured between the snout and the end of the caudal fin. For a smaller number of individuals, the total length (Lt, mm), total weight (Wt, g) and gonad weight (GW, g) were recorded, and the sagittal otoliths were removed and dried to preserve them. Macroscopic maturation was recorded following a seven-stage scale for multiple-batch spawning sciaenid fishes (Haimovici and Cousin, 1989). The maturity stage was determined macroscopically with the following seven-point scale: (1) virginal immature, (2) developing virginal, (3) developing, (4) advanced development, (5) running, (6) partly spent and (7) recovering.

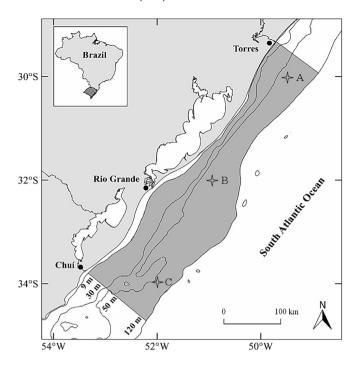


Fig. 1. Bottom-trawl fishing area where *C. jamaicensis* is caught in southern Brazil. The three locations from where sea surface temperature anomalies between 1960 and 2017 were obtained are indicated with the letters: A: 30°S, 50°30′W; B: 32°S, 51°W and C: 34°S, 52°W.

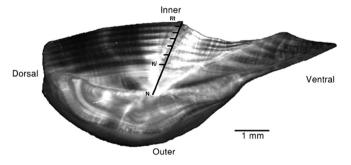


Fig. 2. Thin section examined with reflected light of a sagittae otolith of a seven-year-old female *C. jamaicensis* (*Lt*: 333 mm) caught in southern Brazil in 2016. The black scale side bars indicate the end of each opaque band. *N*: nucleus; *Ri*: the distance from the nucleus to the end of each opaque band; *Rt*: the distance from the nucleus to the inner edge. Opaque bands appear as white bands, whereas translucent bands appear as dark bands.

2.2. Age determinations and validation

Thin transverse sections (0.20–0.25 mm) were cut through the nucleus of the otoliths embedded in polyester resin using a high concentration diamond blade (Buehler-Isomet). All sections were fixed on glass slides with xylol base mounting media (ENTELAN Merck $^{\textcircled{\$}}$).

Sections were examined with transmitted light under a compound microscope $(35\times)$. The number of opaque bands was counted, and the nature (opaque or translucent) of the band at the inner margin of the otolith was recorded. The distances between the nucleus and the end of each opaque band (Ri) and from the nucleus to the otolith margin (Rt) were measured on digitized images of the sections (Fig. 2).

Two readers independently examined the otolith sections. To evaluate the precision between readings, the mean coefficient of variation (*CV*) (Campana and Jones, 1992) was calculated as

follows:

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

where CV_j is the estimated age accuracy for the jth fish; X_{ij} is the age determination of the jth fish by the ith reader; X_j is the mean age of the jth fish; and N is the number of readings. The periodicity of the formation of the growth bands was determined by analyzing the changes in the monthly relative frequencies of opaque and translucent bands along the inner margins of the otoliths and calculating the monthly averages of the marginal increment (MI) according to Campana (2001) as follows:

$$MI = (R - Rn)/R$$

where R = distance from the nucleus to the inner margin of the otolith and Rn = distance from the core to the end of the last opaque band. This formula is suitable for fast-growing fish (Campana, 2001).

2.3. Growth

The total length at the end of the formation of the opaque bands on the otoliths was back-calculated following the procedure proposed by Campana (1990), which assumes a linear relationship between Lt and R and a fixed intercept (biological intercept) for all analyzed individuals. This procedure was preferred instead of the traditional method because several experiments that have controlled or manipulated individual fish growth showed that the greatest variation among individuals occurs in the slope of the relationship between fish length and otolith radius and not the intercept (Marshall and Parker, 1982; Rice et al., 1985; Rosenberg and Haugen, 1982; Secor and Dean, 1989a; Secor et al., 1989b). For C. jamaicensis, a radius of 0.4 mm (O_0) measured on a sectioned otolith from a 63-mm total length (L_0) juvenile was considered the "biological intercept". The back-calculated lengths were obtained according to the following equation:

$$L_a = L_c + (O_a - O_c)(L_c - L_o)(O_c - O_o)^{-1}$$

where L_a is the back-calculated length at age a; L_c is the total length of the fish at the time of capture; O_a is the radius of the otolith at a given age a; and O_c is the total inner radius of the otolith at the time of capture.

Statistical differences in the observed mean length for each age class, the mean weight for each age class and the mean back-calculated length for each age class were tested using an analysis of variance.

Growth in length was described for both periods and sexes with the von Bertalanffy growth model (VBGM) from back-calculated lengths by age as follows:

$$L_t = L_{\infty}(1 - e^{-k(t-to)})$$

where Lt is the total length of the fish; 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). The age-length data were assumed to follow a log-normal 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:

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

The seed values for each parameter were constructed from a noninformative 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 was restricted to the interval of -5 and 5. The probability of $\log L_{\infty}$ was considered to follow a normal distribution with a mean equal to the logarithm of the observed maximum Lt and a variance of 0.001. The probability of t_0 was considered to follow a uniform distribution with a minimum equal to -3 and a maximum equal to zero, and the probability of σ was considered to follow a uniform distribution with a minimum equal to zero and a maximum equal to five.

The posterior distributions of the parameters were obtained through the stochastic process of the Monte Carlo Markov chains (MCMC), which provides an easy and clear way to compare the resulting parameters by analyzing the overlap between the 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 the two remaining values, resulting in a final sample with 10 500 values in the posterior distribution of each parameter (Kinas and Andrade, 2010).

A likelihood ratio test ($\alpha = 0.05$) was used to compare all VBGM parameters at once among sexes and periods (Aubone and Wöhler, 2000; Cerrato, 1990).

The asymptotic weight (W_{∞}) was estimated by the transformation of length by age data to weight-by-age data, based on the potential weight-length equations.

2.4. Weight-length relationships

The relationship between weight and length was described by the potential model ($Wt = a_x L t^b$). For comparisons between the weight–length relationships, the data were transformed into decimal logarithms, and the linear regression models were compared between sexes and between periods through covariance analysis ($\alpha = 0.05$) (Zar, 1984).

2.5. Allometric condition factor (K)

Allometric condition factors (K) (Heincke, 1908; Le-Cren, 1951) were calculated as follows:

$$K = Wt/Lt^b$$

where *b* is the coefficient of the potential equation of the weightlength relationship corresponding to each period.

Mean condition factors by length classes (3 cm interval) were compared between periods and sexes with an analysis of variance (ANOVA, P < 0.05).

2.6. Reproductive cycle

The reproductive cycle was determined by analyzing the changes in the monthly averages of the gonadosomatic index (GSI) for the most recent period. GSI was calculated as $GSI = 100 \times (Wg/Wt)$ (Wooton, 1998), where Wg is the gonad weight in grams.

2.7. Length and age at first maturity

The length (L_{50}) and age (A_{50}) at first maturity were calculated with a Bayesian approach to the logistic model (Cardoso and Haimovici, 2014; Kinas and Andrade, 2010). To avoid misidentification between spent and immature stages, only specimens collected during the peak of the reproductive period were selected for the estimation of maturity ogives. This period was estimated visually based on the results of the maturation seasonality. The macroscopic stage (3) was considered the onset of maturation.

The total number (n_i) and the total number of mature individuals (y_i) were calculated for both sexes for each age class and for each class of length with a 10-mm interval for both periods, where Θ_i expresses the probability that an individual of a certain age i and determined length class i be sexually mature y_i . It was assumed that this probability followed a binomial distribution $Bin(n_i, \Theta_i)$.

The data were adjusted to a logistic model defined by the logit-link function, which transforms the parameter Θ_i restricted to the interval [0, 1] into a binomial distribution m, defined between $(-\infty, +\infty)$ (Kinas and Andrade, 2010). The logistic model was defined as follows:

$$m_i = g(\Theta_i) = \log(\Theta_i/1 - \Theta_i)$$

$$m_i = \beta_0 + \beta_1.x_i$$

where m_i is the probability for each x_i , which is calculated for each age or length class.

