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Demographical analysis of the pink ling *Genypterus blacodes* (Schneider 1801) in the austral demersal fishery: A matrix approach evaluating harvest and non-harvest states

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ABSTRACT

In this work we model the population dynamics of *Genypterus blacodes* of the demersal fishery on Chilean southern-austral region, using stage structured matrices, from a 17-year time-series of annual age-specific female abundances. For the parameterized matrices obtained, we calculated population growth rates with confidence intervals, net reproductive rate, reproductive value, stable stage structure, and we performed a sensitivity analysis.

We also generated and analyzed an analogous stage structured matrix model for the same population assuming no harvesting. The main results are (1) a negative growth rate for the observed population data; (2) a positive growth rate for the population without the capture effect which is significantly different from the growth rate of the harvested population; (3) the sensitivity analysis revealed that λ is more sensitive to variations in adult survival in the age class 7–10 years; (4) the observed population exhibits a stable stage structure.

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1. Introduction

The pink ling (*Genypterus blacodes*) is a demersal species distributed on the coasts of South America, Australia, Tasmania and New Zealand (Chong, 1984; Withell and Wankowski, 1989; Chong and Aguayo, 1990; Horn, 1993; Colman, 1995; Ward et al., 2001; Morioka and Machinandiarena, 2001). This species also named pink cusk-eel (Wiff et al., 2007), golden ling (Paredes and Bravo, 2005) or golden kinglip (Larrain et al., 2002; Seco Pon et al., 2007), is found around the southern tip of South America, between Coquimbo, Chile (30°00'S) along the Pacific Ocean, up to Río Grande in the boundary between Brazil and Uruguay in the Atlantic Ocean.

The austral demersal fishery (ADF) is development in the Chilean southern-austral zone 41°28'–57°00'S from 1997, with a multi-specific character in which diverse resources were extracted simultaneously from approximately 100 species (Aguayo et al., 1986; Arana, 1990), among them the southern hake (*Merluccius*

australis) and the pink ling (Ojeda et al., 1986; Pérez, 2000). Both species have been declared in state of “fully exploited”, a term that is used to qualify a stock which is probably neither being overexploited nor underexploited and is producing, on average, close to its maximum sustainable yield (Restrepo, 1999). Since the southern hake is the main target period of the fishery, it has been managed through closed seasons during reproduction; these measures affect the whole fishery.

In spite of the apparent stabilisation in the last years, decrease of the pink ling landings in the ADF, as well as other fisheries indicators suggest a decreasing trend in population size. This could be explained by overexploitation due to the lack of biological and ecological knowledge about the main species exploited, including the pink ling.

At present, the knowledge about the ecological processes in this species is fragmentary at best, due to a lack of basic biological and fishery information (Wiff et al., 2007) and previous studies carried out on this species were dedicated to other aspects, but they were not directed towards gaining knowledge on demographical processes of the population.

We studied the population dynamics of *G. blacodes* through the formulation and analysis of a discrete time stage-structured matrix model. This matrix model was parameterized from a

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17-year temporal series of data obtained from the Fishery Development Institute of Chile (Instituto de Fomento Pesquero, IFOP) and we consider that the used methodology can be applied to a more extensive temporal series employing the information available at IFOP.

Specifically, we were interested in estimating the stage-specific survival and fecundity rates, and in calculating the sensitivity of the growth rate to variations in vital rates. We reconstruct the temporal series observed under zero capture assumption and we evaluated the effect of fishery on the *G. blacodes* demographical features. However, a series of assumptions are necessary with respect to the quality of data employed such as the age of the specimens of pink ling obtained from the sample used has been correctly identified; the abundances obtained from the matrix of capture are well estimated; all individuals within an age class are identical, the stochastic environment changes are not considered on the population dynamic and so on.

In short, the specific aims of this work are (1) to construct and parameterize a matrix model for *G. blacodes* in the ADF, from the available information about the estimated age-specific abundances; (2) to describe the growth of the pink ling population; (3) to carry out a prospective perturbation analysis of the vital rates; (4) to estimate the pink ling population dynamics without the fishing effect and to contrast this with the results obtained from the model of the harvest population.

