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First Approach to the Application of Life Table Models to Portuguese Dogfish (*Centroscymnus coelolepis*, Bocage and Capello, 1864)

(Elasmobranch Fisheries – Oral)

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Abstract

Life table models are an example of demographic models. In a very simple way, life table models can be considered as the direct transcription of the species life cycle into a matrix format. In this sense life table models can easily accommodate particularities of species dynamics, which are hardly introduced into the traditional stock assessment models. As a matter of fact the matrix formulation, which constitutes the basic tool for evaluating and projecting the stock structure, might be continuously updated at the same time as species knowledge increases. In addition the use of such models, which do not involve so many parameters as other models currently used in fisheries, does not get rid of uncertainty it only hides it away. To be more confident about the future developments of the species dynamics there is the need for further improvements. This work presents the results from a first approach of the adjustment of basic matrix model to Portuguese dogfish.

Introduction

Many of the deep-water stocks in the Northeast Atlantic are heavily exploited and some are severely depleted (Anon., 2001). In 2000, this led ICES to conclude "most exploited deep-water species [in the Northeast Atlantic] are, at present, considered to be harvested outside safe biological limits" and to provide management advice recommending "immediate reductions in these fisheries unless they can be shown to be sustainable. New fisheries should be permitted only when they expand very slowly, and are accompanied by programs to collect data which allow evaluation of stock status." (Anon., 2001).

The high vulnerability of deep-sea fish stocks to exploitation raises the question as to the extent to which yields from these resources are sustainable. This question is particularly pertinent in case of the deep-water sharks.

At the Northeast Atlantic there is an increasing interest for the commercial exploitation of several deep-water shark species. Simultaneously with this interest emerge the necessity for the development of specific fishery management strategies. The emphasis put in this objective is a natural consequence of the unarguable belief on shark vulnerability to exploitation which is supported by the slow-growing rates, late to mature, long-lived and small brood sizes that characterise these species (Smith *et al*., 1998). However, as argued by Walker (1998), the same characteristics that make these species vulnerable to the effects of overexploitation also provide for stable populations and stable fisheries. In fact life-history traits of sharks are more like those of marine and terrestrial mammals, which are also K-selected animals (Walker, 1998).

In many fisheries where sharks are target or taken as part of multispecies fisheries localised stock depletion is expected to occur. This phenomenon involves greater levels of reduction on the density of one species in a specific area but not at other adjacent areas where the species exists and it is commonly associated with fishing pressure or habitat modification. In the first case the local depletion is related to fact that the exploited areas of shark fisheries, given that they do not fall in nursery grounds or in major aggregation of species breeding, are considerably smaller than the general distribution area of the species (Walker, 1998).

In a restricted area off the Portuguese continental slope (ICES Sub-area IX), a longline fishery for black scabbardfish takes place at depths between 800 and 1200 m on hard bottoms along canyon slopes. In 2000, 15 vessels were engaged in this fishery, which has a by-catch of Portuguese dogfish (*Centroscymnus coelolepis*; Bocage & Capello, 1864) (Figueiredo *et al*., 2000). The commercial interest on this species has increased during the last decade. There are also several fisheries for deep-water sharks at Northeast Atlantic. The trawl fishery that developed in the Rockall Trough and on the slopes of the Porcupine Bank is one of the most intensive. Besides Portuguese dogfish, the Leafscale gulper shark (*Centrophorus squamosus*, Bonnaterre, 1788) are the two species routinely landed (Clarke, Connonly and Bracken, 2001). These species are collectively called "siki" in the French fishery records (Gordon, 1999).

Although the biological characteristics of the shark impede the application of many accepted models for stock assessment (Wood, Ketchen and Beamish, 1979) considerable advances have been made towards the modelling population dynamics and assessing stocks of individual shark species (Punt and Terence, 1998).

Life history modelling and demographic analysis have already being explored and applied to several species. Particularly, matrix models allow to describe the evolution, in discrete time, of a population classified in a finite number of states (Caswell, 1989).

This paper constitutes a simple contribution to the use of matrix population models in demographic studies of shark populations and to do this the Portuguese dogfish was used as the case study.