From this model, the length and age of first maturation are defined as follows:

$$L_{50}$$
 or $A_{50} = -\beta_0/\beta_1$

To compare the estimates of length and age of first maturation for both sexes between the different periods, the posterior distribution $p(\beta_0, \beta_1|D)$, where $D = \{(y_i, n_i, x_i); i = 1, \ldots, k\}$, was also obtained via MCMC. To obtain the posterior distribution of β_0 and β_1 , the variables were considered independent, and a normal distribution with a zero mean and wide variance (1000) was used as the *a priori* distribution. The number of chains and simulated iterations were the same as those used for the simulation of the VBGM parameters. The posterior distribution of the parameters results in a simple and clear way of visually comparing through the overlap or lack of overlap of the distributions, avoiding the need for subsequent statistical tests (Kinas and Andrade, 2010).

2.8. Spawning potential ratio (SPR)

The spawning potential was estimated by the length-based spawning potential ratio (LBSPR) method developed by Hordyk et al. (2015a,b), which compares a modeled length composition of a stock without fishing mortality (pristine condition) with the current length composition observed from the catches. LBSPR is an equilibrium-based method with the following assumptions: (i) the von Bertalanffy equation adequately describes the growth, (ii) a single growth curve can be used for both sexes that have equal catchability, (iii) growth rates remain constant across the cohorts within a stock, (iv) the selectivity is asymptotic, (v) the length at age is normally distributed, (vi) the recruitment remains constant over time, (vii) natural mortality remains constant across adult age classes, and (vii) recruitment is constant over time (Hordyk et al., 2015a). The SPR for the exploited population is a function of the ratio of fishing mortality to natural mortality (F/M), selectivity and the two life history ratios M/k and L_{50}/L_{∞} . k is the von Bertalanffy growth coefficient, L_{50} is the size at maturity and L_{∞} is asymptotic size. The virginal length composition was obtained through the von Bertalanffy growth parameters (L_{∞} and k), natural mortality (M), and size at 50% and 95% maturity (L_{50} and L_{95}). The life history parameters of the first period (1977– 1980) were used to estimate the spawning potential, assuming that they adequately represented the pristine situation of the population.

Natural mortality was calculated as the average of the values resulting from the three empirical estimators based on the maximum age (Then et al., 2014). Two maximum ages were used for the calculations, namely, the age of the oldest fish sampled and one year more. This procedure was employed because the removal of older age classes by fishing still occurs at moderate

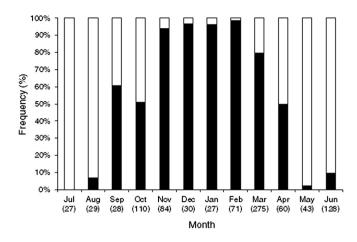


Fig. 3. Frequency by month of opaque (\blacksquare) and translucent (\square) edges of thin sections of *C. jamaicensis* sagittae otoliths sampled in southern Brazil. The sample sizes are in parentheses.

levels of exploitation (Berkeley et al., 2004), and *C. jamaicensis* has been fished by the bottom trawl fishery in southern Brazil since the 1950s (Cardoso and Haimovici, 2016; Yesaki and Bager, 1975).

The current length composition was obtained by random samplings of pair trawler landings in Rio Grande in 2016 and 2017. The SPR was calculated by considering the two estimated natural mortality values and the mean of each life history parameter.

2.9. Sea surface temperature

To investigate the possible effect of climate changes on the population dynamics of *C. jamaicensis*, the monthly sea surface temperature anomalies (SST, °C) were calculated for the period between 1960 and 2017 considering the climatology from 1950 to 2010 for three locations along southern Brazil (Fig. 1). The monthly average SSTs were obtained from the Physical Oceanography Distributed Active Archive Center (PODAAC, 2019). These average SST values were calculated using the "optimum interpolation method" for satellite data and *in situ* measurements (ship and buoy) to generate high-resolution sea surface climatology (Reynolds and Smith, 1995).

All statistical analyses were performed in the software R (R Core Team, 2013), version 3.3.1, using the OpenBUGS package and the libraries R2 WinBUGS (Sturtz et al., 2005) and BRugs (Thomas et al., 2006). SPR was estimated using the LBSPR package version 0.1.2 in R (Hordyk, 2017).

3. Results

3.1. Age readings and validation

The coincidence between the number of opaque bands counted by the two independent readers was 75.5%, corresponding to a CV of 6.33%, which is considered acceptable according to Campana (2001). A joint reading of otoliths that differed in one band in the independent readings increased the percent of aged specimens to 96.6%.

Ages were determined for 282 individuals from 1977–1980 (158 males and 124 females), ranging from 152 mm to 316 mm in total length (*Lt*), and for 461 individuals from 2016–2017 (239 males and 222 females), ranging from 180 mm to 346 mm in *Lt*.

The otolith thin sections showed an alternating pattern of opaque and translucent bands (Fig. 2). The frequency of otoliths with opaque margins was higher than 80% between November

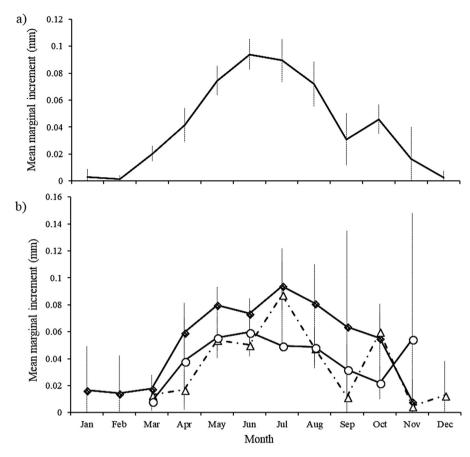


Fig. 4. Mean translucent marginal increment (mm) of otolith thin sections of *C. jamaicensis* sampled in southern Brazil: (a) all pooled ages; (b) discriminated by ages: 2 (----); 3 (-----) and 4-9 (-----). Vertical bars indicate the confidence intervals ($\alpha = 0.05$).

Table 1Observed mean length (Lt, mm) by age of C. jamaicensis fished in southern Brazil. The results of the Kruskal–Wallis test between sexes by age are shown in the right column. S.D. = standard deviation; n = number of sampled individuals.

1977-19	980								
Age	Males			Females			χ^2	df	<i>p</i> -value
	Mean Lt (mm)	n	S.D.	Mean Lt (mm)	n	S.D.			
1	213.1	28	14.7	214.5	26	21.4	0.03	1	0.863
2	247.6	28	17.9	249.9	33	16.2	0.66	1	0.417
3	272.0	63	12.1	267.0	40	24.3	0.79	1	0.373
4	286.6	19	11.3	286.8	13	8.6	0.00	1	0.985
5	293.6	11	9.0	298.5	4	7.0	0.91	1	0.341
6	290.0	2	7.1	305.3	3	13.6	1.33	1	0.248
2016-20	017								
Age	Males	Males			Females			df	<i>p</i> -value
	Mean Lt (mm)	n	S.D.	Mean Lt (mm)	n	S.D.			
1	211.2	57	17.6	216.7	40	16.2	3.28	1	0.070
2	252.4	58	20.3	251.5	62	20.2	0.10	1	0.747
3	291.0	39	13.5	290.9	35	18.5	0.12	1	0.733
4	305.8	50	11.0	309.4	59	9.7	2.21	1	0.137
5	305.9	12	12.8	316.2	11	10.0	3.09	1	0.079
6	319.7	10	6.9	329.1	8	12.4	4.38	1	0.053
7	314.7	3	2.5	339.0	3	9.6			
8	331.5	2	9.2	321.0	1				

and March and lower than 10% between May and August (Fig. 3). The monthly variation in the average translucent MIs followed the same pattern; high values were observed from May to August, and low values were observed from September to March (Fig. 4a). The pattern was similar for all ages (Fig. 4b). The annual patterns of the edge types and the average translucent MIs indicated the formation of one opaque band during the summer and spring and

one translucent band during the fall and winter. These results validate the age readings in the *C. jamaicensis* otoliths thin sections from southern Brazil.

