Study of the bay of Biscay anchovy population dynamics 
using spatialised age-specific matrix models

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Abstract
The anchovy population of the bay of Biscay displays an important variability both in abundance and spatial distribution. Using the population age and abundance structure derived from survey data, five areas, each containing a sub-population of distinct demographic feature, were defined. Demographic models for subdivided population offer an useful investigation tool to study the effect of varying demographic parameters on population growth. An age-specific matrix model was applied to a stable average population and in each area fertility, mortality and migratory rates at age were determined. The model analysis revealed the strong effect of first year mortality on population growth as well as the important weight of the sub-population located the Gironde River plume on the global population of the bay. The major role of migratory flows into restoring and maintaining a stable population structure was also discussed. Tentative conclusions on the population dynamic links with physical and hydrological feature of the bay of Biscay are drawn and possible future developments of the model are presented.

Keywords: anchovy, demographic models, subdivided population

1. Introduction
The anchovy population (Engraulis encrasicolus, L.) of the bay of Biscay displays an important variability both in abundance and spatial distribution (spawning ground). The study of the anchovy population over 20 years revealed that, at reproduction time, fish within a particular length or age class are often found on some preferential habitats (1). These different spawning habitats coincide with major hydrological structures, such as river plumes, vertical instability at the shelf break, coastal upwelling, oceanic gyre) (2).
Demographic models for subdivided population offer an useful investigation tool to study the effect of varying demographic parameters on population growth (3, 4). Such models may take into account the spatial distribution and migratory patterns of the population as individuals grow and age, as well as the effect of different habitats on fish biological functions. We applied an age-specific matrix model to the anchovy population and, using the population age-structure derived from survey data, we defined five distinct areas in the bay of Biscay. For each area fertility, mortality and migratory rates at age were determined. The matrix sensitivity and elasticity to the variation of vital rates were calculated to study the mechanisms underlying population growth of anchovy. The general implications for population dynamics are discussed.

2. Definition of sub-populations and zones

From 1992 to 2001, data on the anchovy population was available from seven scientific surveys: DAAG92, ERAG93-94, PEGASE97-98 and PEL00-01. The population abundance was estimated from acoustic data. The age distribution was reconstituted using the length distribution of each trawl haul and the length-age key defined for the bay of Biscay anchovy population (1). A Principal componant analysis (PCA) was used to explore the variation of abundance at age (Fig.1). The matrix lines were the trawl hauls and the columns represent the four adult age classes. The value of the matrix were the abundance of anchovies in each age class. The abundance data was transformed logarithmically ($x' = \log(x+1)$) to reduce the data skewness (5).

![Figure 1: PCA on anchovy abundance at age from 1992 to 2001.](image-url)
The scores of the trawl hauls on the four resulting axes were further classified (using divisive hierarchical clustering based on euclidean distance measure) to distinguish groups within the population. Four distinct groups were detected (Fig.1, thumbnail biplot). Each of these groups can be interpreted as a characteristic sub-population with particular abundance and demographic patterns. The first group (■) is representative of a relatively abundant but ageing population. The second group (◆) correspond to an abundant young population. The third and forth groups (● △) corresponded to low abundance populations of varying demographic quality. The classified trawl hauls were mapped and five zones could be distinguished (Fig.2).

![Figure 2: Spatial projection of classified trawl hauls](image)

The zone A and D were dominated by abundant young populations (●=◆) and coincided with the Adour and Gironde river plumes. The zone B was characteristic of an abundant but aging population (■). The zone C represented a transition from the young population in D to the older population in B. The zone E was more variable both in term of abundance and demography (● ■ ●).
3. Model Structure

Simple growth model
The well known Leslie matrix ($A$) describes the projection of a population from time $t$ to time $t+1$ in terms of the vital rates of each age class.

$$AN_t = N_{t+1} \quad (3.1)$$

Where $N_t$ is a vector describing the age distribution of population at time $t$, $n$ is the number of age class and $t$ is measured in year. $A$ is the population projection matrix

$$A = \begin{pmatrix}
F_1 & \cdots & F_{n-1} & F_n \\
P_1 & \cdots & 0 & 0 \\
\vdots & \ddots & \vdots & \vdots \\
0 & \cdots & P_{n-1} & 0
\end{pmatrix} \quad (3.2)$$

Where $P_n$ is the probability of surviving from the age $n$ until the next age class, $F_n$ is the yearly fertility of an individual aged $n$.

