Density-dependent changes in the feeding behaviour of *Macrodon atricauda* of southern Brazil

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Long-term density-dependent changes in the population dynamics of the king weakfish *Macrodon atricauda* of southern Brazil between 1976 and 2013 may be related to a change in diet and an increase in feeding intensity. The importance of the small crustacean, *Artemesia longinaris,* increased in the diet of adults, whereas the importance of teleosts decreased and the frequency of full stomachs increased. *Macrodon atricauda* currently benefits from a high availability of *A. longinaris*, which results in a higher energy intake per individual, which, in turn, induces faster body growth and an earlier onset of sexual maturation.

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Worldwide overfishing has caused long-term changes in the population dynamics of severely exploited marine fish species (Hutchings, 2000; Worm *et al.*, 2009). Several studies have reported density-dependent changes in growth and sexual maturation of bony fishes due to intense fishing pressure (Law, 2000; Saborido-Rey & Kjesbu, 2005; Pérez-Rodríguez *et al.*, 2013). The widely used explanation for these changes is that the steady removal of biomass leads to a decrease in population density, which increases food availability and relaxes density-dependent effects responsible for slower growth and delayed maturation (Dieckmann & Heino, 2007). Testing this hypothesis requires a long-term dataset on the feeding, growth and the onset on sexual maturation, such as the one collected over the last four decades for king weakfish *Macrodon atricauda* (Günther 1880) from southern Brazil (Haimovici, 1987, 1998; Cardoso & Haimovici, 2011, 2014).

The sciaenid *M. atricauda* inhabits shallow coastal waters from Espírito Santo state in south-eastern Brazil down to northern Argentina. From the five genetically distinct populations of *M. atricauda* (Rodrigues *et al.*, 2013), the most abundant inhabits southern Brazil, between Chui and Cape Santa Marta Grande (28° 0′ S–34° 40′ S), where it has been exploited by the industrial bottom pair-trawl fishery since the late 1950s (Yamaguti & Moraes, 1965; Haimovici, 1998).

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TABLE I. Preponderance index for the prey items of *Macrodon atricauda* from southern Brazil by Juras & Yamaguti (1985) (left column) and then present study (right column) for immature and mature females and males

Prey items	Juras & Yamaguti (1985)				Present study			
	Females		Males		Females		Males	
	Immature	Mature	Immature	Mature	Immature	Mature	Immature	Mature
All crustaceans	82·1	32·8	84·2	52·6	98·1	74·8	90·8	98·0
Artemesia longinaris	81·8	32·8	83·5	52·6	95·3	71·9	79·1	97·5
Pleoticus muelleri					0·03	0·04	0·02	0·1
Sergestidae					2·8	2·9	11·7	0·4
Gammaridae						0·0	0·0	
Stomatopoda	0·3		0·7					
All teleosts	16·3	67·1	7·5	47·0	1·8	25·1	8·9	2·0
Paralonchurus brasiliensis	8·2	37·0	6·1	26·4		0·9		
Macrodon atricauda	8·1	23·7	1·4	7·2	0·02	0·3	0·1	0·1
Engraulidae		3·5		11·1		1·4	0·1	
Gadidae		2·0		1·1				
Trichiurus lepturus		0·9		1·2				
Teleostei not identified					1·8	22·5	8·8	1·9
All molluscs	1·3	0·2	8·2	0·1	0·02		0·2	0·0
Lolignidae	1·3	0·1	8·2	0·1	0·02	0·03	0·2	0·02
Bivalvia	0·02	0·1						

Recent studies on long-term effects of fishing on the life history of *M. atricauda* show an increase in growth between 1977 and 2009 (Cardoso & Haimovici, 2011) and a decrease in the age and size of first maturity between 1976 and 2011 (Cardoso & Haimovici, 2014). The decrease in size at maturity was interpreted as an effect of the selective fishing pressure (Cardoso & Haimovici, 2014). In contrast, the changes in growth and in the age at maturity were interpreted as density-dependent effects, resulting from the decrease in abundance of *M. atricauda* (Cardoso & Haimovici, 2015), and also of striped weakfish *Cynoscion guatucupa* (Cuvier 1830) (Miranda & Haimovici, 2007), its main competitor for shrimps, squids and small fishes along the inner shelf of southern Brazil (Martins, 2000). This interpretation was based on the hypothesis of increased food availability. To test this hypothesis, the diet of the *M. atricauda* population over the past 5 years was compared with the diet of the same population in the 1970s reported by Juras & Yamaguti (1985). In addition, the long-term trend in feeding intensity between the 1960s and 2010s was analysed.