The spawning of *C. jamaicensis* in southern Brazil and the formation of opaque bands mostly occur from November to March; therefore, January 1 was assumed to be the nominal date of birth of all specimens for the classification of age classes. The oldest

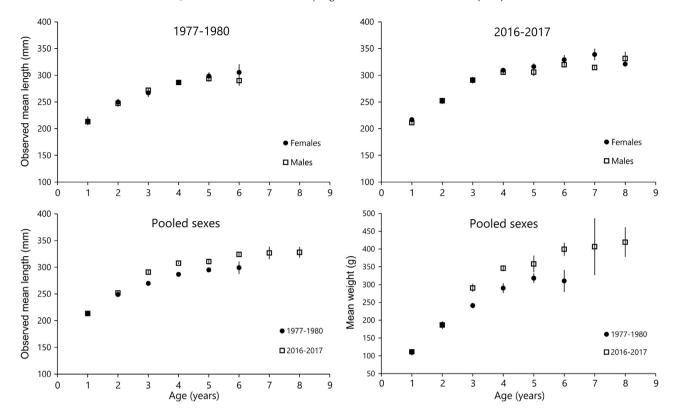


Fig. 5. Observed mean length by age of males and females of *C. jamaicensis* sampled in southern Brazil in both periods (upper panel). Observed mean length by age of pooled sexes by period (lower right panel). Vertical bars indicate the confidence intervals ($\alpha = 0.05$).

specimens sampled in the 1977–1980 period were two 7-year-old females, while the oldest specimen was one 9-year-old male in the 2016–2017 period. This result does not indicate that the lifespan had been enhanced; instead, it is probably the result of a sampling issue.

3.2. Growth

The mean Lt and weight in all age classes did not significantly differ between males and females in either sampled period (Table 1, Fig. 5); therefore, both sexes were pooled together for the comparison between periods. The average Lt and weight were significantly higher (P < 0.05) in the second period than in the first period (Tables 2, 3).

The mean back-calculated length at age was between the previous and former ages observed in the samples for both periods and for both sexes, which is evidence of the adequacy of the back-calculation procedure (Tables 4 and 5). The back-calculated length at age decreased with increasing age, which was interpreted as Rosa Lee's phenomenon (Chugunova, 1963). The large difference between the length observed in the landings and the back-calculated length at age one was attributed to the selectivity of trawl nets (Tables 4 and 5). The mean back-calculated length in each age class was higher in the second period than in the first period (Tables 4 and 5).

The credibility intervals of all three von Bertalanffy growth parameters of both sexes overlapped, indicating no significant differences between the growth curves of males and females (Table 6). Between the periods, a significant increase was observed only in L_{∞} for females. Despite the overlapping growth curves (Fig. 6), when the von Bertalanffy growth parameters were considered together, a significant difference ($X_{\rm obs}^2=76.52$; P<0.05) was observed between the 1977–80 and 2017–17 periods.

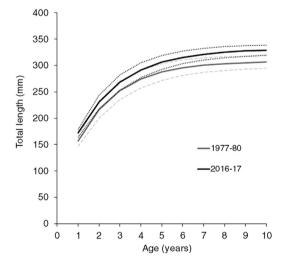


Fig. 6. Von Bertalanffy's growth curves of *C. jamaicensis* in southern Brazil by period. 2016–2017: average values modeled (continuous black line) and their credibility intervals (dotted black lines); 1977–1980: average values modeled (continuous gray line) and their credibility intervals (dashed gray lines).

3.3. Weight-length relationships

The covariance analysis of the relationship between weight and length did not show significant differences between the sexes (Fig. 7) in either 1977–1980 (P=0.561) or 2016–2017 (P=0.269). For pooled sexes, significant differences were observed between periods (P<0.001), resulting in the following equations:

Period (1977–1980): $Wt_{pooled sexes}$

Table 2 Observed mean length (Lt, mm) by age of C. interpolate Interpo

Age	1977-1980	1977–1980			2016–2017			df	p-value
	Mean Lt (mm)	n	S.D.	Mean Lt (mm)	n	S.D.			
1	212.8	54	17.6	213.5	97	17.2	0.25	1	0.621
2	248.8	61	16.9	251.9	120	20.2	1.84	1	0.175
3	269.8	103	18.0	291.0	74	15.9	57.35	1	< 0.001
4	286.7	32	10.1	307.7	109	10.5	52.26	1	< 0.001
5	294.9	15	8.5	310.8	23	12.5	14.31	1	< 0.001
6	299.2	5	13.3	324.2	18	10.4	8.31	1	0.004
7				326.8	6	14.7			
8				328.0	3	8.9			

Table 3 Mean weight (Wt, g) by age of C. jamaicensis fished in southern Brazil with the sexes pooled. The results of the Kruskal-Wallis test between periods are shown in the right column. S.D. = standard deviation; n = number of sampled individuals.

Pooled	sexes								
Age	1977-1980	1977-1980			2016–2017			df	p-value
	Mean Wt (g)	n	S.D.	Mean Wt (g)	n	S.D.			
1	109.7	54	31.0	111.4	97	27.7	0.57	1	0.450
2	186.3	61	44.3	186.6	120	46.6	0.05	1	0.823
3	241.2	103	39.0	290.9	74	50.4	41.04	1	< 0.001
4	290.2	32	39.6	346.0	109	43.2	31.91	1	< 0.001
5	318.2	15	28.8	358.0	23	59.6	5.93	1	0.015
6	310.4	5	35.4	399.4	18	39.6	10.28	1	0.001
7				406.5	6	99.6			
8				419.3	3	36.5			

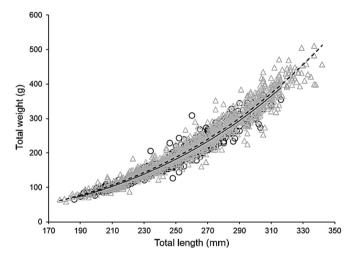


Fig. 7. Weight–length relationship for pooled sexes of *C. jamaicensis* sampled in southern Brazil for the periods 1977–1980 (o) and 2016–2017 (Δ). Continuous line indicates the regression line for 1977–1980. Dashed line indicates the regression line for 2016–17.

=
$$3.23 \times 10^{-6} \times Lt^{3.23}$$
 ($R^2 = 0.9521$, $n = 482$)
Period (2016–2017): $Wt_{\text{pooled sexes}}$
= $3.70 \times 10^{-6} \times Lt^{3.21}$ ($R^2 = 0.9630$, $n = 1405$).

3.4. Allometric condition factor (K)

No significant differences were observed between sexes for the allometric condition factor (K) according to a two-way ANOVA (P=0.353) (Table 7). For pooled sexes, significant differences were observed between periods and length classes (two-way ANOVA, P<0.001) (Table 7). The mean K in different TL classes was higher in the second period than in the first period

(Table 8, Fig. 8). Significant differences in K in the different length classes were observed between periods (one-way ANOVA, P < 0.001) (Table 8). The percentage increases in the total weight by length class between periods were as follows: 0.03% at 180 mm, 0.13% at 210 mm, 0.12% at 240 mm, 0.63% at 270 mm and 2.29% at 300 mm.

3.5. Reproductive cycle

The highest values of the gonadosomatic index were observed between November and March, with few GSI values > 1 in April (Fig. 9). Therefore, it can be concluded that the reproductive season of *C. jamaicensis* in the southern region of Brazil occurs from austral late spring to early autumn.

3.6. Length and age at first maturity

The length and age at first maturity were calculated using data from 887 individuals sampled in the peak of the reproductive season from November to March (93 females and 97 males (1977 to 1980) and 319 females and 378 males (2016–2017)).

Significant relationships between length, age and sexual maturity were observed for both sexes and periods, as the posterior distributions of β_1 did not include zero (Table 9).

For both analyzed periods, the age and length at first maturity did not differ between sexes, as can be observed by the overlapping of the posterior distributions (Table 9). On the other hand, the length at first maturity decreased significantly between periods for both sexes, from 230 mm to 205 mm for females and from 234 mm to 205 mm for males, as shown by the nonoverlapped posterior distributions (Table 9, Fig. 10). The age at first maturity also decreased from 2.29 years to 1.9 years for females and from 2.55 years to 1.82 years for males (Table 9, Fig. 11).

Table 4Observed mean length (Lt, mm) in the landings and back-calculated mean lengths by age for males, females and pooled sexes of C. jamaicensis fished in southern Brazil between 1977 and 1980. n = Number of sampled individuals.