Simple migration model
In the case of two constant populations with migration between them, we denote $p$ and $q$ the proportion of individuals moving from population 1 and 2 respectively. Thus, between $t$ and $t+1$ the migration model can be written as

$$\begin{pmatrix}
N_1 \\
N_2
\end{pmatrix}(t+1) = \begin{pmatrix}
1-p & q \\
p & 1-q
\end{pmatrix}\begin{pmatrix}
N_1 \\
N_2
\end{pmatrix}(t) \quad (3.3)$$

and the total number of individuals does not change over time. This model can easily be extended to $n$-sites and movements may be restricted to neighbouring sites using a random walk process (3).

Coupling growth and migration
The use of discrete time multisite models requires to know the number of individuals aged $n$ in site $k$ at time $t$ and to group them in a column vector $N_t$. Assuming constant parameters, $N_{t+1}$ is obtained from $N_t$ by a transition matrix that generalises the Leslie matrix model. In the case of two populations, each growing according to their own demographic parameters (described in the $A$ and $B$ Leslie matrices respectively), they will grow according to:
\[
\begin{pmatrix}
N_1 \\
N_2
\end{pmatrix}
(t+1) = 
\begin{bmatrix}
1-p & q \\
p & 1-q
\end{bmatrix}
\begin{bmatrix}
A & 0 \\
0 & B
\end{bmatrix}
\begin{pmatrix}
N_1 \\
N_2
\end{pmatrix}
(t)
\]
\[
= 
\begin{bmatrix}
A(1-p) & Bq \\
Ap & B(1-q)
\end{bmatrix}
\begin{pmatrix}
N_1 \\
N_2
\end{pmatrix}
(t)
\]

(3.4)

In the case of a population with 3 age classes, the projection matrix will be in the form of:

\[
\begin{bmatrix}
F_{1,A}(1-p) & F_{2,A}(1-p) & F_{3,A}(1-p) \\
P_{1,A}(1-p) & 0 & 0 \\
0 & P_{2,A}(1-p) & 0
\end{bmatrix}
Bq
\]

(3.5)

If we chose to get the movers of each population to reproduce first into each site and then to migrate, the projection matrix will simplify to the form:

\[
\begin{bmatrix}
F_{1,A} & F_{2,A} & F_{3,A} \\
P_{1,A}(1-p) & 0 & 0 \\
0 & P_{2,A}(1-p) & 0
\end{bmatrix}
B'q
\]

(3.6)

In order to model the anchovy population of the bay of Biscay we have chosen to consider four age classes within the five zones defined earlier and their migratory behaviour between zones. In this model, anchovy do not survive after their third year. Anchovy can be considered as a birth pulse species although their reproduction period sprayed out on 2 to 3 months (6). The birth pulse was assumed to take place immediately after the census date and individuals should enter the population at age 1. The first year mortality \(P_0\) is incorporated into the fertility coefficients (7). However, since the migratory patterns of the newborns appeared essential to the population structure, they constituted an additional age class, that do not reproduce or die (their mortality \(P_0\) being already
taken into account) but do migrate. The recurrence equation for population numbers is, in block matrix notation:

\[
M = \begin{bmatrix}
1 - \sum \text{MIG}_{k,0} & P_1 \text{F}_{k} & P_2 \text{F}_{k} & P_3 \text{F}_{k} \\
0 & 1 - \sum \text{MIG}_{k,1} & 0 & 0 \\
0 & 0 & 1 - \sum \text{MIG}_{k,2} & 0 \\
\text{MIG}_{k-0} & \text{MIG}_{k-1} & \text{MIG}_{k-2} & 0 \\
\text{MIG}_{k-C} & \text{MIG}_{k-D} & \text{MIG}_{k-E} & 0 \\
\text{MIG}_{k-A} & \text{MIG}_{k-B} & \text{MIG}_{k-C} & \text{MIG}_{k-D} \\
\text{MIG}_{k-E} & \text{MIG}_{k-E} & \text{MIG}_{k-E} & \text{MIG}_{k-E} \\
\end{bmatrix}
\]

where the block matrices A, B, C, D and E are the growth models (generalised Leslie matrices) of the 5 zones considered, MIG \( k-l \) are the transition matrices from zone \( k \) to zone \( l \), including the proportion of movers in each age class and their survival rates. The dominant eigenvalue of the matrix \( M \), \( \lambda \), measures the population growth over one year.