Material and Methods

Portuguese Dogfish Data

The Projection matrix constructed for Portuguese dogfish is based on information mainly derived from samples collected from landings at Sesimbra port, which is located at the centre of Portugal Mainland. As stated before, this species is the major by-catch of the artisanal longline fishery that takes place off Sesimbra and that has black scabbardfish as the target species.

Size at birth

26.8 cm for both males and females is the length at birth assumed for Portuguese dogfish. This value was established taken into consideration the length of embryos at the latest state of development, i.e. near birth, which were collected from Sesimbra samples (Veríssimo, 2001).

This size is slightly smaller than the one adopted for specimens from the West off British Isles (Clarke, Connoly and Bracken, 2001).

Although the Portuguese data are insufficient to determine the duration of gestation time so the value of 26 months pointed out by Girard (2000) is adopted, which is close to the value (22 months) as demonstrated for the related species *Squalus acanthias* (Hanchett, 1988)

Growth parameters

Although the present analysis of population data is not done in terms of age groups it is necessary to have some indications about species' growth pattern and rates. Such information is necessary in order to have an idea about time duration of the each category into which the population will be divided.

Age determination of sharks, particularly of deep-water sharks, is not an easy task. The choice of the shark structure for age determination, of the preparation method and of the ageing criteria together with the lack of validation studies are important sources that affect the level of uncertainty on age determinations and consequently the variance of growth parameter estimates. These age data preliminary nature, but have been used in this analysis to illustrate the utility of the matrix model for this species.

In this study, the growth parameter estimates are determined based on age and length data available from ageing studies, which were based on species samples collected following the Portuguese landing sampling program. In these studies ages were assigned through the analysis of spine's structure, namely, through the counting of the growth bands inscribed on fine spine sections. For establishment of ageing criteria it has been assumed that:

- Growth bands are annually deposited;
- Only one growth band is deposited in each year;
- Species' growth pattern is adequately described by the Von Bertallanffy model (VBF);
- L_∞ is assumed to be 0.95 of maximum species' observed length, Lmax (130.15 cm in Hareide *et al*., 2000).

The VBF models as well as the estimates of its growth parameters are presented in Fig. 1.

Renovation rate

The renovation rate in each year is the product of:

- mean number of embryos liberated by pregnant females;
- sex ratio of terminal embryos per pregnant female;
- females' fraction liberating embryos each year.

To determine the renovation rate for Portuguese dogfish it is assumed that:

- there are no differences on renovation rates among geographic areas;
- the mean number of embryos do not vary according to the length/age of females;
- the sex ratio of liberated embryos is constant;
- the proportion of pregnant females liberating embryos in each year is constant.

Based on biological information from specimens sampled at Sesimbra the following results are obtained (Veríssimo, 2001):

- 10 is the mean number of terminal embryos by female;
- 43% is the sex ratio of the liberated embryos;
- 5.6% is the fraction of pregnant females liberating embryos in each year.

The estimated renovation rate is equal to 0.24.

Natural mortality

For all the species natural mortality parameter; M, is very difficult to determine. Consequently M is commonly treated as a fixed constant, although it is known that it is a random variable that varies over time, age and year-class.

Despite this difficulty on its determination, natural mortality is often estimated following different approaches, namely: I) catch curve analysis; ii) LFA and related analyses, iii) mark and recapture experiments; iv) collection of dead organisms; v) fitting populations models; vi) life history (or meta-) analysis.

The last approach, life history analysis or meta-analysis, has as starting point several estimates of life history parameters calculated for a variety of species and environments. These estimates are jointly used in order to establish predictive relationships or statistical distributions for the parameters of interest.

In the case of natural mortality different estimates of this parameter are used to develop predictive regression relationships in which natural mortality is a dependent variable. Although several models are available, at the present study natural mortality is estimated using Pauly's Model: Pauly, 1980).

$$\log_{10} M = -0.0066 - 0.279 \log_{10} L_\infty + 0.6543 \log_{10} K + 0.4634 \log_{10} T$$

The value of 5ºC which, corresponds to minimum temperature registered for the species (Compagno, 1994), is adopted. Although observational temperature data registered onboard of a Portuguese longline fishing vessel indicated a considerably higher value (11.5ºC). This value is not used in present study and the resulting M estimate for the 5ºC temperature is 0.16.