Males — 1977-		Observed man It (mm)	Ammulaia						
Age (years)	n	Observed mean Lt (mm)	Annulus 1		111	13.7	17		
			I	II	III	IV	V	VI	
1	17	213.1	172.2						
2	31	247.6	151.9	220.3					
3	58	272.0	150.6	213.5	257.4				
4	26	286.6	145.8	202.2	243.9	278.5			
5	16	293.6	128.9	183.2	225.7	260.2	289.6		
6	3	290.0	128.8	159.7	190.5	221.4	257.4	288.3	
7									
Total	151		151	134	103	45	19	3	
Back-calculated	mean Lt ((mm)	149.7	208.1	247.1	268.2	284.5	288.3	
Growth increme	ent (mm)			58.3	39.0	21.1	16.3	3.7	
Females – 1977	7-1980								
Age (years) n Ol		Observed mean Lt (mm)	Annulus 1	number					
			I	II	III	IV	V	VI	VII
1	16	214.5	167.1						
2	30	249.9	155.8	224.3					
3	44	267.0	148.5	211.6	251.8				
4	20	286.8	143.5	198.6	245.9	276.0			
5	6	298.5	126.6	184.7	233.5	264.2	294.9		
6	1		135.6	164.7	208.2	251.8	280.9	305	
7	2	303.0	127.8	160.4	192.9	231.8	257.8	277.73	303
Total	119		119	103	73	29	9	3	2
Back-calculated	mean Lt ((mm)	150.4	209.7	246.5	269.7	285.1	288.0	303.0
Growth increme	ent (mm)			59.3	36.7	23.1	15.4	2.9	14.9
Pooled sexes –	1977-198	0							
Age (years)	n	Observed mean Lt (mm)	Annulus 1	number					
			I	II	III	IV	V	VI	VII
1	33	212.8	169.7						
2	61	248.8	153.9	222.3					
3	102	269.8	149.7	212.7	255.0				
4	46	286.7	144.8	200.6	244.7	277.4			
5	22	294.9	128.2	183.6	227.8	261.3	291.1		
6	4	299.2	130.5	160.9	195.0	229.0	263.3	293.7	
7	2	303.0	127.8	160.4	192.9	231.8	257.8	277.0	303.0
Total	270		270	237	176	74	28	6	2
Back-calculated	mean Lt ((mm)	150.0	208.8	246.8	268.8	284.7	288.1	303.0
Growth increment (mm)				58.7	38.0	21.9	15.9	3.4	14.8

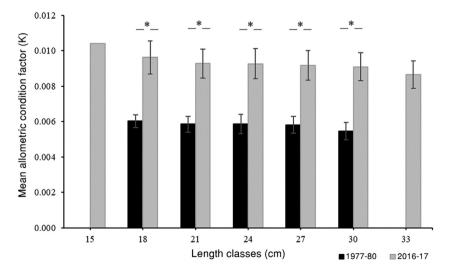


Fig. 8. Mean of the allometric condition factor (K) of C. jamaicensis sampled in southern Brazil by period: 1977–1980 (black bars) and 2016–2017 (gray bars) at length classes with standard deviation. The -*- indicates significant differences between periods (p < 0.05).

Table 5Observed mean length (Lt, mm) in landings and back-calculated mean lengths by age for males, females and pooled sexes of C. jamaicensis fished in southern Brazil between 2016 and 2017. n = Number of sampled individuals.

Age (years)	-	Observed mean Lt (mm)	Annuluc	number							
Age (years)	n	Observed mean Li (mm)	I	II	III	IV	V	VI	VII	VIII	IX
1	43	211.2	194.6				•	**	*11	V 111	
2	61	252.4	162.2	235.6							
3	39	291.0	156.4	226.6	274.9						
4	47	305.8	148.6	211.9	259.9	295.5					
5	24	305.9	142.1	198.1	242.1	279.0	305.3				
6	10	319.7	137.8	186.0	226.1	259.1	286.7	313.0			
7	4	314.7	127.9	167.8	211.1	239.2	264.2	289.2	311.0		
8	1	31	134.7	182.5	218.4	254.3	278.2	302.1	314.0	338.0	
9	1		134.4	1582	205.9	229.7	241.6	265.4	289.2	313.0	325.
Total	230		230	187	125	87	40	16	6	2	1
Back-calculate	d mean	Lt (mm)	160.5	218.2	256.0	283.0	294.3	303.4	307.9	325.5	325.
Growth increr	nent (mi	m)		57.6	37.8	26.9	11.3	9.0	4.5	17.6	-0.5
Females – 20	16-2017										
Age (years) n Observed mean Lt (mm)			Annulus	number							
			I	II	III	IV	V	VI	VII	VIII	
1	27	216.7	197.7								
2	68	251.5	164.3	235.8							
3	33	290.9	158.4	229.9	273.3						
4	48	309.4	149.5	216.0	263.1	298.6					
5	29	316.2	146.4	208.8	250.2	287.4	313.0				
6	6	329.1	142.5	190.2	233.3	262.1	292.9	316.1			
7	5	339.0	129.9	189.1	226.5	261.1	290.4	314.5	335.6		
8	3	321.0	123.8	172.5	209.0	241.3	265.7	298.0	318.4	330.6	
9											
Total	219		219	192	124	91	43	14	8	3	
Back-calculate	d mean	Lt (mm)	160.0	222.1	258.6	288.7	304.3	311.6	329.1	330.6	
Growth increr	nent (mi	m)		62.1	36.4	30.0	15.6	7.3	17.4	1.4	
Pooled sexes	- 2016-	2017									
Age (years)	n	Observed mean Lt (mm)	Annulus	number							
			I	II	III	IV	V	VI	VII	VIII	IX
1	70	213.5	195.8								
2	129	251.9	163.3	235.7							
3	72	291.0	157.3	228.1	274.2						
4	95	307.7	149.1	214.0	261.5	297.1					
5	53	310.8	144.4	204.0	246.6	283.6	309.5				
6	16	324.2	139.6	187.6	228.8	260.2	289.0	314.1			
7	9	326.8	129.0	179.6	219.7	251.4	278.8	303.2	324.6	00	
8	4	328.0	126.5	175.0	211.4	244.6	268.8	299.0	317.3	332.5	00-
9	1		134.4	158.2	205.9	229.7	241.6	265.4	289.2	313.0	325
Total	449		449	379	250	178	83	30	14	5	1
Back-calculate	d mean	Lt (mm)	160.2	220.2	257.3	285.9	299.5	307.2	320.0	328.6	325
Growth increr	nent (mi	m)		59.9	37.1	28.5	13.5	7.7	12.7	8.5	-3.

Table 6 Von Bertalanffy's growth parameters and their respective credibility intervals (*Cr. I*, $\alpha = 0.05$) for *C. jamaicensis* fished in southern Brazil.

	Periods	Females		Males		Pooled sexes	
		1977–1980	2016-2017	1977-1980	2016–2017	1977–1980	2016-2017
	Lower Cr.I.	294.42	330.12	297.22	311.87	297.98	323.49
L_{∞}	Mean	308.02	343.24	311.89	322.97	308.21	331.66
	Upper Cr.I.	323.52	357.61	329.65	335.63	319.87	340.45
	Lower Cr.I.	0.41	0.36	0.41	0.42	0.44	0.41
k	Mean	0.50	0.42	0.49	0.50	0.50	0.46
	Upper Cr.I.	0.58	0.49	0.58	0.57	0.56	0.51
	Lower Cr.I.	-0.64	-0.82	-0.61	-0.75	-0.55	-0.72
t_0	Mean	-0.46	-0.65	-0.43	-0.56	-0.42	-0.59
	Upper Cr.I.	-0.29	-0.48	-0.27	-0.39	-0.30	-0.48
	Lower Cr.I.	-	-	-	-	316.82	385.39
W_{∞}	Mean	_	_	_	_	353.31	416.15
	Upper Cr.I.	_	_	_	_	398.34	451.05

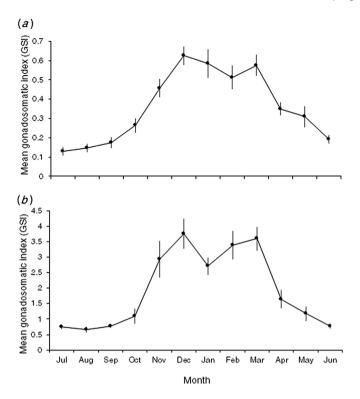


Fig. 9. Monthly mean gonadosomatic indices for males (a) and females (b) of *C. jamaicensis* sampled in southern Brazil. Vertical bars indicate the confidence interval ($\alpha = 0.05$).

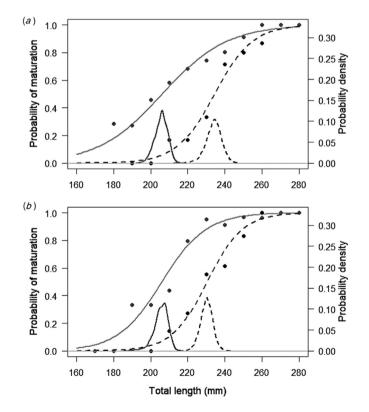


Fig. 10. Length maturity ogives and their respective posterior distributions of the estimated L_{50} by period for males (a) and females (b) of *C. jamaicensis* caught in southern Brazil. Dashed black lines (1977–1980). Continuous gray lines (2016–2017).