2. Materials and methods

The information employed in this work was obtained for the fisheries of inner and outer waters of the ADF according to the compiled logbooks. The data of inner waters corresponds mainly to small-scale and industrial longline fishery, and the data of outer waters corresponds to the trawler fishery including factory and freezer vessels (Aránguiz-Acuña and González-Olivares, 2004). Historically, the pink ling has been caught as an incidental species in the ADF where captures are carried out by industrial vessels operating with bottom trawls and longlines as fishing gear (Wiff et al., 2007).

The data was obtained from the indirect estimate of the pink ling abundances by age class through the Sequential Population Analysis (SPA) gauged with the Catch per Unit of Effort (CPUE) (Payá et al., 2000).

The pink ling abundances series of 3 to 14+ years old, estimated in this way for the period 1982–1998 (Fig. 1) was provided by the Chilean Fishery Secretariat (SUBPESCA) and estimated

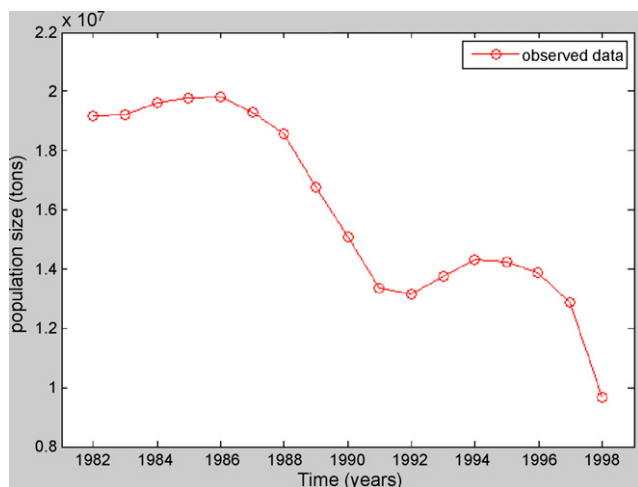


Fig. 1. The female pink ling abundance series of 3 to 14+ years old, estimated for the period 1982–1998.

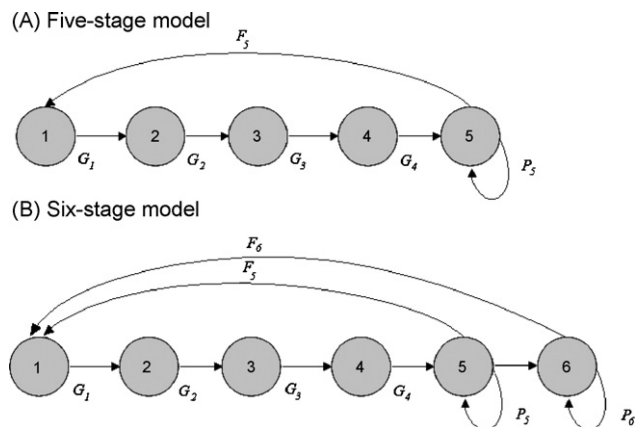


Fig. 2. Life-cycle for the five- and six-stage matrix models.

by the Fishery Development Institute (IFOP) on basis of the landed biomass of these commercial fisheries (Aguayo et al., 2000, 2001).

2.1. Model construction

We developed a stage structured matrix model for the female pink ling (*G. blacodes*) population known as stage-classified matrix model (Caswell, 2001). The matrix model is a discrete model that uses age distributions to project population densities as time progresses (Banks et al., 2007). Mortality is the only mechanism included to remove individuals from the population and a balance between emigration and immigration is assumed.

The beginning of sexual maturity for *G. blacodes* was determined at 7 years old, considering that the 50% age at maturity is 6 years estimated by microscopic observations, and that the contribution to the 3–6-year-old classes is smaller than the 1.4% of the total eggs production in a year (Aguayo et al., 2001).

Models with at least five stages were considered, so that each juvenile age class (3–6 years old) would be represented in a separate stage with a maximum of 12 stages, so that each age group (3–14 years old) would be also represented in a separate stage.

