

# Application of an age-structured model to better understand the fishing effects on a fish population: the case of anchovy fishery in north Aegean waters (E. Mediterranean)

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## Abstract

Anchovy (*Engraulis encrasicolus*) is an important commercial small pelagic fisheries resource in the northern Aegean sea (eastern Mediterranean). The objectives of the paper are to improve our understanding of anchovy population variability under the current harvesting regulations applied for anchovy fishery and explore the impacts of alternate fishing strategies on anchovy survival and annual catches. The model simulates the anchovy biomass by combining a continuous McKendrick-Von Foerster age-structured population dynamics model and an age-specific growth equation which describes anchovy weight. Model results were generally consistent within the field biomass ranges and annual reported catches for the period 2003-2006 and 2008. Fishing scenarios results indicated that: i) the scenario of closing the fishing period during spring can be an alternate management option that could contribute to increase of anchovy biomass without significant change in catches, ii) the imposition of an extra month closure especially in spring is a favorable measure on anchovy variability, iii) measures based on fishing selectivity are time consuming to induce positive results but the protection of older individuals compared to younger ones as applied now, could have a positive effects on the structure of the population. Finally, as a criterion of population survival, we have considered the notation of persistence. The theoretical and numerical consideration of persistence - under the specific model assumptions - indicated that anchovy population can be thought as a viable population, although a different modelling approach would require its reconsideration.

*Keywords:* age structured model, McKendrick-Von Foerster equation, anchovy, Northern Aegean Sea

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## 1. Introduction

Anchovy (*E. encrasicolus*) is an important pelagic fish for commercial fisheries in Greece and one of the main target species in north Aegean sea [26]. In recent years, anchovy stock production show signs of declining and highly fluctuating trend and it is generally recognized that an integrated management system is required although

several regulation measures (closed fishing season for purse-seine fleet, minimum legal landing sizes, mesh size regulation etc) are implemented by policy makers [27].

Understanding population dynamics of fish stocks is essential in developing optimal fisheries management strategies [6]. A task of high practical and ecological significance is the estimation of a fish population reaction to changes in fishing strategy. Fishing mortality can be changed through direct but also indirect methods, such as regulating mesh size to make fish of certain age or size less vulnerable to the gear, area closures and effort limits. The development and application of a harvesting model can serve as a tool for quantitatively synthesize the current knowledge and explore these aspects. In [7], the authors proposed measures for the stock recovery of Kuwait's shrimp fishery, while the effectiveness of closed fishing seasons as a management measure is examined for *Cymbula gratanina* [2].

Several biological processes such as mortality rate and reproduction capacity show significant interannual variations depending on the age structure of a population. The study and application of an age-dependent model is a more realistic representation of a fish population dynamics than simple production models [33].

In this work, we apply an age-structured model to simulate the evolution of anchovy biomass by combining an age-specific growth model which describes anchovy weight and the continuous model of McKendrick-Von Foerster to study the population abundance [15]. Several applications based on the McKendrick-Von Foerster equation can be found in the literature; on fish population [3], on demography [1], on population economics [10]. From these applications, it occurs that the applicability of this kind of model on other species is acceptable.

The objective of this paper is the integration of existing biological and fishery knowledge on anchovy into a unified modelling framework, contributing by this way to better understanding of anchovy population dynamics under the different fishing strategies. The model components are based on specific field data and specific characteristics of anchovy biology and ecology. Using age-specific weight and the available natural mortalities, fishing mortalities and fertilities data, we fitted an age-structured model with available acoustic biomass estimates during the period 2003-2006 and 2008 and reported catches. Long-time series of data on mass and biological parameters of anchovy throughout the Greek waters are incomplete [26]. Although we recognize that the study period is short, we decided to work on this period as the available data are the most recent and reliable.

## 2. Model set up

Fish biomass is a key quantity in stock assessment. Fisheries policy makers usually set their management decisions by the total weight of catch [33]. The fish biomass ( $B_f$ ) is calculated as the product of the mean weight of an individual fish weight ( $W$ ) and the population abundance ( $N$ ),

$$B_f = W \cdot N. \quad (2.1)$$

The importance of considering both growth and mortality functions that vary simultaneously with population density has been recognized [3]. In this section, we describe: 1) the components of the population model through the processes of natural, fishing mortality and reproduction and 2) anchovy weight.