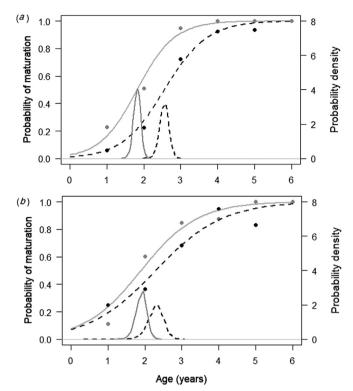


Fig. 11. Age maturity ogives and their respective posterior distributions of the estimated A_{50} by period for males (a) and females (b) of *C. jamaicensis* caught in southern Brazil. Dashed black lines (1977–1980). Continuous gray lines (2016–2017).

Table 7Results of the two-way ANOVA for comparison of the allometric condition factor K of *C. jamaicensis* fished in southern Brazil.

Variables	D.f.	F-value	p-value
Periods	1	7070.914	< 0.001
Sexes	1	0.862	0.353
Length classes	5	7.919	< 0.001
Periods: Sexes	1	0.015	0.902
Periods: Length classes	4	0.728	0.573
Sexes: Length classes	5	0.107	0.991
Periods: Sexes: Length classes	4	0.149	0.963
Residuals	1864		

3.7. Spawning potential ratio (SPR)

The instantaneous coefficient of natural mortality (M) for a maximum age of 9 years was estimated as 0.6, and the SPR for 2016–2017 was 43%, ranging from 37 to 71%, when the uncertainty of the life history parameters was considered (Table 10). For a maximum age of 10 years, M was estimated at 0.55, and the SPR was 38%, ranging from 33 to 65% (Table 10). These scenarios suggest losses between 57 and 62% of the spawning potential in relation to the virginal condition. However, these estimates presented large confidence intervals due to the low precision of the life history parameters.

3.8. Sea surface temperature (SST)

An increasing trend in the SST anomalies from 1960 to 2017 was observed at the three locations along the coast of southern Brazil (Fig. 12). The main increase was observed in the late 1990s when almost only positive anomalies were registered. The highest values occurred after 2015.

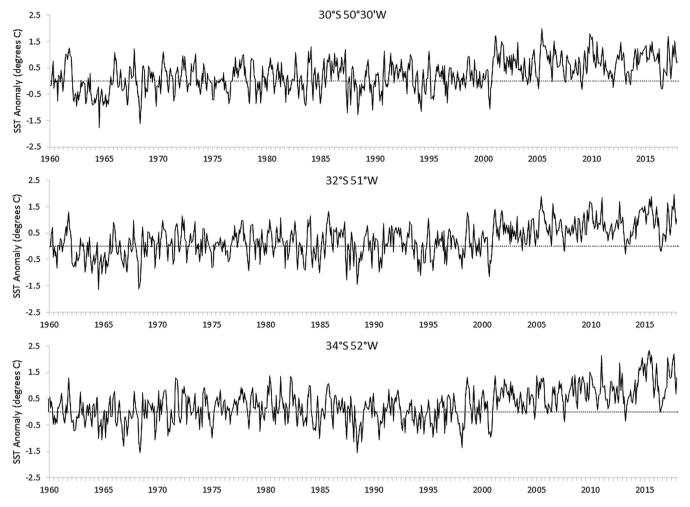


Fig. 12. Monthly means sea surface temperature anomalies from 1960 to 2017 for three locations along the continental shelf of southern Brazil. Dashed lines indicate anomalies equal to zero.

Table 8Mean allometric condition factor (K) by length class (3 cm) of C. *jamaicensis* fished in southern Brazil in different periods. The one-way ANOVA results are shown in the right column. S.D. = standard deviation; n = number of sampled individuals.

Length classes (cm)	1977-1980			2016–2017			F-value	p-value	
	Mean K Factor	S.D.	n	Mean K Factor	S.D.	n			
15				0.0104		1			
18	0.0060	0.0004	35	0.0096	0.0009	84	489.928	< 0.001	
21	0.0058	0.0004	122	0.0093	0.0008	373	1963.2410	< 0.001	
24	0.0059	0.0005	198	0.0093	0.0008	395	2622.2500	< 0.001	
27	0.0058	0.0005	112	0.0092	0.0008	342	1614.4950	< 0.001	
30	0.0055	0.0005	15	0.0091	0.0008	200	302.0980	< 0.001	
33				0.0087	0.0008	10			
Total	0.0058	0.0005	482	0.0092	0.0008	1405			

4. Discussion

This study validated the age readings in thin sections of *C. jamaicensis* sagittal otoliths. A well-defined pattern of annual deposition of one opaque ring during the months with warm waters (late austral spring and summer) and one translucent ring during the months with cold water (late austral autumnwinter) was demonstrated. To the best of our knowledge, the deposition of calcium carbonate with different opacities throughout the year occurs due to a combination of endogenous factors, such as reproduction and diet, and exogenous factors, such as water temperature (Green et al., 2009; Morales-Nin, 2000). The continental shelf and slope of southern Brazil (29°–34°S) are under the influence of marked latitudinal displacements of the

Subtropical Convergence, resulting in seasonal variations of up to 10 °C in the SSTs from the warmer months (February and March) to the colder months (July to August) (Castello et al., 1998). The same seasonality in the translucent and opaque bands was observed in sagittal otoliths for other demersal sciaenid species in southern Brazil that have different spawning seasons, such as *Macrodon atricauda* (spawns during spring and summer) (Cardoso and Haimovici, 2011), *Cynoscion guatucupa* (spawns during spring and autumn) (Vieira and Haimovici, 1993), *Umbrina canosai* (spawns during winter and spring) (Haimovici and Reis, 1984) and *Micropogonias furnieri* (spawns in late spring and summer) (Schwingel and Castello, 1990). Therefore, temperature rather than the reproductive season may be related to the seasonality

Table 9 Mean and credibility intervals (*Cr.I.*, $\alpha = 0.05$) for model parameters (β_0 and β_1) and estimated length (L_{50}) and age at maturity (A_{50}) from each period for *C. jamaicensis* sampled in southern Brazil.

Periods	Parameters	Females			Males	Males			
		Cr.I .2.5%	Mean	Cr.I. _{97.5%}	Cr.I. _{2.5%}	Mean	Cr.I. _{97.5%}		
	L ₅₀ β ₁	0.07	0.109	0.159	0.062	0.102	0.142		
	L_{50} β_0	-36.851	-25.132	-15.997	-33.558	-23.946	-13.272		
1977-1980	L_{50} (mm)	223.14	230.09	236.34	225.01	233.99	241.54		
1977-1960	A_{50} β_1	0.705	1.169	1.709	1.252	1.794	2.416		
	A_{50} β_0	-4.148	-2.694	-1.403	-6.296	-4.591	-3.054		
	A_{50} (years)	1.85	2.29	2.69	2.29	2.55	2.79		
	L ₅₀ β ₁	0.058	0.085	0.108	0.046	0.058	0.072		
	L_{50} β_0	-22.486	-17.419	-11.417	-14.982	-11.916	-9.134		
2016-2017	L_{50} (mm)	196.71	205.56	211.75	198.45	205.69	211.73		
2010-2017	A_{50} β_1	0.97	1.366	1.812	1.519	2.046	2.686		
	A_{50} β_0	-3.648	-2.607	-1.658	-5.034	-3.731	-2.648		
	A_{50} (years)	1.57	1.9	2.17	1.61	1.82	2.01		

Table 10 Input values of *C. jamaicensis* life history parameters used to fit the length-based spawning potential ratio model (Hordyk et al., 2015b) and the output of the spawning potential ratio (SPR) for each parameter combination. M = natural mortality; k and $L_{\infty} =$ Von Bertalanffy growth coefficients; $L_{50} =$ length at first maturity; $L_{95} =$ length at 95% of maturation.

M	K	$M k^{-1}$	L_{∞}	L ₅₀	L_{95}	SPR
Estimated	average values					
0.61	0.50	1.22	308.2	232.0	261.3	43%
0.55	0.50	1.09	308.2	232.0	261.3	38%
Lower cred	libility interval					
0.61	0.44	1.38	298.0	224.1	250.5	71%
0.55	0.44	1.25	298.0	224.1	250.5	65%
Upper cred	libility interval					
0.61	0.56	1.09	319.9	238.9	275.8	37%
0.55	0.56	0.98	319.9	238.9	275.8	33%

in the deposition of the translucent and opaque bands in *C. jamaicensis* otoliths.