To characterize the present diet of *M. atricauda*, 630 stomach contents of immature and mature individuals from different seasons (spring: 98; summer: 320; autumn: 152; winter: 60) were examined. They had been landed by commercial bottom trawlers fishing between 28° 28′ S (Cape Santa Marta Grande) and 33° 40′ S (Chui) between 2008 and 2013. Sex, total mass (M, g) and total length (L_T, mm) of every *M. atricauda* individual were recorded. When food items were present, the stomach was removed, its total mass was recorded, and it was fixed in 10% formalin. The prey items were identified to the lowest possible taxonomic level, and the number and mass of individuals of each taxon recorded.

To compare the present diet with the past diet described by Juras & Yamaguti (1985), the same preponderance index (I_P) (Ramakrishnaiah, 1972) as in Juras & Yamaguti
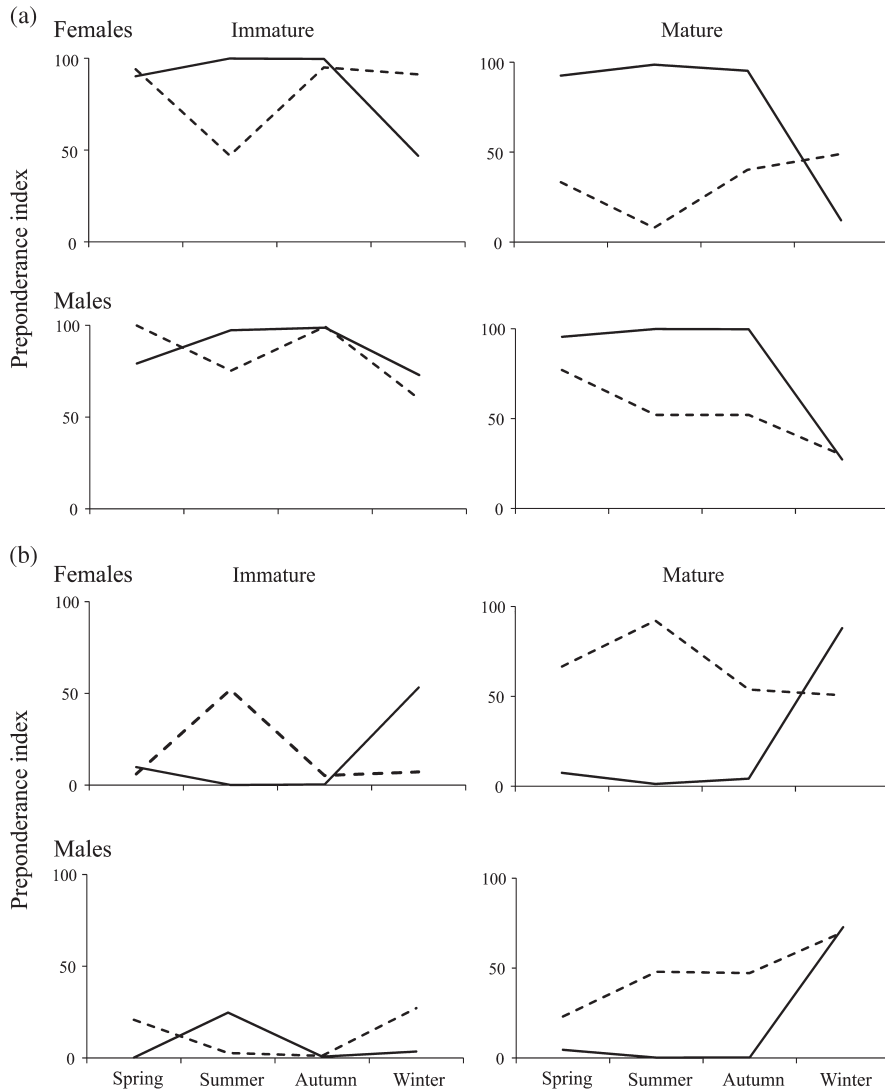
FIG. 1. Preponderance index (I_P) for all (a) crustaceans and (b) teleosts in the diet of *Macrodon atricauda* from southern Brazil by Juras & Yamaguti (1985) (‒ ‒ ‒) and the present study (——) by year and season for immature and mature females and males.

(1985) was used: $I_P = V_i O_i \left(\sum V_i O_i \right)^{-1}$, where V_i is the volume and O_i is the frequency of occurrence of each prey item. The volume, however, was replaced by the mass (M_i) of the prey items. I_P was calculated and compared between sexes, immature and mature fishes, and between seasons.