\[
MN_t = \lambda N_t = N_{t+1}
\]

The natural logarithm of \( \lambda \) measures the intrinsic rate of increase. The corresponding right eigenvector (\( W \)) is the stable age distribution.

\[
MW = \lambda W
\]

The sensitivity of population growth, \( \lambda \), to the change of any vital rate (\( x \)) can be measured by:

\[
S_x = \frac{\delta \lambda}{\delta x}
\]

When a parameter \( x \) of the model is varied by \( \alpha \% \), the growth rate \( \lambda \) changes by \( \alpha Ex\% \) where \( Ex \) is the elasticity of \( \lambda \) to changes in \( x \).

\[
E_x = \left( x / \lambda \right) S_x
\]

Elasticity is similar to sensitivity, but takes the size of the parameter into account. They both allow to determine which parameters have the greatest impact on population growth.

4. Data available and model parameters determination

Abundance data were available only for seven surveys that did not constitute continuous time series (Fig. 3).
Figure 3: Total biomass distribution of anchovy over the five zones

The model parameters can be determined between any consecutive years but the series available were always, at best, that of a relatively stable population (1993-1994, 2000-2001) or, otherwise, that of a strongly decreasing abundance (1992-1993, 1997-1998). With such year to year variability, the determined population vital rates were highly unbalanced and the corresponding model projections resulted in population extinction within one or more zones or, on the contrary, an unlikely demographic explosion. We chose to present here the asymptotic evolution of a stable average population (Fig. 4) which population abundance was averaged over the seven observed years. Although, such situation does not exist in nature, this model will enable the identification of the most sensitive demographic parameters and help the understanding of the effect of change in the observed parameters.
Fertility determination

Motos (6) described the average fertility per age class of adult anchovy in the bay of Biscay. He determined that the total annual realised fecundity of one year old female anchovy (< 140mm) was 11188 eggs/g and 8750 eggs/g for older females. Based on these information, the individual weight and age of individual fish was required to calculate the fertility rates. Such detailed biometric data existed for five surveys (ERAG94, PELGAS98, PEL00-02). The average weight at age in each trawl haul was calculated and, using Motos results and assuming equal numbers of male and female in the catch, the average fertility per individuals (fertility per females/2) and per age class was calculated. These fertilities were further averaged over each of the five zones and over the five studied years (table 1). Therefore, the fertility rates applied to the model were assumed constant and independent from other population vital rates or structure. The fertility rates were higher in the B, C and E zones and generally increased with age.
Table 1: Age by site anchovy fertility

<table>
<thead>
<tr>
<th>Age</th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
<th>E</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>108385 (35%)</td>
<td>124862 (19%)</td>
<td>111536 (8%)</td>
<td>82405 (30%)</td>
<td>126463 (25%)</td>
</tr>
<tr>
<td>2</td>
<td>103870 (17%)</td>
<td>131231 (14%)</td>
<td>126389 (10%)</td>
<td>82405 (30%)</td>
<td>136295 (13%)</td>
</tr>
<tr>
<td>3</td>
<td>124031 (42%)</td>
<td>148937 (16%)</td>
<td>155121 (8%)</td>
<td>94874 (41%)</td>
<td>146408 (25%)</td>
</tr>
</tbody>
</table>

In the pre-breeding census birth pulse model, the first year mortality $P_o$ must be incorporated into the fertility coefficients so that

$$F'_{k,n,t} = F_{k,n,t} \times P_{k,0,t}$$  \hspace{1cm} (4.1)$$

where $F$ is the fertility, $P$ the survival probability, $k$ the zone, $n$ the age class and $t$ the year.