The differences in the von Bertalanffy growth curves, the increase in the observed lengths and weights by age classes and the large back-calculated lengths at age support the conclusion that growth was faster in recent years (2016-2017) than in the former period (1977-1980). The increase in length by age for both sexes promoted the increase in L_{∞} and the decrease in k, except for males. A decrease in k does not necessarily mean a decrease in the growth rate since it can reflect a restriction of the von Bertalanffy model for the description of the growth when there is a strong increase in L_{∞} . Pauly (1979) associates a decrease in L_{∞} and an increase in k with an increase in stress factors, such as temperature, fish density and food availability; thus, the observed increase in L_{∞} and decrease in k could be a result of the relaxation of these stress factors. The increasing trend of the SST anomalies towards positive values observed in the study region (Fig. 12) would be expected to cause a decrease in the L_{∞} and a reduction in body size at each age (Daufresne et al., 2009; Cheung et al., 2013). Thus, the observed changes in growth and the increase in the condition factors by length class (Fig. 8) may be associated with a decrease in the fish density due to the decrease in the demersal fish density in the region, including the densities of Jamaican weakfish and other species with similar trophic spectra targeted by the bottom trawl and bottom gillnet fisheries (Cardoso and Haimovici, 2016).

The Jamaican weakfish shares several prey species with *M. atricauda* on the inner continental shelf of southern Brazil (Martins, 2000; Martins and Haimovici, 2016), mainly the shrimp *Artemesia longinaris*. Cardoso and Haimovici (2016) reported an increase in the feeding intensity of *M. atricauda* over the last 40 years when crustaceans, especially the shrimp *A. longinaris*, increased in importance in the analyzed stomachs. According to the authors, the main cause of the increase in the feeding

intensity was the decrease in the abundance of *M. atricauda* and of its competitor, the stripped weakfish *C. guatucupa*, which was caused by the long-term biomass removal by fishing (Cardoso and Haimovici, 2016). The growth of both species, *M. atricauda* (Cardoso and Haimovici, 2011) and *C. guatucupa* (Miranda and Haimovici, 2007), also increased over the last few years. Therefore, the observed changes in the growth of Jamaican weakfish and other species can be considered a result of the decrease in the abundance of neritic and macrobenthic species affected by demersal fishing, resulting in increased availability of prey.

The observed changes in the reproductive parameters, such as age (A_{50}) and length (L_{50}) at first maturity, are more difficult to explain since there are three possible drivers, and we do not have enough knowledge to disentangle the effects. A decline in stock abundance may be one driver of the decrease in A_{50} since it increases individual food availability and relaxes the densitydependent effect that is responsible for increasing A_{50} (Barot et al., 2004; Saborido-Rey and Kjesbu, 2005; Audzijonyte et al., 2016). For C. jamaicensis, a decrease in A_{50} was observed for both sexes over time, between the second and third year of life in the first period and between the first and second year of life in the most recent period. The same decreasing pattern of A_{50} was observed for M. atricauda between the 1970s and 2010 (Cardoso and Haimovici, 2014), which was also interpreted as a result of changes to density-dependent factors, that is, increased individual food availability due to decreased intraspecific and interspecific competition (Cardoso and Haimovici, 2016). However, increasing water temperatures may also be a driver since one of the physiological responses of this process is earlier energy allocation to reproduction, resulting in shifts in the age and size at maturation (Audzijonyte et al., 2016).

The length at first maturity also decreased over time for both sexes, and the possible drivers of these changes also differed. One driver is increasing temperatures, as stated above, and another

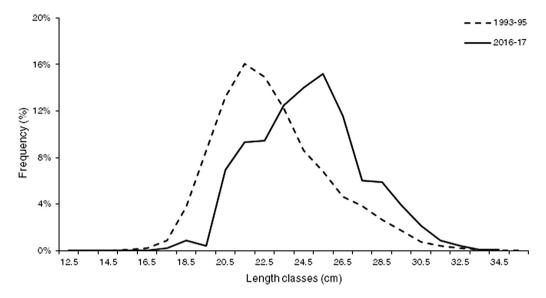


Fig. 13. Length frequencies of *C. jamaicensis* sampled between 1993 and 1998 in southeastern Brazil from bottom pair-trawl landings by Castro et al. (2002) (dashed line), and in southern Brazil from the same fleet between 2016 and 2017 (continuous line).

driver is increased mortality at the potential sizes at maturity that were selected for determination of the early onset of maturation. In other words, biased removal of individuals who mature at large sizes increases the proportion of genotypes associated with reproduction at small sizes in the long term (Dieckmann and Heino, 2007). A decrease in the size at first maturity was also observed for *M. atricauda* in the same region (Cardoso and Haimovici, 2014), and the possible causes may be the same as those postulated for the observed changes in *C. jamaicensis*.

A relevant question for management purposes is whether the stocks along the coast of southern and southeastern Brazil belong to the same population. Along the coast of São Paulo State (23°S-26°S), C. jamaicensis landed by pair trawlers are smaller than those recorded by the same gear in southern Brazil (Fig. 13). The reproductive period in São Paulo is between late spring and late summer, which is the same as that in southern Brazil, (Carneiro, 2007; Castro, 2000); however the lengths at first maturity observed in 1997 (195.1 mm for females and 191.6 mm for males Carneiro, 2007) were smaller than those observed in this study in both periods (Table 9). The differences in the TL composition and length at first maturity could be a consequence of slow growth in southeastern Brazil, suggesting limited exchange between the regions. However, these differences in growth should be tested with new comparable aging and growth studies because Santos (1963) aged whole otoliths, while David (1997) examined transversal sections of mostly young fishes under 200 mm, and aging was not validated in either study. Thus, despite the coincidence in reproductive dynamics, other studies are necessary to investigate the existence of one or two stocks exploited in southern and southeastern Brazil.

Regarding the assessment of the state of exploitation in southern Brazil, *C. jamaicensis* is not a target of industrial fisheries; therefore, there are no sufficiently accurate data available to use traditional assessment models, which rely on catch and effort or reliable estimates of fishing mortality. However, knowledge of their life history (maximum age and sexual maturity, growth parameters and estimates of natural mortality) combined with a representative length composition allowed for the preliminary assessment of the stock status using the model developed by Hordyk et al. (2015a,b). This model estimates the SPR with assumptions of recruitment equilibrium conditions, length data as representative of the stock, unilateral asymptotic selectivity, normal distribution of the modeled virginal length composition, a

fixed k and a positive proportionality between egg production and fish length. For Jamaican weakfish in southern Brazil, a representative length composition obtained from the bottom trawl fishery, which utilizes fishing gear with unilateral asymptotic selectivity, was used. The value of k was assumed to be fixed since it did not vary significantly between periods (Table 6).

The estimated SPR values for the *C. jamaicensis* population in southern Brazil were sensitive to the maximum age used to calculate natural mortality. Depending on the assumed maximum age (9 or 10 years old), fish removal may have resulted in losses of approximately 57% or 62% of the spawning potential, respectively. It is plausible to assume that the maximum age is greater than the observed age in this study since the bottom trawl fishery has existed in the region for at least 40 years (Haimovici and Cardoso, 2016), and the removal of the older age classes is one of the observed effects in exploited populations (Berkeley et al., 2004). Thus, it is safe to assume that the fishery removed at least 60% of the C. jamaicensis population with spawning potential in southern Brazil. Considering the uncertainty in the estimated life history parameters and the fact that the model does not consider a probable decrease in the stock abundance over time, this removal may have been even greater.

5. Conclusion

Jamaican weakfish, C. jamaicensis, in southern Brazil are growing faster and maturing earlier than forty years ago. The changes in growth are likely due to density-dependent processes because of the intense fishing that decreased the abundance of the species and of its main competitors. However, the changes in maturation parameters are difficult to explain since there are three possible drivers, density-dependent processes and increasing water temperatures for the changes in the age at first maturity and increasing water temperatures and genotypic responses to differential selection for the changes in the size at first maturity. The SPR of the stock decreased to between 57% and 62% of the virginal situation. Although C. jamaicensis can be considered a resilient species due to its life history characteristics, such as early maturity at a small size, long spawning period, and fast growth, the intense biomass removals by fishing in southern Brazil have changed its population dynamics and reduced its spawning potential.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

CRediT authorship contribution statement

Abner Ventura Alves: Formal analysis, Writing - original draft. **Manuel Haimovici:** Investigation, Methodology, Writing - original draft, Writing - review & editing. **Luís Gustavo Cardoso:** Supervision, Writing - original draft, Writing - review & editing, Resources, Project administration.