Fishing mortality

Fishing mortalities are estimated based on equivalence Z=F+M, where Z is the total mortality, F fishing mortality and M, natural mortality.

Under equilibrium assumptions and assuming that fishing mortality do not differ among length classes, Z, can be determined through Beverton and Holt (1957) model:

$$Z = k \frac{L\infty - \overline{L}}{\overline{L} - L_c} L\infty$$

where:

- $\overline{L}$ is the mean length of capture;
- Lc is the length at first capture;

K	0,17
$L\infty$	137
$\overline{L}$	104.1
Lc	74
F	0.189

Fishing gear selectivity

Results of Irish longline surveys support Gordon's (1999) view that longlines are not a selective fishing method for sharks as trawl (Clarke *et al*., this conference). In effect while longlines tend to select larger teleost fish than trawls (Hareide, 1995; Jørgensen, 1995) this statement may not apply to all deepwater shark species (Clarke, 2000). Longlines are not size-selective; on longlines the probability of capturing small Portuguese dogfish females is higher than on trawl. Furthermore, squalid sharks as small as 27 cm TL were taken on long-lines (Connolly, Kelly and Clarke, 1999).

In addition results from Irish longline surveys (Clarke, 2000; Connolly, Kelly and Clarke, 1999) show that commercial (13/0 EZ) hooks and baits select for a broad size *spectrum* of squaliform sharks representing the entire length range of free-swimming specimens of the species under study. It appears that small sharks are well adapted to prey on relatively large food items.

Population length histograms

Female length frequency distributions are established based on samples obtained from the length sampling program carried out in Sesimbra landing port (Fig. 2).

Matrix Population Model

A matrix population model is adjusted to Portuguese dogfish data as a way to investigate the demographic dynamics of the exploited population at the Portuguese continental slope.

This matrix approach is one of the several mathematical frameworks for demographic modelling particularly useful whenever the life cycle of a species is most appropriately described in terms of size classes or developmental stages, rather than age classes (Caswell, 1989).

Matrix population models are applied to populations in which individuals are classified into discrete categories or stages. Although some stages are naturally discrete others are naturally continuous and must be made discrete (e.g. size). Dividing continuous variables into discrete categories involves trade-offs. In this last case the model treats all individuals within a category as identical so creating only a few large categories reduces the accuracy of the dynamics within each stage. Alternatively, creating many small categories leads to a large model and make it hard to estimate parameter values because sample sizes in each category are small (Caswell, 1997).

The stages describe the life cycle, or as much of it as is believed to be demographically important. Species' *life cycle graph* is a simple graphical description of the life cycle, which is isomorphic to the *population projection matrix* **A**.

A matrix population model operates in discrete time projecting a population from t_0 to t_0+1. At the present approach only the simpler time invariant and density independent model will be considered:

$$\mathbf{n(t_0 + t) = A^{\mathit{t}}\ ´\ n(t_0)} \quad \mathbf{for\ \ t}\ {}^{3}\ \mathbf{1\ with\ t_0} \quad \mathbf{initialtime.}$$

Using this model the analysis of the population dynamics is based on the analysis of the asymptotic behaviour of the projection matrix $\mathbf{A}^{\mathbf{t}}$, through the study of the eigenvalues and eigenvectors of the matrix **A**.

If $\mathbf{A} = \{a_{ij}\}$ (i, j = 1,...,k) is a square matrix of dimension $k \times k$, the eigenvalues, λ_i (i = 1,...k) are determined as the solutions of the characteristic equation $| \mathbf{A} - \lambda\mathbf{I} | = 0$.