Mortality determination

The number of newborn anchovies ($N_n$) in any zone ($k$) and any year $t$ was estimated from the number of adults ($N_n$) and from their respective individual fertility ($F_n$).

$$N_{k,0,t} = \sum_{n=1}^{3} F_{k,n,t} \times N_{k,n,t}$$  \hspace{1cm} (4.2)$$

The survival probability $P$ in the zone $k$ from the age class $n$ to age class $n+1$ over the year $t$ was calculated as follow:

$$P_{k,n,t} = \frac{N_{k,n+1,t+1}}{N_{k,n,t}}$$  \hspace{1cm} (4.3)$$

and the global survival probability over all the zones was

$$P_{n,t} = \sum_k N_{k,n+1,t+1} / \sum_k N_{k,n,t}$$  \hspace{1cm} (4.4)$$

The total mortality of any age class $n$, within any zone $k$ and any year $t$ can be determined as follow

$$Z_{k,n,t} = -Ln(P_{k,n,t})$$  \hspace{1cm} (4.5)$$

The resulting total mortality rates are summarised in Table 2.
We found that the mortality rate during the first year of life of anchovy (from birth to adulthood) was very important and equivalent to a survival probability of 0.8 survivors from an initial cohort of 100000 eggs spawned. The mortality rates of one year old anchovy were very variable from zone to zone. Since the large majority of the adult population is between 1 and 2 years old, such differences may have major effect on the population dynamics. The mortality of age class 2 was relatively constant over the 5 zones studied. The natural mortality of anchovy was evaluated at 1.2 therefore our results suggested that the fishing mortality should be approximately 0.7 for this age class which represented about a third of the total mortality. The rare three years old individuals had much higher mortality rates.

The growth model is coupled to a migration model and the survival equation must account for the migration rates. Movers have left the zone and the local mortality is only applied to the stayers. 

$$P'_{k,n,t} = (1 - Mig_{k,n,t}) \times P_{k,n,t} \quad (4.6)$$

$Mig_{k,n,t}$ is the total migration rate of the local population to all other zones and its calculation is developed in the next section.

**Migration determination**

From the abundance data available, it is difficult to distinguish between mortality and migration. No mark-recapture data and no direct observation of migratory flow of the anchovy population were available. Migrations are often deduced from fishing effort displacement (8, 9) but such methods do not permit to distinguish variation in migratory behaviour in the different age class and miss out the first age class. In this study, the migration rates were determined by the observation of differences in the cohort relative distribution from one year to the next. The relative distribution $R_d$ of individuals age $n$ in the zone $k$ and the year $t$ is calculated as:

$$Rd_{k,n,t} = N_{k,n,t} / \sum_k N_{k,n,t} \quad (4.7)$$
The relative migration rate (relative loss of individuals from the zone expressed as a fraction of the total population) is determined as:

$$R_{mig}^{k,n,t} = R_{d}^{k,n+1,t+1} - R_{d}^{k,n,t}$$  \hspace{1cm} (4.8)

This value is negative when individuals are lost from the zone and positive when individuals are gained. To separate the migration rates from the zone $k$ to any other zone $l$, the relative migration rate value is distributed to the closest zone that had gain individuals. However, if this receiving zone had gained less individuals than was lost by the source zone, the remaining individuals are sent to the second closest zone that had gain individuals and so on until all the movers are distributed.

$$R_{mig}^{k,n,t} = \sum_{l} R_{mig}^{k-l,n,t}$$  \hspace{1cm} (4.9)

These migration rates are still expressed as proportion of the total population over the five zones so the absolute migration rate of each zone is equal to:

$$M_{ig}^{k-l,n,t} = R_{mig}^{k-l,n,t} / R_{d}^{k,n,t}$$  \hspace{1cm} (4.10)

And the total proportion of movers leaving any zone $k$ is

$$M_{ig}^{k,n,t} = R_{mig}^{k,n,t} / R_{d}^{k,n,t}$$  \hspace{1cm} (4.11)

The apparent migration patterns of the three first age classes of the average anchovy population in the five pre-defined zones were illustrated in Figure 5. The B, C and E zones contributed a large proportion of the newborns toward the coastal zones A and D, that coincided to the Gironde and Adour river plumes. This apparent migration pattern certainly partly resulted from passive transport processes but also from habitat preferences of juvenile and very young adults. One year old individual displayed an inverted migration pattern and after their first reproductive year, a large proportion of individual moved towards open sea and the South before their second reproduction period. This pattern was similar although much attenuated for the older age class.
The transition matrix must also include the age class mortality. However, some movers may have died before leaving their zone, in their destination zone or on their way there, and it is unclear which mortality rate should be used. Therefore, the global survival probability of each age class over all the considered zones was applied to the movers.