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References

- Aubone, A., Wöhler, O.C., 2000. Aplicación del método de Máxima Verosimilitud a la estimación de parámetros y comparación de curvas de crecimiento de von Bertalanffy. INIDEP Inf. Tec. 37, 21, http://hdl.handle.net/1834/2541.
- Audzijonyte, A., Fulton, E., Haddon, M., Helidoniotis, F., Hobday, A.J., Kuparinen, A., Morrongiello, J., Smith, A., Upston, J., Waples, R., 2016. Trends and management implications of human-influenced life-history changes in marine ectotherms. Fish Fish. 17, 1005–1028. http://dx.doi.org/10.1111/faf. 12156
- Barot, S., Heino, M., O'brien, L., Dieckmann, U., 2004. Long-term trend in the maturation reaction norm of two cod stocks. Ecol. Appl. 14, 1257–1271. http://dx.doi.org/10.1890/03-5066.
- Berkeley, S.A., Hixon, M.A., Larson, R.J., Love, M.S., 2004. Fisheries sustainability via protection of age structure and spatial distribution of fish populations. Fish 29, 23–32, https://doi.org/10.1577/1548-8446(2004)29[23:FSVPOA]2.0.
- Campana, S.E., 1990. How reliable are growth back-calculations based on otoliths? Can. J. Fish. Aquat. Sci. 47, 2219–2227. http://dx.doi.org/10.1139/ f90-246.
- Campana, S.E., 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. J. Fish. Biol. 59, 197–242. http://dx.doi.org/10.1111/j.1095-8649.2001.tb00127. x.
- Campana, S.E., Jones, C.M., 1992. Analysis of otolith microstructure data. In: Stevenson, D.K., Campana, S.E. (Eds.), Otolith Microstructure Examination and Analysis. Canadian Special Publication of Fisheries and Aquatic Sciences, Canada, pp. 73–100.
- Cardoso, L.G., Haimovici, M., 2011. Age and changes in growth of the king weakfish *Macrodon atricauda* (Günther, 1880) between 1977 and 2009 in southern Brazil. Fish. Res. 111, 177–187. http://dx.doi.org/10.1016/j.fishres. 2011.06.017.
- Cardoso, L.G., Haimovici, M., 2014. Long term changes in the sexual maturity and in the reproductive biomass of the southern king weakfish *Macrodon atricauda* (Günther, 1880) in southern Brazil. Fish. Res. 160, 120–128. http://dx.doi.org/10.1016/j.fishres.2014.05.012.
- Cardoso, L.G., Haimovici, M., 2016. Density-dependent changes in the feeding behavior of *Macrodon atricauda* of the southern Brazil. J. Fish. Biol. 89, 1002–1008. http://dx.doi.org/10.1111/jfb.12974.
- Carneiro, M.H., 2007. Diagnóstico dos recursos pesqueiros marinhos, *Cynoscion jamaicensis*, *Macrodon ancylodon* e *Micropogonias furnieri* (perciformes: sciaenidae), da região sudeste-sul do Brasil entre as latitudes 23° e 28°40'S (Ph.D. thesis). Federal University of São Carlos, Brazil.
- Castello, J.P., Haimovici, M., Odebrecht, C., Vooren, C.M., 1998. A plataforma e o talude continental. In: Seelinger, U., Odebrecht, C., Castello, J.P. (Eds.), Os ecossistemas costeiros e marinhos do extremo sul do Brasil. Ecoscientia, Rio Grande, Brazil, pp. 189–197.

- Castro, P.M.G., 2000. Estrutura e dinâmica da frota de parelhas do Estados de São Paulo e aspectos biológicos dos principais recursos pesqueiros demersais costeiros da região Sudeste/Sul do Brasil (23°-29°S) (Ph.D. thesis). University of São Paulo, Brazil.
- Castro, P.M.G., Cergole, M.C., Carneiro, M.H., Mucinhato, C.M.D., Servo, G.J.M., 2002. Crescimento, mortalidade e taxa de explotação do goete *Cynoscion jamaicensis* (*Perciformes: Sciaenidae*), na região sudeste/sul do Brasil. Bol. Inst. Pesca 28, 141–153.
- Cerrato, R.M., 1990. Interpretable statistical tests for growth comparisons using parameters in the Von Bertalanffy equation. Can. J. Fish. Aquat. Sci 47, 1416–1426. http://dx.doi.org/10.1139/f90-160.
- Cheung, W.W., Sarmiento, J.L., Dunne, J., Frölicher, T.L., Lam, V.W., Palomares, M.D., Pauly, D., 2013. Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems. Nat. Clim. Change 3 (3), 254.
- Chugunova, N.I., 1963. Age and Growth Studies in Fish. National Science Foundation and the Israel Program for Scientific Translations, Washington.
- Daufresne, M., Lengfellner, K., Sommer, U., 2009. Global warming benefits the small in aquatic ecosystems. Proc. Natl. Acad. Sci. 106 (31), 12788–12793.
- David, G.S., 1997. Idade e crescimento de *Cynoscion guatucupa* e *Cynoscion jamaicensis* na plataforma de Ubatuba, São Paulo, Brasil (M.Sc. thesis). University of São Paulo, Brazil.
- Dieckmann, U., Heino, M., 2007. Probabilistic maturation reaction norms: their history, strengths, and limitations. Mar. Ecol. Prog. Ser. 335, 253–269.
- Dowling, N.A., Dichmont, C., Haddon, M., Smith, D., Smith, T., Sainsbury, K., 2014. Empirical harvest strategies for data-poor fisheries. A review of the literature. Fish. Res. 171, 141–153. http://dx.doi.org/10.1016/j.fishres.2014.11.005.
- Green, B.S., Mapstone, B.D., Carlos, G., Begg, G.A., 2009. Tropical Fish Otoliths: Information for Assessment, Management and Ecology, first ed. Springer, Netherlands.
- Haimovici, M., 1987. Estratégia de amostragens de comprimentos de teleósteos demersais nos desembarques da pesca de arrasto no litoral sul do Brasil. Atlântica 9, 65–82.
- Haimovici, M., Absalonsen, L., Velasco, G., Miranda, L.V., 2006. Diagnóstico do estoque e orientações para o ordenamento da pesca de *Umbrina canosai* (Berg, 1895). In: Rossi-Wongtschowski, C.L.D.B., Ávila-da-Silva, A.O., Cergole, M.C. (Eds.), Análise das Principais Pescarias Comerciais da Região Sudeste-Sul do Brasil: Dinâmica Populacional das Espécies em Explotação II. São Paulo, Brazil, pp. 77–85.
- Haimovici, M., Cardoso, L.G., 2016. Long-term changes in the fisheries in the Patos Lagoon estuary and adjacent coastal waters in Southern Brazil. Mar. Biol. Res. 13, 135–150. http://dx.doi.org/10.1080/17451000.2016.1228978.
- Haimovici, M., Cousin, J.C.B., 1989. Reproductive biology of the castanha *Umbrina canosai* (Pisces, Scianidae) in southern Brazil. Rev. Bras. Biol. 49, 523–537.
- Haimovici, M., Ignácio, J.M., 2005. Micropogonias furnieri (Desmarest, 1823).
 In: Rossi-Wongtschowski, C.L.D.B., Ávila-da-Silva, A.O., Cergole, M.C. (Eds.),
 Análise das Principais Pescarias Comerciais da Região Sudeste-Sul do Brasil:
 Dinâmica Populacional das Espécies em Exploração. São Paulo, Brazil. In:
 Série Documentos Revizee-Score Sul, São Paulo, pp. 101-107.
- Haimovici, M., Martins, A.S., Vieira, P.C., 1996. Distribuição e abundância de teleósteos demersais sobre a plataforma continental do sul do Brasil. Rev. Bras. Biol. 56, 27–50.
- Haimovici, M., Reis, E.G., 1984. Determinação de idade e crescimento da castanha *Umbrina canosai*, (Pisces, Sciaenidae) do Sul do Brasil. Atlântica 7, 25–46.
- Heincke, F., 1908. Bericht über die Untersuchungen der Biologischen Anstalt auf Helgoland zur Naturgeschichte der Nutzfische. Die. Beteil. Deutschl. Int. Meeresforsch. 1908. 67–155.
- Hordyk, A., 2017. LBSPR: Length-based spawning potential ratio. R package version 0.1.1. Available at: https://CRAN.R-project.org/package=LBSPR.
- Hordyk, A.R., Ono, K., Sainsbury, K.J., Lonergen, N., Prince, J.D., 2015a. Some explorations of the life history ratios to describe length composition, spawning-per-recruit and the spawning potential ratio. ICES J. Mar. Sci. 72, 204–216. http://dx.doi.org/10.1093/icesjms/fst235.
- Hordyk, A.R., Ono, K., Valencia, S.R., Lonergan, N.R., Prince, J.D., 2015b. A novel length-based empirical estimation method of spawning potential ratio (SPR) and tests of its performance, for small-scale, data-poor fisheries. ICES J. Mar. Sci. 72, 217–231. http://dx.doi.org/10.1093/icesjms/fsu004.
- Jørgensen, T., 1990. Long-term changes in age at sexual maturity of northeast artic cod (*Gadus morhua*). ICES J. Mar. Sci 46, 235–248.
- Kinas, P.G., Andrade, H.A., 2010. Introdução à Análise Bayesiana (com R), first ed. Mais Oue Nada, Porto Alegre.
- Law, R., 2000. Fishing, selection and phenotypic evolution. ICES J. Mar. Sci. 57, 659–668. http://dx.doi.org/10.1006/jmsc.2000.0731.
- Le-Cren, E.D., 1951. The length-weight relationship and seasonal cycle in gonadal weight and condition in the perch (*Perca fluviatilis*). J. Anim. Ecol. 20, 201–219.
- Marshall, S.L., Parker, S.S., 1982. Pattern identification in the microstructure of sockeye salmon (*Oncorhynchus nerka*) otoliths. Can. J. Fish. Aquat. Sci. 39, 542–547. http://dx.doi.org/10.1139/f82-077.
- Martins, A.S., 2000. As assembleias e as guildas tróficas de peixes ósseos e cefalópodes demersais da plataforma continental e talude superior do estremo sul do Brasil (Ph.D. thesis). Federal University of Rio Grande, Brazil.