Each eigenvalue, λ_i, has an associated right eigenvector, $\mathbf{w_i}$, of dimension $(k\times1)$, that satisfies the equation $\mathbf{A}.\mathbf{w_i} = \lambda_i.\mathbf{w_i}$, i = 1,...,k

Analogously each eigenvalue, λ_i has an associated left eigenvector, $\mathbf{v_i}$, of dimension $(k\times1)$, that satisfies the equation $\mathbf{v^*_i}\,.\mathbf{A^*} = \lambda_i.\mathbf{v^*_i}$, i = 1,...,k, where $\mathbf{v^*_i}$ - transposed of v_i, is a right eigenvector of $\mathbf{A}^*$, transposed of **A**.

Both the dominant eigenvalue λ_1, $\lambda_1 > |\lambda_i|$, $i\neq1$, and its corresponding right eigenvector $\mathbf{w}_1$ will govern **the resultant asymptotic population structure assuming that the actual environmental conditions are maintained indefinitely constant.**

- if $\lambda_1 > 1 \rightarrow$ the population will increase exponentially
- if $\lambda_1 < 1 \rightarrow$ the population will decrease exponentially

λ_1 is called the population growth rate and its logarithm expresses the intrinsic change rate of the population, $\ln(\lambda_1) = r$. The stable population structure is given by the right eigenvector associated with the dominant eigenvalue. The stage specific reproductive value is given by the left eigenvector, $\mathbf{v_1}$, associated with the dominant eigenvalue.

Multiregional models, also designated metapopulation models by ecologists, may be used in cases when it is needed to incorporate spatial variation in the processes associated with the population (Caswell, 2001).

In the present study a multiregional model is constructed for the Portuguese dogfish. However due to the lack of information about the migration pattern of the species between the commercially exploited region and adjacent areas leads to assume the simplest form of dispersal of individuals between those areas, diffusion. According to this approach the flux of individuals between regions is proportional to the differences in their densities (Caswell, 2001).

In this case the projection matrix of the model includes the projection submatrices A_1 and A_2, which describe the within-region demography of Regions 1 and 2 respectively. The entries of each of matrix correspond to the transitions and reproduction of individuals from the corresponding region. Differences between the two submatrices are due to the fact that fishing mortality takes only place at Region 1.

$$\boldsymbol{A} = \left(\begin{array}{c|c} A_1 & 0 \\ \hline 0 & A_2 \end{array}\right) = \left[\begin{array}{cccc|cccc} P_{11} & 0 & R & R & 0 & 0 & 0 & 0 \\ G_{11} & P_{12} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & G_{12} & P_{13} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & G_{13} & P_{14} & 0 & 0 & 0 & 0 \\ \hline 0 & 0 & 0 & 0 & P_{21} & 0 & R & R \\ 0 & 0 & 0 & 0 & G_{21} & P_{22} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & G_{22} & P_{23} & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & G_{23} & P_{24} \end{array}\right]$$

where:

- P_{ki} is the probability of an individual from region k and stage i survives and remains at stage i;
- G_{ki} is the probability of an individual from region k and stage i survives and passes to stage i+1;
- R is the renovation rate, which is assumed to be equal for the two stages contributing with embryos.

The model also comprehends the 4x4 diffusion matrix, D = diag (d_1, d_2, d_3, d_4) where d_i is the probability that an individual in category i leaves the region and goes to the other. In our case estimates of d_i from Region 1 to region 2 correspond to the proportion of the mean observed number of individuals in category i at region 1 *versus* the expected number under the theoretical underlying length distribution assumed for the whole area.

The population vector is $\boldsymbol{n} = \left(\begin{array}{c} n_{Region\ 1} \\ \hline n_{Region\ 2} \end{array}\right) = \left(\begin{array}{c} n_1 \\ n_2 \\ n_3 \\ n_4 \\ \hline n_5 \\ n_6 \\ n_7 \\ n_8 \end{array}\right)$ and considering that demography occurs first the

within-region demography transforms the vectors $n_{region1}$ (t) and $n_{region2}$ (t) into to intermediate vectors m_1(t) and m_2(t) according to $\left(\begin{array}{c} m_1 \\ \hline m_2 \end{array}\right)(t) = \left(\begin{array}{c|c} A_1 & 0 \\ \hline 0 & A_2 \end{array}\right) \left(\begin{array}{c} n_{Region\ 1} \\ \hline n_{Region\ 2} \end{array}\right)(t)$. Then considering that the dispersal moves individuals between the two regions the population vector at time t+1 follows