The five-stage model was structured with the following stages: (1) 3-year-old recruits; (2) 4-year-old juveniles; (3) 5-year-old juveniles; (4) 6-year-old juveniles; (5) 7–14-year-old adults. The six-stage model was arranged in a similar way but with stage (5) 7–10-year-old adults and (6) 11–14-year-old adults.

We found that the methodology employed to obtain the coefficients of the projection matrix was not sensitive enough to estimate the fecundity parameters in matrices with more than six stages, i.e., matrices including more than two fertile stages. So, these models were rejected and only the five- and six-stage models were considered.

In vector matrix notation the model employed can be expressed in a general form as

$$\mathbf{x}(t + 1) = \mathbf{A} \cdot \mathbf{x}(t) \tag{1}$$

where \mathbf{A} is the transition matrix also known as Leslie matrix, $\mathbf{x}(t)$ is the abundance vector at the time t and $\mathbf{x}(t + 1)$ is the abundance vector at time $t + 1$. The life-cycle graphs for five and six stages are shown in Fig. 2.

The transition matrices for the five and six stages are

$$\mathbf{A}_1 = \begin{pmatrix} 0 & 0 & 0 & 0 & F_5 \\ G_1 & 0 & 0 & 0 & 0 \\ 0 & G_2 & 0 & 0 & 0 \\ 0 & 0 & G_3 & 0 & 0 \\ 0 & 0 & 0 & G_4 & P_5 \end{pmatrix} \quad \text{and}$$

$$A_2 = \begin{pmatrix} 0 & 0 & 0 & 0 & F_5 & F_6 \\ G_1 & 0 & 0 & 0 & 0 & 0 \\ 0 & G_2 & 0 & 0 & 0 & 0 \\ 0 & 0 & G_3 & 0 & 0 & 0 \\ 0 & 0 & 0 & G_4 & P_5 & 0 \\ 0 & 0 & 0 & 0 & G_5 & P_6 \end{pmatrix}$$

where the parameters are all positives having the following meanings:

G_i indicates the part of the population in the age or stage group i at time t that survives to reach the age or stage group $i + 1$ at time $t + 1$;

P_i corresponds to the part of the population in the age or stage group i at time t which remains in the same stage at time $t + 1$;

F_i expresses the female average contribution from i class to the 3-year-old class.

These parameters were estimated through the quadratic programming method (quadprog) of Wood (1994) described in Caswell (2001) and implemented with the software MATLAB, obtaining a matrix for temporal series of 17 years. The quadprog method allows to determine the complexity of the population model in a statistically optimum manner using cross-validation (Wood, 1994). Specifically, the confidence intervals obtained for population size and death rates give a 95% probability that the true population dynamics are within the intervals.

2.2. Construction of a matrix model in absence of exploitation

With the purpose of estimating the pink ling population dynamics since 1982 in the absence of commercial exploitation, we defined the fraction abundance to the fishing occurred at time t as $H_i(t) = n_i(t)/x_i(t)$, where $x_i(t)$ is the population size of the stage i at time t , known from the abundance estimates, which are assumed to have been measured previous to the capture, and $n_i(t)$ is the population size of the stage i immediately after the capture, known from the capture series by age class.

The original projection matrix A was modified in order to obtain a transition matrix B applied to the unexploited population. Thus, b_{ij} is the element of the matrix B obtained from the relation $b_{ij}(t) = a_{ij}/H_i(t)$. In this way, the transition matrices B_t were obtained for each instant t , describing the unexploited population from the initial age vector, yielding a new series of population abundance for each instant t . These resulting vectors were used in the quadratic programming routine to obtain a transition matrix for the population (Aránguiz-Acuña, 2002).

2.3. Model analysis

In each model, the goodness of fit between the observed data curve and the curve obtained from the model projection was tested through the permutation method, according to the description of Manly (1997), with 2000 randomizations obtained through Monte Carlo re-sampling.