- Martins, A.S., Haimovici, M., 2016. Seasonal mesoscale shifts of demersal nekton assemblages in the subtropical south-western atlantic. Mar. Biol. Res. 13, 88–97. http://dx.doi.org/10.1080/17451000.2016.1217025.
- Menezes, N.A., Figueiredo, J.L., 1980. Manual de peixes marinhos do sudeste do Brasil. IV. Teleostei 3. Museu de Zoologia, University of São Paulo, Brazil.
- Miranda, L.V., Haimovici, M., 2007. Changes in the population structure, growth and mortality of striped weakfish *Cynoscion guatucupa* (Sciaenidae, Teleostei) of southern Brazil between 1976 and 2002. Hydrobiologia 589, 69–78.
- Morales-Nin, B., 2000. Review of the growth regulation processes of otolith daily increment formation. Fish. Res. 46, 53–67.
- Morrongiello, J.R., Thresher, R.E., 2015. A statistical framework to explore ontogenetic growth variation among individuals and populations: a marine fish example. Ecol. Monograph 85, 93–115.
- Newman, D., Berkson, J., Suatoni, L., 2015. Current methods for setting catch limits for data-limited fish stocks in the United States. Fish. Res. 164, 86–93.
- Olsen, E.M., Heino, M., Lilly, G.R., Morgan, M.J., Brattey, J., Ernande, B., Dieckmann, U., 2004. Maturation trends indicative of rapid evolution preceded the collapse of northern cod. Nature 428 (6986), 932.
- Pauly, D., 1979. Gill Size and Temperature as Governing Factors in Fish Growth: A Generalization of Von Bertalanffy's Growth Formula (Ph.D. thesis). Kiel University, Germany.
- R Core Team, 2013. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Available at http://www.R-project.org/. (Accessed 15 September 2018).
- Reynolds, R.W., Smith, T.M., 1995. A high resolution global sea surface temperature climatology. J. Clim. 8, 1571–1583.
- Rice, J.A., Crowder, L.B., Binkowski, F.P., 1985. Evaluating otolith analysis for bloater *Coregonus hoyi*: do otoliths ring true? Trans. Am. Fish. Soc. 114, 532–539.
- Rijnsdorp, A.D., 1993. Fisheries as a large-scale experiment in life-history evolution: disentangling phenotypic and genetic effects in changes in maturation and reproduction of North Sea Plaice, *Pleuronectes platessa*. L. Oecologia 96, 391–401
- Rondineli, G.R., Braga, F.M.S., Tutui, S.L.S., Bastos, G.C.C., 2007. Dieta de *Menticirrhus americanus* (Linnaeus, 1758) e *Cynoscion jamaicensis* (Vaillant and Bocourt, 1883) (*Pisces, Sciaenidae*) no sudeste do Brasil, estado de São Paulo. Bol. Inst. Pesca 33, 221–228.
- Rosenberg, A.A., Haugen, A.S., 1982. Individual growth and size-selective mortality of larval turbot (*Scophthalmus maximus*) reared in enclosures. Mar. Biol. 72, 73–77.
- Saborido-Rey, F., Kjesbu, O.S., 2005. Growth and maturation dynamics. p. 26, http://hdl.handle.net/10261/47150.

- Santos, E.P., 1963. Growth of goete: Quantitative aspects. Bol. Inst. Oceanogr. Sao Paulo 13. 185–190.
- Schwingel, P.R., Castello, J.P., 1990. Validacion de La Edad Y Crecimiento de La Corvina (*Micropogonias furnieri*) En El Sur de Brasil. Frente Marítim. 7, 19–24.
- Secor, D.H., Dean, J.M., 1989a. Somatic growth effects on the otolith-fish size relationship in young pond-reared striped bass, *Morone saxatilis*. Can. J. Fish. Aquat. Sci. 46, 113–121.
- Secor, D.H., Dean, J.M., Baldevarona, R.B., 1989b. Comparison of otoliths growth and somatic growth in larval and juvenile fishes based on otolith length/fish length relationships. Rapp. P-v Rèun. Cons. Perm. Int. Explor. Mer 191, 431–438.
- Sturtz, S., Ligges, U., Gelman, A., 2005. R2WinBUGS: A package for running WinBUGS from R. J. Stat. Softw. 12, 1–16.
- Then, A.Y., Hoenig, J.M., Hall, N.G., Hewitt, D.A., 2014. Evaluating the predictive performance of empirical estimators of natural mortality rate using information on over 200 fish species. ICES J. Mar. Sci. 72, 82–92.
- Thomas, A., O'Hara, B., Ligges, U., Sturtz, S., 2006. Making BUGS open. R News 6, 12–17.
- Tresher, R.E., Koslow, J.A., Morison, A.K., Smith, D.C., 2007. Depth mediated reversal of the effects of climate on long-term growth rates of exploited marine fish. Proc. Natl. Acad. Sci. USA 104, 7461–7465.
- Trippel, E.A., 1995. Age at maturity as a stress indicator in fisheries. Bioscience 45, 759–771.
- Vaillant, L.L., Bocourt, F., 1883. Études sur les Poissons. In: Mission scientifique au Mexique et dans l'Amérique centrale. Rech. Zool. 4, 121–200.
- Valentini, H., Castro, P.M.G., Servo, G.J.M., Castro, L.A.B., 1991. Evolução da pesca das principais espécies demersais da costa sudeste do Brasil, pela frota de arrasteiros de parelha baseada em São Paulo, de 1968 a 1987. Atlântica 13, 87–95.
- Vazzoler, A.E.A.M., Braga, F.M.S., 1983. Contribuição para o conhecimento da biologia de *Cynoscion jamaicensis* (Vaillant and Bocourt, 1883), na área entre Cabo de São Tomé (22°04'S) e Torres (29°21'S), Brasil. Bol. Inst. Oceanogr. S. Paulo. Bol. Inst. Oceanogr. Sao Paulo 32, 125–136.
- Vieira, P.C., Haimovici, M., 1993. Idade e crescimento da pescada olhuda Cynoscion striatus (Pisces, Sciaenidae) no sul do Brasil. Atlântica 15, 73-91.
- Wooton, R.J., 1998. Ecology of Teleost Fishes, second ed. Kluver Academic Publishers, Dordrecht.
- Yesaki, M., Bager, K.J., 1975. Histórico da evolução da pesca industrial em Rio Grande. Série Documentos Técnicos SUDEPE/PDP No. 11, Rio Grande, Brazil. Zar, J.H., 1984. Biostatistical Analysis, second ed. Prentice-Hall, Englewood Cliffs,