$\left(\begin{array}{c} n_{Region1} \\ \hline n_{Region2} \end{array}\right)(t+1) = \left(\begin{array}{c|c} I-D & D \\ \hline D & I-D \end{array}\right) \left(\begin{array}{c} m_1 \\ \hline m_2 \end{array}\right)(t)$, where **I** is the identity matrix. This process yields a single

Projection matrix, which is constructed from the demography and diffusion matrices and that can be analysed in the same way as the projection matrix **A** referred at the beginning.

Results and Discussion

The female length frequency distributions of Portuguese dogfish females caught by the commercial Portuguese longlines are bimodal, the second mode being heavier than the first one. Such bimodality is probably the reflection of a differential geographic distribution of females along the species' distribution area.

Taking into consideration the K species' strategy assigned to the Portuguese dogfish several trial and error fittings of gamma distributions to model the length of the female population were essayed. As a result, a gamma distribution with mean equal to 95 and a variance of 412.5 is admitted for the underlying theoretical length distribution for the female population (Fig. 3). Based on this distribution and on the fact that the fishing area of the longline fleet is quite restricted and did not greatly change since the beginning of its activity, it is further assumed that the life cycle of the species takes places at two different regions:

- Region 1 corresponds to the area where the Portuguese fishing fleet activity takes place. It is admitted that at this region the length frequency distribution of the female subpopulation is similar to the one obtained for the commercial longliners;
- Region 2 includes the remaining area of species occurrence that is not commercially exploited.

Considering the length frequency distributions and the length of first maturity, the following four different categories for the female population are adopted in the two regions:

Categories	**Total length Range**	**Observation**
1	< 74	
2	[74 - 100[	100 length of 1st maturity (Veríssimo, 2001)
4	[100, 118[	
5	[118, 137)	137 cm maximum length

Based on the demography and diffusion processes admitted for the Portuguese dogfish the *life cycle graph* is presented in Fig. 4.

The estimated projection matrix of Portuguese dogfish data is:

$$\begin{pmatrix} 0.31 & 0 & 0.23 & 0.23 & 0.02 & 0 & 0.01 & 0.01 \\ 0.10 & 0.12 & 0 & 0 & 0.34 & 0.43 & 0 & 0 \\ 0 & 0.08 & 0.18 & 0 & 0.00 & 0.18 & 0.41 & 0 \\ 0 & 0 & 0.16 & 0.59 & 0.00 & 0 & 0.03 & 0.12 \\ 0.02 & 0 & 0.01 & 0.01 & 0.38 & 0 & 0.23 & 0.23 \\ 0.28 & 0.35 & 0 & 0 & 0.12 & 0.15 & 0 & 0 \\ 0 & 0.15 & 0.34 & 0 & 0 & 0.10 & 0.22 & 0 \\ 0 & 0 & 0.03 & 0.10 & 0 & 0 & 0.19 & 0.71 \end{pmatrix} =$$

$$= \left(\begin{array}{cccc|cccc} 0.95 & 0.00 & 0 & 0 & 0.05 & 0 & 0 & 0 \\ 0 & 0.26 & 0 & 0 & 0 & 0.74 & 0 & 0 \\ 0 & 0 & 0.35 & 0 & 0 & 0 & 0.65 & 0 \\ 0 & 0 & 0 & 0.86 & 0 & 0 & 0 & 0.14 \\ \hline 0.05 & 0 & 0 & 0 & 0.95 & 0 & 0 & 0 \\ 0 & 0.74 & 0 & 0 & 0 & 0.26 & 0 & 0 \\ 0 & 0 & 0.65 & 0 & 0 & 0 & 0.35 & 0 \\ 0 & 0 & 0 & 0.14 & 0 & 0 & 0 & 0.86 \end{array}\right) \times \left(\begin{array}{cccc|cccc} 0.33 & 0 & 0.24 & 0.24 & 0 & 0 & 0 & 0 \\ 0.38 & 0.48 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.23 & 0.52 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.18 & 0.68 & 0 & 0 & 0 & 0 \\ \hline 0 & 0 & 0 & 0 & 0.39 & 0 & 0.24 & 0.24 \\ 0 & 0 & 0 & 0 & 0.46 & 0.58 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.28 & 0.63 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0.22 & 0.82 \end{array}\right)$$