The dominant eigenvalue λ of the transition matrix A gives the population growth rate; and the effects of matrix entries on λ were assessed using sensitivity and elasticity analysis on the matrices (Benton and Grant, 1999). Sensitivity refers to the change in λ resulting from perturbations in the matrix's elements (Morrison and Hik, 2007). The population elasticity (Buhle et al., 2005) of λ refers to the proportional response of λ to a proportional change in a matrix element (Caswell, 2000, 2001).

Using the percentile method (Meyer et al., 1986; Manly, 1997), we employed a jack-knife re-sampling proceeding to construct 95% confidence intervals for λ . Non-overlapped 95% confidence intervals indicated significant differences.

The stability of age structure of the observed population was tested through the calculus of the age structure for every year and then averaged over the study period, obtaining a stage vector w^{obs} (Brault and Caswell, 1993). This structure was compared with the stable age through a χ^2 test.

3. Results

The five- and the six-stage matrices for the exploited population, parameterized using the quadratic programming routine are

$$A_1 = \begin{pmatrix} 0 & 0 & 0 & 0 & 1.021 \\ 0.773 & 0 & 0 & 0 & 0 \\ 0 & 0.764 & 0 & 0 & 0 \\ 0 & 0 & 0.740 & 0 & 0 \\ 0 & 0 & 0 & 0.309 & 0.815 \end{pmatrix},$$

$$A_2 = \begin{pmatrix} 0 & 0 & 0 & 0 & 0.986 & 1.219 \\ 0.773 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.764 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.740 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.609 & 0.623 & 0 \\ 0 & 0 & 0 & 0 & 0.003 & 0.852 \end{pmatrix} \quad (2)$$

From the permutation analysis it is possible to affirm that for $\alpha=0.05$ there are not significant differences between the observed abundance curve and those predicted by both models (see Figs. 3 and 4).

For the unexploited population represented in five and six stages the following transition matrices were obtained:

$$A'_1 = \begin{pmatrix} 0 & 0 & 0 & 0 & 1.069 \\ 0.989 & 0 & 0 & 0 & 0 \\ 0 & 1.000 & 0 & 0 & 0 \\ 0 & 0 & 0.885 & 0 & 0 \\ 0 & 0 & 0 & 0.382 & 0.817 \end{pmatrix},$$

$$A'_2 = \begin{pmatrix} 0 & 0 & 0 & 0 & 1.023 & 1.283 \\ 0.974 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1.000 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.875 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.808 & 0.553 & 0 \\ 0 & 0 & 0 & 0 & 0.009 & 0.856 \end{pmatrix} \quad (3)$$

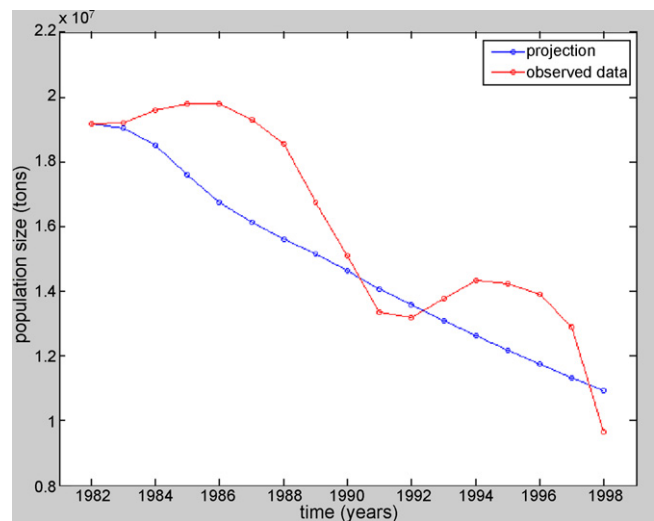


Fig. 3. Comparison of the projection of the five-stage matrix obtained by means of the programming quadratic method and the observed data of the female pink ling abundance series of 3 to 14+ years old estimated for the period 1982–1998.