The absolute migration rate including overall survival probability (defined by eq. 4.4) was calculated as follow:

$$Mig^1_{k,n,t} = Mig_{k,n,t} \times P_{n,t}$$ \hspace{1cm} (4.12)

5. Model Projection and analysis

To run and analyse the model presented herein, ULM (Unified Life Models) program, a powerful tool especially designed for discrete time matrix models, was used (10). The asymptotic behaviour of the population projected over 20 years was calculated and plotted. The total numbers of adult in every (Fig. 6) and each zone (Figs 7-11) was shown to oscillate toward stability as a result of strong migration (3). The computed growth rate was 1.01 corresponding to near stability.
Figure 6: Total numbers of adults in the 5 zones

Figure 7: Adult abundance in zone A

Figure 8: Adult abundance in zone B

Figure 9: Adult abundance in zone C
Model Properties

The model matrix was shown to be non negative (all its element are greater than or equal to zero). However, the matrix was reducible as it is often the case in spatially structured populations with one-way dispersal patterns (7). Some habitats may contribute individual to others but not vice versa. In the present case, the zone D contributed individuals to the zone A but the reverse did not occur. Moreover, individuals from zone A were never exchanged with zones C or E. However, in metapopulation model the entire matrix is of interest and cannot be reduced. The long term dynamics of such model may depend on the initial conditions (7).

The dominant eigenvalue ($\lambda_1$) determined the properties of the population growth and the trajectory resulting from the initial condition will grow at a rate equal to $\lambda_1$. The analysis of the present projection matrix showed that $\lambda_1$ was equal to 1.01 thus confirmed the computed growth rate. The intrinsic rate of increase was of 0.01. This result confirmed the near stability of the population modelled. Stability was not achieved due to small approximations in the matrix parameters.

The stable age by site population structure (Table 3) reflected the initial population distribution over the zones (Fig. 4). This confirmed the stability of the structure of population modelled. The age one class was very abundant in the zone D but the age 2 and 3 classes were more abundant in zone B.
Table 3 Stable scaled age by site adult population structure

<table>
<thead>
<tr>
<th>Age class</th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
<th>E</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age class 1</td>
<td>4.0</td>
<td>4.2</td>
<td>8.2</td>
<td>62.1</td>
<td>6.8</td>
</tr>
<tr>
<td>Age class 2</td>
<td>0.8</td>
<td>5.2</td>
<td>3.2</td>
<td>1.3</td>
<td>2.2</td>
</tr>
<tr>
<td>Age class 3</td>
<td>0.1</td>
<td>0.9</td>
<td>0.5</td>
<td>0.2</td>
<td>0.3</td>
</tr>
</tbody>
</table>

**Sensitivity and elasticity analyses**

Sensitivity and elasticity of the population growth ($\lambda$) to variation of the matrix parameters were computed. Overall, the coefficient of variation of $\lambda$ was 0.455 times that of the matrix entries. The sensitivity analysis revealed that variation in the vital rates in the zone D for the 2 first age classes resulted in the largest change in the population growth rate (Table 4).

**Table 4: Sensitivity of $\lambda$ to matrix entries**

<table>
<thead>
<tr>
<th>Sensitivity of $\lambda$ to growth variation ($F'$ defined in eq. 4.1)</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
</tr>
<tr>
<td>---</td>
</tr>
<tr>
<td>Age class 1</td>
</tr>
<tr>
<td>Age class 2</td>
</tr>
<tr>
<td>Age class 3</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Sensitivity of $\lambda$ to survival (including migration) variation ($P'$ defined in eq 4.6)</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
</tr>
<tr>
<td>---</td>
</tr>
<tr>
<td>Age class 0</td>
</tr>
<tr>
<td>Age class 1</td>
</tr>
<tr>
<td>Age class 2</td>
</tr>
</tbody>
</table>

The elasticity of $\lambda$ to changes in the original vital rates were computed (Table 5). These results illustrated the strong elasticity of the present model growth rate in response to first year mortality variation. The vital rates applied to one year old individuals in the zone D, which contributed the most to the total adult population, affected the most the population growth rate. Change in migration rates had little effect on the population growth. However, the migration pattern of the age class 1 appeared to be more important to the population stability than any other age class. The relatively small contribution of the zone A to the total population is also revealed by this analysis.
The population growth rate were relatively unaffected by variation of any vital rates of the sub-population in A.