eigenvector associated with the dominant eigenvalue and the stage specific reproductive value given by the left standardised eigenvector, associated with the dominant eigenvalue are:

right eigenvector		**left eigenvector**	
w1	0.101	**v1**	0.575
w2	0.138	**v2**	0.785
w3	0.103	**v3**	1.106
w4	0.128	**v4**	0.905
w5	0.131	**v5**	0.731
w6	0.123	**v6**	0.890
w7	0.100	**v7**	1.383
w8	0.177	**v8**	1.474

Despite the insufficiency knowledge about the spatial distribution of the female population if this fact is not taken into consideration a possible life table model will be reduced to the demographic model adopted for Region 1, which corresponds to submatrix projection $\mathbf{A_1}$ (the light green highlighted submatrix previously presented. In this case the computed eigenvalues are: l_1 = 0.818**;** l_2= 0.500**;** l_3 = 0.345-0.206i and l_4= 0.345+ 0.206i. The right and left standardised eigenvectors, associated with the dominant eigenvalue are:

right eigenvector		**left eigenvector**	
w1	0.242	**v1**	0.668
w2	0.269	**v2**	0.866
w3	0.208	**v3**	1.292
w4	0.281	**v4**	1.198

The analysis of two models indicates that, under stable conditions, a medium term decrease of the population in both. In the case of the multiregional model the decreasing rate is slower than the one estimated for the model that does not incorporate migration processes.

In both approaches the vulnerabilities and deficiencies of our knowledge about the Portuguese dogfish dynamics are not considered. Nevertheless the multiregional model seems to provide a more adequate perspective of the population evolution in the future since the information available from the fishing exploitation of the species does not indicate a dramatic decrease on the yields. Also the length structure of the landed specimens, especially in the two last categories, does not put into evidence a marked change, which is more probable to occur if the simple demographic model is adopted.

Finally to be more confident on species' dynamics knowledge there is the need for further improvements on:

- Length population structure both on a geographic and temporal basis;
- Migratory processes acting in the whole or part of the population.

Better estimates of the biological parameters are used as inputs for the construction of the Projection matrix are also required, namely:

- Natural mortality, which is one of the most problematic parameters;
- Total and fishing mortality estimates, through the implementation of other approaches and on the subsequent analysis of the consistency of different estimates obtained;
- Age determinations and age validation;
- Investigation on the degree of the well fit adjustment of other growth models, specially models with higher flexibility than VBF;
- Study of species' embryonic development;

Those improvements will certainly allow a better description of the population Projection matrix and consequently the study of its dynamics. Nevertheless it is also important to point out that the development of more complex models, usually implying an increase of the parameter's set to be estimated and of variability associated with the whole model will determine a more difficult interpretation of model's output.

On the other hand the use of simpler models, not involving so many parameters, as it was tried in the present study, do not allow to get rid of the whole uncertainty about the knowledge of species' dynamic it only hides it away. So the results obtained should be regarded with caution and considered just as a rough approach to the underlying and unknown trajectory of the population under study.

Consequently with the increase on comprehension of the species it will be possible to proceed with a stepwise upgrading of the simple model. This will allow a finer perception of the most problematic parameter(s) and due to this they might be inputted into the model as random variables. By this approach, theoretical probability distributions are adjusted to parameters. In this way it will be able to relax the strong model's assumption of a constant environment by the probabilistic study of different trajectories.

Catch and effort data at a species-specific level are only slowly becoming available for this and other deep-water species. In many cases they are incomplete and do not cover the earlier, high catch phase of the fisheries (1990's). In the interim, another approach is to use life history models as described above. This will involve collecting more life history data, including refining estimates of age, age-specific natural mortality and knowledge of the population structure. It is suggested that internationally coordinated sampling programs may achieve the goal of collecting these data. Such an approach may be a more fruitful means of supporting the rational assessment of these species, than mere reliance on the catch and effort data.