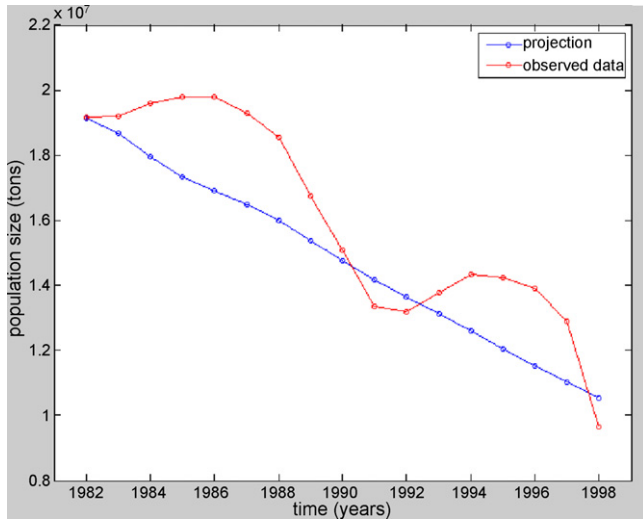


Fig. 4. Comparison of the projection of the six-stage matrix obtained by means of the programming quadratic method and the observed data of the female pink ling abundance series of 3 to 14+ years old estimated for the period 1982–1998.

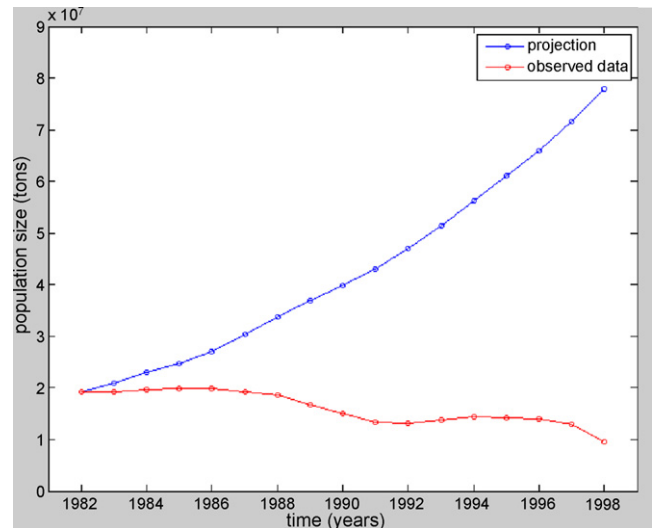


Fig. 6. Comparison of the projection of the six-stage matrix without considering harvest and the observed data of the female pink ling abundance series of 3 to 14+ years old estimated for the period 1982–1998.

From the permutation analysis it is possible to affirm that for $\alpha = 0.05$ there are significant differences between the observed data curve and those curves predicted by both models as it is shown in Figs. 5 and 6 for the unexploited population.

The estimated population growth rate for the five-stage model with harvest corresponds to 0.971 and its confidence interval is (0.967–0.972). The estimated population growth rate for the six-stage model with harvest corresponds to 0.953 and its confidence interval is (0.945–0.968). The estimated population growth rate for the five-stage model without harvest is 1.080 and its confidence interval is (1.079–1.092). The estimated population growth rate for the six-stage model without harvest corresponds to 1.086 and its confidence interval is (1.086–1.100). From these results it follows that there exists significant differences between the dynamics of exploited population and the one with no harvest.

The reproductive net rates R_0 for the five- and six-stage models with capture are 0.748 and 0.712, and for the five- and six-stage models without capture are 1.950 and 1.709 respectively.

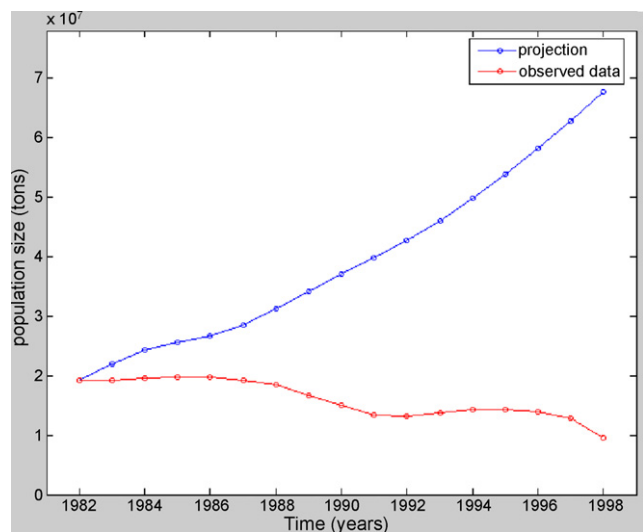


Fig. 5. Comparison of the projection of the five-stage matrix without considering harvest and the observed data of the female pink ling abundance series of 3 to 14+ years old estimated for the period 1982–1998.