Table 5. Elasticity of $\lambda$ to vital rates variation

<table>
<thead>
<tr>
<th>Elasticity of $\lambda$ to fertility variation ($F$ defined in Table 1)</th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
<th>E</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age class 1</td>
<td>&lt;0.1 \cdot 10^{-3}</td>
<td>0.013</td>
<td>0.028</td>
<td>0.310</td>
<td>0.050</td>
</tr>
<tr>
<td>Age class 2</td>
<td>&lt;0.1 \cdot 10^{-4}</td>
<td>0.016</td>
<td>0.012</td>
<td>0.006</td>
<td>0.018</td>
</tr>
<tr>
<td>Age class 3</td>
<td>&lt;0.1 \cdot 10^{-5}</td>
<td>0.003</td>
<td>0.002</td>
<td>0.001</td>
<td>0.003</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Elasticity of $\lambda$ to mortality variation ($Z$ defined in eq. 4.5, Table 2)</th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
<th>E</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age class 0</td>
<td>-0.008</td>
<td>-0.419</td>
<td>-0.536</td>
<td>-3.841</td>
<td>-0.887</td>
</tr>
<tr>
<td>Age class 1</td>
<td>&lt;0.1 \cdot 10^{-3}</td>
<td>-0.006</td>
<td>-0.013</td>
<td>-0.022</td>
<td>-0.018</td>
</tr>
<tr>
<td>Age class 2</td>
<td>&lt;0.1 \cdot 10^{-4}</td>
<td>-0.006</td>
<td>-0.004</td>
<td>-0.002</td>
<td>-0.005</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Elasticity of $\lambda$ to site to site migration rates variation ($M_{igkl}$ defined in eq. 4.10, Fig. 5)</th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
<th>E</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age class 0</td>
<td>A</td>
<td>B</td>
<td>C</td>
<td>D</td>
<td>E</td>
</tr>
<tr>
<td>B</td>
<td>-0.0008</td>
<td>0.0014</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C</td>
<td>0.0011</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>E</td>
<td>-0.0065</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Age class 1</td>
<td>A</td>
<td>B</td>
<td>C</td>
<td>D</td>
<td>E</td>
</tr>
<tr>
<td>D</td>
<td>-0.0016</td>
<td>0.0341</td>
<td>0.0198</td>
<td>0.0581</td>
<td></td>
</tr>
<tr>
<td>Age class 2</td>
<td>A</td>
<td>B</td>
<td>C</td>
<td>D</td>
<td>E</td>
</tr>
<tr>
<td>A</td>
<td>0.00035</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>D</td>
<td>-0.00007</td>
<td>-0.00003</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Model sensitivity to initial conditions, the stabilising role of migration

Because the model proposed was reducible, the population structure and projection may depend on initial conditions. Variable initial conditions can be seen as resulting from different environmental conditions that have affected the population structure. The population abundance distributions determined from the seven years of data were used in turn as initial conditions. The population growth rate remained constant ($\lambda=1.01$) and the stable age by site population structure described
earlier (Table 3) was also conserved. Similarly, if any zone was initially set as containing no individuals, the population structure was restored within ten years. Finally, only one reproducing adult in any one zone was required for the asymptotic population structure to be restored after variable time laps (from few years for an individual set in zone D to few centuries for an individual set in zone A). These results illustrated the importance of migration to stabilise the population structure.

**Effect of retention on the first age class**

The migration pattern defined for the first age class supposedly mostly reflected physical processes responsible for the passive transport of anchovy eggs, larvae and juveniles in the bay of Biscay. In order to simulate the possible effect of retention of the first age class within their birth place the migration rates were set to zero. The absence of transport of this age class toward the coast resulted in population extinction in every zones but E (Table 6). In the remaining populated zone the population growth rate was $\lambda=1.05$.

**Table 6: Stable scaled age by site adult population structure resulting from no migration of age class 0**

<table>
<thead>
<tr>
<th></th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
<th>E</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age class 1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>86.4</td>
</tr>
<tr>
<td>Age class 2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>11.8</td>
</tr>
<tr>
<td>Age class 3</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1.8</td>
</tr>
</tbody>
</table>

This result illustrated the importance of the transport processes involved in the apparent migration of the first age class. Although the rate of population increase is more important than in the model including first year migration, the population distribution is reduced to the northern most zone.