Changes in feeding intensity were analysed using stomach fullness data from 9318 individuals sampled over four time periods from landings of commercial bottom pair trawlers: 1976–1979 ($n = 1283$), 1980–1986 ($n = 5158$), 2005–2009 ($n = 1056$) and 2010–2013 ($n = 1821$) (Haimovici, 1987; Haimovici, 1998; Cardoso & Haimovici,

TABLE II. Mean and 90% credibility intervals (CrI) of the posterior distributions of the frequencies of each type of stomach by period recorded from *Macrodon atricauda* individuals sampled from the commercial trawl fishery in southern Brazil

	Empty			Half-full			Full		
Period	CrI5%	Mean	CrI95%	CrI5%	Mean	CrI95%	CrI5%	Mean	CrI95%
1976–1979	0·71	0·73	0·75	0·20	0·22	0·24	0·04	0·05	0·06
1980–1986	0·58	0·59	0·60	0·38	0·39	0·40	0·02	0·02	0·03
2005–2009	0·58	0·60	0·63	0·27	0·29	0·31	0·09	0·11	0·12
2010–2013	0·50	0·52	0·54	0·35	0·36	0·38	0·10	0·11	0·12

2011). A stomach was classified as empty when no food was present, as half-full when at least one identifiable item was present, and as full when the stomach was distended and filled with prey items. In each period, the data were analysed by season to avoid the influence of seasonal variation on any long-term trend in feeding intensity.

Due to the polynomial distribution of the data and to visually compare the probabilities of each stomach state (empty, half-full and full) among periods without the need for statistical tests (Kinas & Andrade, 2010), a Bayesian approach (Gelman *et al.*, 2003) was used.

Assuming that y is the counting vector of the number of observations of each of the k possible outcomes, then $p(y|\theta) \propto \prod_{j=1}^{k} \theta_j^{y_j}$, where θ describes the probability of each result, and $\theta_j^{y_j}$ is the probability vector relative to the counting vector of the number of observations for each decade; the sum of the probabilities $\sum_{j=1}^{k} \theta_j$ is 1. The distribution is generally regarded as implicitly conditional on the number of observations: $\sum_{j=1}^{k} y_i = n$. The conjugate a priori distribution is a multivariate generalization of the beta distribution known as Dirichlet: $p(\theta|\alpha) \propto \prod_{j=1}^{k} \theta_j^{\alpha_j - 1}$, where θ is the probability vector, and the distribution is restricted to a non-negative α_s with $\sum_{j=1}^{k} \theta_j = 1$ and $\alpha_1, \ldots + \alpha_k = \alpha_0$. In other words, the sample size is defined a priori as: $\theta \sim Dirichlet (\alpha_1, \ldots, \alpha_k)$ and the probability of each result as: $p(\theta) = Dirichlet (\theta|\alpha_1, \ldots, \alpha_k)$, where $\alpha_j > 0 \equiv \sum_{j=1}^{k} \alpha_j$ (positive real numbers).

The comparison of the diet of mature *M. atricauda* showed that I_P of all crustaceans, mainly *A. longinaris*, increased from 32·8 to 74·8 and from 52·6 to 98·0 in mature females and males, respectively, while the I_P of teleosts decreased from 67·1 to 25·1 and from 47·0 to 2·0 respectively (Table I). Both changes were observed in all seasons except winter (Fig. 1) and led the conclusion that the relative importance of crustaceans, mainly *A. longinaris*, increased while the relative importance of teleost fishes decreased in the diet of mature *M. atricauda* over the study period.

In immature *M. atricauda* changes were small: the I_P of all crustaceans, mainly *A. longinaris*, increased from 82·1 to 98·1 in females and from 83·5 to 90·8 in males. For teleosts the I_P decreased from 16·3 to 1·8 in females, and increased from 7·5 to 8·9 for males (Table I). There was not a consistent pattern of change in the different seasons.