The sensitivity and the elasticity matrices of the five-stage model in the exploited population are

$$S = \begin{pmatrix} 0 & 0 & 0 & 0 & 0.093 \\ 0.122 & 0 & 0 & 0 & 0 \\ 0 & 0.124 & 0 & 0 & 0 \\ 0 & 0 & 0.128 & 0 & 0 \\ 0 & 0 & 0 & 0.306 & 0.609 \end{pmatrix},$$

$$E = \begin{pmatrix} 0 & 0 & 0 & 0 & 0.098 \\ 0.098 & 0 & 0 & 0 & 0 \\ 0 & 0.098 & 0 & 0 & 0 \\ 0 & 0 & 0.098 & 0 & 0 \\ 0 & 0 & 0 & 0.098 & 0.512 \end{pmatrix} \quad (4)$$

From the observation of the five-stage model for exploited population, it is possible to verify a higher sensitivity of λ to the probability P_5 in stage five (from 7 to 14 years old), and followed by the survival G_4 of the last juvenile stage. The rest of the parameters reached lower sensitivity values. The elasticity analysis for the same model showed a higher relative sensitivity of λ to variations in P_5 , while the remaining parameters reached elasticity values lower than 0.10.

The sensitivity and elasticity matrices of the six-stage model in the exploited population are

$$S = \begin{pmatrix} 0 & 0 & 0 & 0 & 0.129 & 0.004 \\ 0.171 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.173 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.178 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.217 & 0.400 & 0 \\ 0 & 0 & 0 & 0 & 1.569 & 0.045 \end{pmatrix},$$

$$E = \begin{pmatrix} 0 & 0 & 0 & 0 & 0.134 & 0.005 \\ 0.139 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.139 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.139 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.139 & 0.261 & 0 \\ 0 & 0 & 0 & 0 & 0.005 & 0.040 \end{pmatrix} \quad (5)$$

In the case of the exploited population represented in six stages, it was observed a higher sensitivity of λ respect to the survival of the stage five G_5 (from 7 to 10 years old), followed by P_5 . The rest of the sensitivity values were lower. The elasticity of exploited population represented in six stages was mainly focussed on the parameter P_5 .

The sensitivity and elasticity matrices of the five-stage model in the unexploited population are

$$S = \begin{pmatrix} 0 & 0 & 0 & 0 & 0.125 \\ 0.134 & 0 & 0 & 0 & 0 \\ 0 & 0.133 & 0 & 0 & 0 \\ 0 & 0 & 0.150 & 0 & 0 \\ 0 & 0 & 0 & 0.349 & 0.507 \end{pmatrix},$$

$$E = \begin{pmatrix} 0 & 0 & 0 & 0 & 0.123 \\ 0.123 & 0 & 0 & 0 & 0 \\ 0 & 0.123 & 0 & 0 & 0 \\ 0 & 0 & 0.123 & 0 & 0 \\ 0 & 0 & 0 & 0.123 & 0.384 \end{pmatrix} \quad (6)$$

The sensitivity and elasticity matrices of the six-stage model for the unexploited population are

$$S = \begin{pmatrix} 0 & 0 & 0 & 0 & 0.161 & 0.007 \\ 0.178 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.173 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.198 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.214 & 0.325 & 0 \\ 0 & 0 & 0 & 0 & 0.896 & 0.038 \end{pmatrix},$$

$$E = \begin{pmatrix} 0 & 0 & 0 & 0 & 0.151 & 0.008 \\ 0.159 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.159 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.159 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.159 & 0.166 & 0 \\ 0 & 0 & 0 & 0 & 0.008 & 0.030 \end{pmatrix} \quad (7)$$

In the unexploited five-stage population model, the sensitivity analysis shows higher sensitivity of P_5 , relative to the other parameters of this model. The elasticity analysis of the unexploited five-stage population model showed higher sensitivity of λ to the parameter P_5 .