**Effect of adult migratory behaviour**

The apparent migration pattern described for the second and third age class probably reflected the migratory behaviour of large adult anchovies in relation of their habitat preferences during the reproduction period. The absence of adult migration corresponding to an alteration of this behaviour was simulated by setting their migration rates to zero. Here again this resulted in population extinction in four of the five zones (Table 7) and in the remaining populated zone, the growth rate was 0.99, indication that even there, the population was not sustainable over very long periods of time.
Table 7: Stable scaled age by site adult population structure resulting from the absence of adult migration

<table>
<thead>
<tr>
<th></th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
<th>E</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age class 1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>94.0</td>
<td>0</td>
</tr>
<tr>
<td>Age class 2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>5.2</td>
<td>0</td>
</tr>
<tr>
<td>Age class 3</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.8</td>
<td>0</td>
</tr>
</tbody>
</table>

Here again this result reflected the importance of adult migratory behaviour to the perpetuation of the population spatial distribution and sustainability. Year to year change in adult migration flows in response to the changing hydrological environment of the bay of Biscay may have strong impacts on the population growth and spatial distribution.

6. Discussion and Conclusion

Standard demographic models, such as Leslie matrices, have been extended to the context of subdivided population and constitute adequate tools to study the dynamics of such population in an empirical context. The high variability of anchovy abundance and distribution in the bay of Biscay led us to consider the study of the dynamics of a stable average population. The study illustrated the large effect of the first year mortality on the population dynamics and confirmed the importance of recruitment for short lived species such as anchovy. A permanent increase of the first year mortality would have resulted in population extinction. On the contrary, a reduction would have resulted in short term population demographic explosion. This study also revealed the importance of the zone D corresponding to the Gironde estuarine where a substantial part of the total spawning population can be found. Changes the first reproducing age class (age class 1) fertility rates or the first age class (age class 0) mortality rates of this sub-population resulted in large variation in the global population growth rate. Therefore, the growth of the modelled population fairly depended on first year mortality and vital rates in zone D.

Although variation in migration rates defined for this stable population did not affect much the population growth rate they had a major role in restoring and maintaining the stable asymptotic population structure. Migratory flows had buffering effects on population trajectory by enabling the transfer of individuals from areas with relatively strong rate of increase to other zones. Migration was also shown to have a cushioning effect over local extinction and permitted the re-colonisation of empty zones. The migration flows of the first age class certainly mostly reflect physical transport of eggs, larvae and juveniles. They were essential in maintaining population structure and their unlikely disappearance resulted in population extinction in four of the five defined zones. Similarly,
large adult apparent migratory behaviour certainly reflected their habitat preferences during the reproduction period and was shown to affect strongly the population distribution.

These results suggested the importance of the bay of Biscay hydrological structures and processes to the anchovy population. The Gironde river plume coincided to zone D, the most abundant and sensitive area to the modelled population dynamic. The first age class mortality may also result directly or indirectly from hydrological variations affecting their environmental condition. Finally, physical transport during the first stages of the anchovy life cycle and habitat preferences of large adults may also be primordial to the perpetuation of population distribution. Therefore, providing that some useful hydrological variables can be linked to variation in the calculated vital rates of the anchovy population, it may be possible to couple the present population model to hydrological model of the bay of Biscay.

7. Perspectives
More abundance data are required to better define model parameters and their evolution through time and varying environmental conditions. Abundance data from 1983, 1984, 1987, 1989, 1990, 1991 and 2002 were made available and will be used jointly to those already available. The fertility rates defined herein were derived from literature and made constant. However, egg counts were undertaken during the three surveys PEL 2000-2002. From these data, fertility will be redefined conjointly with other population parameters and its evolution and effect on population growth during this two year interval will be investigated.

The model parameters will be calibrated using AD model builder, a statistical software allowing the development and statistical inference of model parameters. The optimisation of the parameters is carried out in a stepwise manner and standard deviations of estimated parameters are also produced. The relationships between the parameters variation and environmental condition will be investigated. Ultimately, the population model coupled to its environment will be used to simulate environmental and exploitation scenarios and their effect on anchovy population in the bay of Biscay.
References


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