These changes may be a result of the intense fishing pressure on the demersal fish stocks along the continental shelf of southern Brazil, which have caused a decrease in abundance in the last five decades (Haimovici, 1998; Haimovici *et al.*, 2006). The decreased abundance of fish stocks may have resulted in a lower availability of fishes
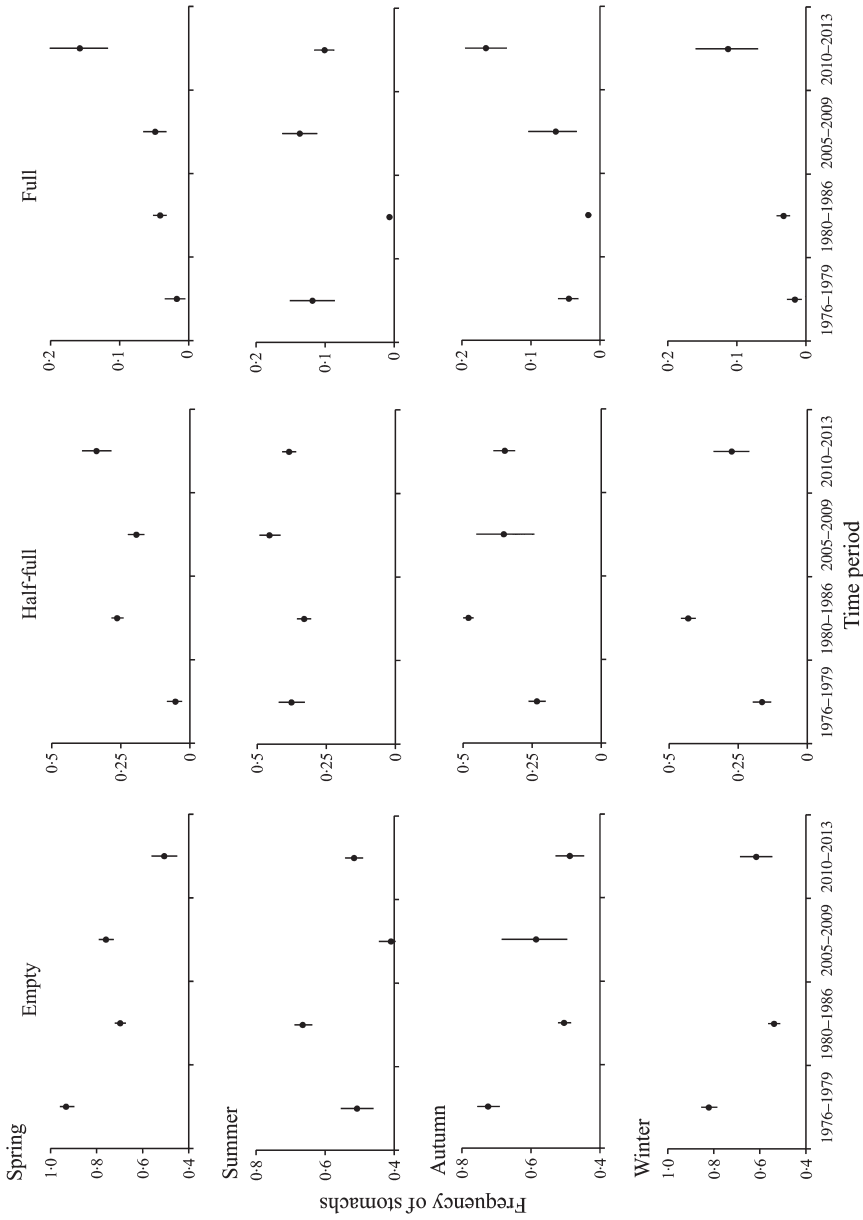
Fig. 2. Mean ±90% credibility intervals frequencies of empty, half-full and full stomachs by season in different time periods for *Macrodon atricauda* landed by pair-trawling in southern Brazil.

and a higher availability of *A. longinaris* as prey for *M. atricauda*, probably due to reduced intra- and interspecific competition for food caused by the decreasing abundance of teleosts (Cardoso & Haimovici, 2015), particularly its main competitor, *C. guatucupa* (Miranda & Haimovici, 2007).

The long-term analysis of stomach fullness of *M. atricauda* showed that the frequency of empty stomachs was, on average, 73% in the 1970s, decreased to *c.* 60% in the 1980s and 2000s, and further to *c.* 50% thereafter (Table II). The same trend was detected in all seasons (Fig. 2), except in summer; when feeding intensity is lower (Juras & Yamaguti, 1985). The frequency of half-full stomachs varied from 22% in the 1970s to 39% in the 1980s, 29% in the 2000s, and 36% after 2010. The frequency of full stomachs increased considerably over time from around 5% in the 1970s to *c.* 10% in the 2000s and after 2010 (Table II). Again, the same increasing trend in the frequency of full stomachs could be detected in all seasons, except in summer (Fig. 2).

The increased feeding intensity over time of the southern Brazilian population of *M. atricauda* corroborates the hypothesis of an increase in food availability (Cardoso & Haimovici, 2014). It may occur due to a relaxation of intra- and interspecific competitive pressure and may result in a faster body growth and a greater accumulation of energy, which, in turn, allows for an advanced acquisition of the minimum energy necessary to reach sexual maturity (Rowe *et al.*, 1991; Hutchings & Jones, 1998). Therefore, these results provide direct evidence of density-dependent effects on the diet of a severely exploited fish stock.

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