In the case of the unexploited six-stage population model we observe a higher sensitivity of λ with respect to the survival of stage five G_5 , followed by $P_5 = 0.325$. The remaining values were less than the sensitivity values indicated for these parameters. The elasticity analysis reflected a higher relative sensitivity of the unexploited six-stage population growth rate P_5 followed very closely by the probability of survival and growth of the all juvenile classes, G_1-G_4 and the fecundity of the stage five F_5 .

The right eigenvector or stable stage structure w , and the left eigenvector or reproductive value ν for the exploited and unexploited five-stage model and the structure of stages observed are given in Table 1.

The right and left eigenvectors for the exploited and unexploited population gathered in six stages and the structure of stages observed are given in Table 2.

The structure of stages observed in the five- and six-stage models does not present significant differences with the stable stage structure of the transition matrices for the harvested population ($P > 0.9$).

Table 1
Right and left eigenvectors for the exploited and unexploited five-stage model and the structure of stages observed.

Stages	Exploited		Unexploited		Observed
	w	ν	w	ν	
1	0.260	0.080	0.224	0.551	0.251
2	0.207	0.100	0.205	0.602	0.213
3	0.163	0.128	0.190	0.650	0.168
4	0.124	0.167	0.156	0.793	0.126
5	0.247	0.525	0.226	0.242	0.241

Table 2
Right and left eigenvectors for the exploited and unexploited six-stage model and the structure of stages observed.

Stages	Exploited		Unexploited		Observed
	w	ν	w	ν	
1	0.255	0.048	0.225	0.707	0.252
2	0.207	0.059	0.202	0.789	0.213
3	0.166	0.073	0.186	0.856	0.168
4	0.129	0.094	0.150	1.063	0.126
5	0.238	0.148	0.227	1.430	0.211
6	0.007	0.578	0.010	3.945	0.030

4. Discussion and conclusions

This work was carried out with the abundance data provided by IFOP estimated by analysis of sequential populations, including methods related to the reconstruction of population size by ages obtained from data of commercial capture.

The models for the pink ling population subjected to exploitation grouped in five and six stages, predict dynamics that fit significantly ($P < 0.05$) to the observed abundance data. The models of five and six stages give similar results for the same population, so any of these two forms of the pink ling population model is appropriate for the analysis.

We think that this methodology is a suitable tool to analyze others exploited populations, in spite of the necessary calculations to obtain the parameters of the unique projection matrix (van Groenendaal et al., 1988) using quadratic programming.

The models presented for the exploited population of *G. blacodes* reflect a rate of population change significantly smaller than the unexploited one ($P < 0.05$). Our results confirm that the current pink ling population presents a decreasing tendency sustained throughout the study period. With the same initial condition, and the fishing effort removed, the population shows an exponential increase with growth rates significantly larger than 1. Therefore, it is possible to affirm that the pink ling population dynamics from the austral demersal fishery has been significantly altered by the capture regime to which they have been exposed. The negative effect of the capture on the *G. blacodes* increase has both quantitative and qualitative consequences, because the fishing extraction reduces the growth rates from positive to negative values.

Considering that the population growth rate λ with a hypothetical absence of capture would be 1.086 and 1.080 (for the proposed models), it is evident that the population has a slow natural increase, comparable to other species such as sea birds, killer whales, whales, squirrels and sharks (Brault and Caswell, 1993; Caswell et al., 1999; Mollet and Cailliet, 2002).

Even though there are not previous matrix models and detailed studies on population dynamics for *G. blacodes* and other species of the genus, population growth rate estimates have been carried out through life tables and population matrices similar as it was done for different elasmobranch species (Mollet and Cailliet, 2002). Our study finds that there are no significant differences between the population growth rates carried out for different stage groupings, which changed between 0.996 and 1.185. Myers et al. (1997) estimated the intrinsic growth rate r of 20 populations of Atlantic cod (*Gadus morhua*), through the Ricker's stock-recruit model. Making the calculation for λ , their results show values between 1.161 and 2.801, which are comparatively higher than the maximum observed for pink ling in our work.