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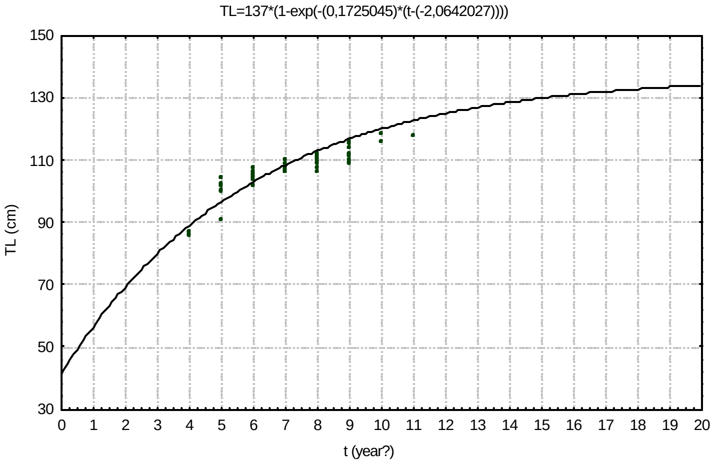

Fig. 1. Growth curve adjusted for female data.

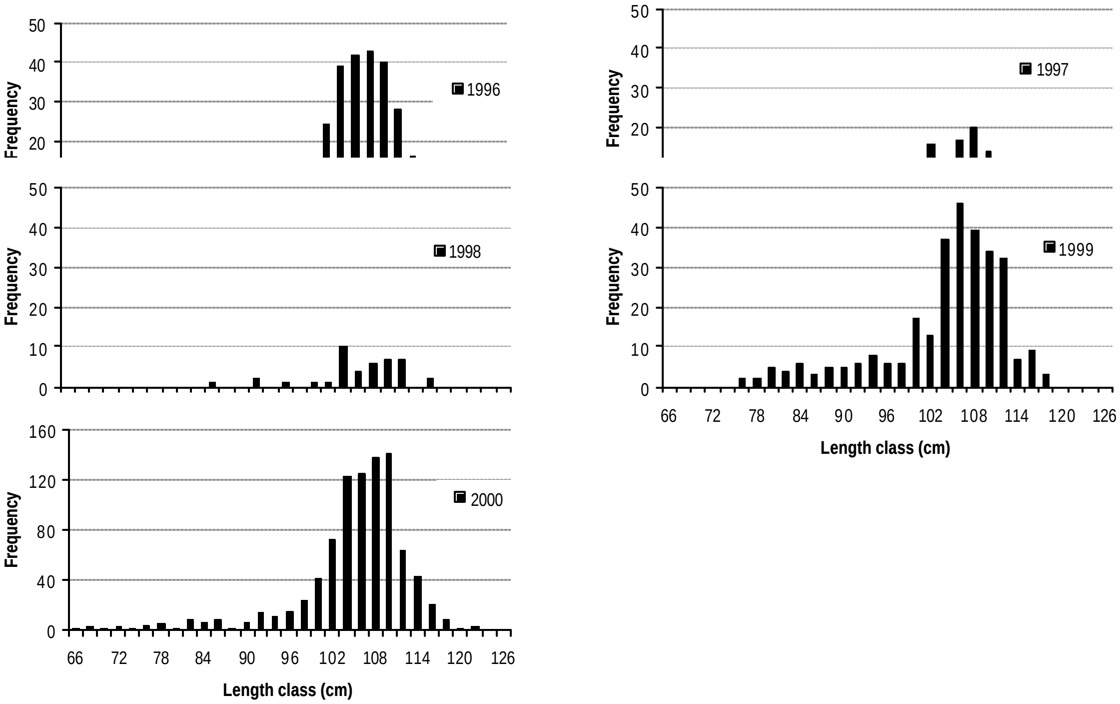

Fig. 2. Female length frequency distributions based on samples taken by the commercial longline fishery at Sesimbra landing port from 1996 to 2000.