The sensitivity and elasticity analyses of the five-stage model in the exploited population, revealed a stronger functional dependence of the growth rate on the survival and retention P_5 of adult females. The sensitivity matrix for the six-stage model showed a greater dependence on the parameter G_5 of survival and devel-

opment to the following stage, while the elasticity results of the six-stage model showed higher estimates for the parameter P_5 of survival and permanence in the stage five, i.e., female in the 7–10-year-old class.

The perturbation analysis of the population matrices under the assumption of no harvest showed similar results to those obtained for the observed series. Likewise, the five-stage model showed a stronger dependence of the growth rate on the survival and permanence P_5 of the adult females. The sensitivity matrix for the six-stage model revealed a higher dependence on hypothetical variations in the survival and development parameter G_5 , while the elasticity analysis showed larger estimates for the survival and permanence parameter into the stage five P_5 , closely followed by the juvenile survival and development G_1 – G_4 and F_5 the fecundity of the stage five.

Nevertheless, when the sum of elasticities e_{G_5} and e_{P_5} is considered, it can be confirmed that the parameter whose hypothetical variation would affect to a greater extent the population growth rate is the survival and permanence or the survival and growth of the adult class, as it is usual for species with long life-cycles (Brault and Caswell, 1993; Heppell et al., 2000).

For a correct interpretation of the results, de Kroon et al. (2000) forewarn on the use of elasticities to address the management of populations. The prospective perturbation analysis carried out here determines the kind of functional dependence of λ with regard to the vital rates, that is, how the population growth responds to the changes in the projection matrix entries. This functional dependence is a property of the life history, and it is therefore independent from any environment-induced variation in these rates. For this reason, it does not explain neither how the vital rates have varied in the past, nor how they can vary at present or in the future (Caswell, 2000). The retrospective analysis indicates a relation between the high elasticity and the low variability of parameters, which it would contribute to a small variability of λ .

On the other hand, some authors forewarn that high variances in a_{ij} could make that this parameter a non-interesting object since it is subjected to a bigger environmental variation (Caswell, 2000; de Kroon et al., 2000). For the pink ling case, it would be very useful to complement the results given here, with retrospective analysis for which a source of variation of λ is required (Caswell, 2000).

The left eigenvector structure or population reproductive value of the pink ling grouped in five stages corroborates the importance of the adult stage, just as the results of the perturbation analysis suggest. It shows that stage five (7-year females and older) has a higher reproductive value (0.525), i.e., it contributes to a larger extent to future births. For the six-stage model, the higher reproductive value of the older stage (0.578) corresponds to 11–14-year-old adult females. These results partially agree with those obtained by Aguayo et al. (2001), from the calculation of the egg production by age class. These authors inform a bigger contribution from the class 7–9-year olds.

The right eigenvector, or stable stage structure, shows that the population is mainly concentrated in the juvenile stages one and two and adult stage five, for both the exploited and the unexploited population. In a constant environment the proportion of individuals within different age classes should tends to a stable distribution, as it was observed for the pink ling population studied. Their effects diminish in proportion to the sub-dominant eigenvectors (transient dynamics), e.g., the population approaches asymptotically to the stable stage structure given for the λ dominant eigenvalue (Caswell, 2001).

We consider of special interest to carry out subsequent quantitative ecological studies about this resource, including spatial aspects and inter-specific relations, based on exact estimates of the population sizes. Nonetheless, from this work it is possible to affirm that the pink ling population of the ADF exhibits a low growth rate. It

is advisable therefore, that a special care should be taken in relation with its exploitation regime. Under these circumstances, it is also possible to recommend management strategies that preserve the 7–10-year-old adult individuals, since small variations in the survival of these individuals will highly alter the dynamics of the whole population, risking the sustainability of the pink ling fishery.

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