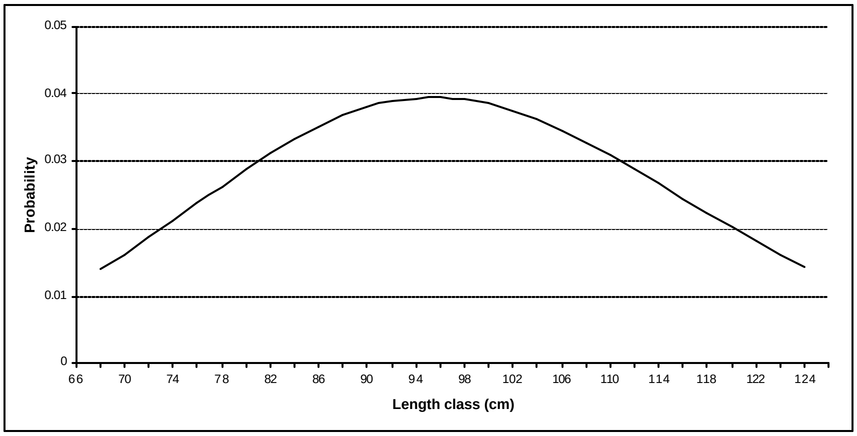

Fig. 3. Theoretical length frequency distribution of the female population of Portuguese dogfish.

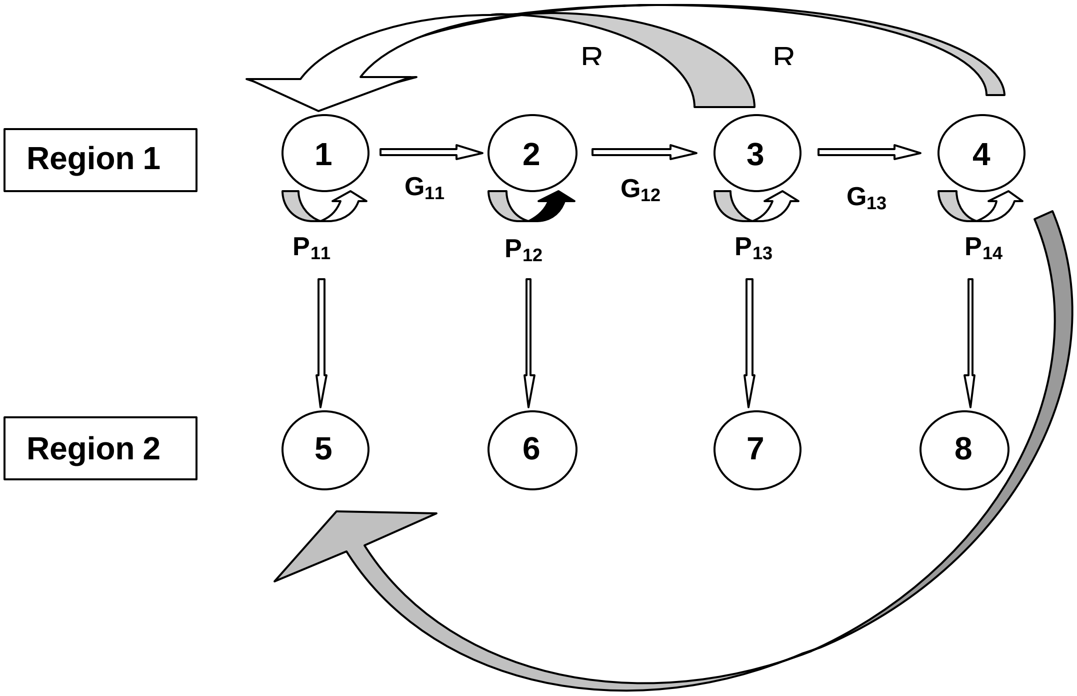

Fig. 4. Multiregional life cycle of the Portuguese dogfish with four categories and two regions. Only transitions beginning in Region 1 are drawn; Region 2 is symmetrical.