### 2.1. Population model

Motivated by Sánchez [21], the age-structured continuous harvesting population model adopted in this work is a modification of McKendrick model [15] by augmenting the death rate with a harvesting term. The population dynamics of anchovy is described by the following problem:

$$\frac{\partial n(a, t)}{\partial t} + \frac{\partial n(a, t)}{\partial a} = -m(a)n(a, t) - f(a, t)n(a, t), \quad 0 < a < M, \quad t > 0, \quad (2.2a)$$

$$n(0, t) = \int_0^M B(a, t; N)n(a, t)da, \quad t > 0, \quad (2.2b)$$

$$n(a, 0) = n_0(a), \quad 0 \leq a \leq M, \quad (2.2c)$$

$$N(t) = \int_0^M n(a, t)da, \quad t > 0, \quad (2.2d)$$

where

- $n(a, t)$  is the number of individuals of age  $a$  at a particular time  $t$ ,
- $m(a)$  is the natural mortality function following the property:

$$0 < m(a) \leq \bar{m} = \max_a m(a),$$

- $f(a, t)$  is the fishing mortality function coefficient such that

$$f(a, t) = h(a)e(t),$$

which satisfy

$$0 \leq h(a) \leq \bar{h} = \max_a h(a) \quad \text{and} \quad \underline{e} = \min_a e(a) \leq e(t) \leq \bar{e} = \max_a e(a),$$

- $B(a, t; N)$  expresses the birth function assumed to be separable in the variables  $a$ ,  $t$  and  $N = N(t)$ ,

$$B(a, t; N) = b(t)\beta(a)\beta_0(N),$$

such that  $0 < \underline{b} = \inf_t b(t) \leq b(t) \leq \bar{b} = \sup_t b(t)$ ,  $\beta(a)$  has a compact support on  $[0, \infty]$  and  $\beta_0(N(t))$  is a decreasing and bounded function with  $\underline{\beta}_0 = \inf_t \beta_0(N) \leq \beta_0(N(t)) \leq \bar{\beta}_0 = \sup_t \beta_0(N)$ ,

- $n_0(a)$  is the initial age distribution,
- $M$  denotes the maximal age of the species and
- $N(t)$  is the total population at time  $t$ .

#### 2.1.1. Existence of solutions

The standard method to show existence for a first-order, linear partial differential equation like (2.2), is to apply the method of characteristics, determine the characteristics curves in the  $at$ -plane, along which equation (2.2) reduces to an ordinary differential equation [4]. However, when this method is applied, the unknown function  $n(a, t)$  is involved implicitly in the expression of the solution and by using the boundary condition (2.2b) we result to an integral equation [12]. Thus, by specifying the characteristic curves of (2.2), the solution is represented by the following expression

$$n(a, t) = \begin{cases} n(t-a, 0) \exp\left(-\int_0^t (m(s+t) + f(s+a-t, s)) ds\right), & a \geq t, \\ n(0, t-a) \exp\left(-\int_0^a (m(s+t-a) + f(s, s+t-a)) ds\right), & a \leq t. \end{cases} \quad (2.3)$$

Substituting the two expressions of  $n(a, t)$  into the boundary condition (2.2b) we obtain the integral form

$$\begin{aligned} n(0, t) = \int_0^M B(a, t; N)n(a, t)da = & b(t)\beta_0(N(t)) \int_0^t \beta(a)n(0, t-a)G(a, t)da \\ & + b(t)\beta_0(N(t)) \int_t^M \beta(a)n(t-a, 0)F(a, t)da, \end{aligned} \quad (2.4)$$

where

$$G(a, t) = \exp\left(-\int_0^t (m(s+t) + f(s+a-t, s)) ds\right) \quad (2.5)$$

and

$$F(a, t) = \exp\left(-\int_0^a (m(s+t-a) + f(s, s+t-a)) ds\right). \quad (2.6)$$

Thus, the solution of (2.2) lies to the solution of the integral equation (2.4) which constitutes the basis for analytical results and some numerical methods. As the study of stability in non autonomous problems, as (2.2), is quite complicated, we focus our attention to a more biological stability aspect, called persistence.

### 2.1.2. Persistence

Persistence has emerged as a relevant stability concept for population models. Although its questionable credibility, it is recognized as an indicator of a long term population survival [4]. A brief mathematical definition of the persistence term is illustrated below:

1. A population  $n(a, t)$  which is described by the system (2.2) is said to be persistent if  $\liminf_{t \rightarrow \infty} n(a, t) > 0$ ,
2. If  $\limsup_{t \rightarrow \infty} n(a, t) = 0$ , then we say that the population goes to extinction.

For the study of persistence for (2.2) we will recall the comparison technique applied in [18].

We consider again the original system (2.2) and the two auxiliary ones (for comparison purposes).

$$\begin{aligned} \frac{\partial n(a, t)}{\partial t} + \frac{\partial n(a, t)}{\partial a} &= -(m(a) + h(a)e(t))n(a, t), \quad 0 < a < M, \quad t > 0, \quad (2.7) \\ n(0, t) &= b(t)\beta_0(N) \int_0^M \beta(a)n(a, t)da, \quad t > 0, \\ n(a, 0) &= n_0(a), \quad 0 \leq a \leq M. \end{aligned}$$

$$\begin{aligned} \frac{\partial \underline{n}(a, t)}{\partial t} + \frac{\partial \underline{n}(a, t)}{\partial a} &= -(m(a) + \bar{e}h(a))\underline{n}(a, t), \quad 0 < a < M, \quad t > 0, \quad (2.8) \\ \underline{n}(0, t) &= \underline{b}\underline{\beta}_0 \int_0^M \beta(a)\underline{n}(a, t)da, \quad t > 0, \\ \underline{n}(a, 0) &= \underline{n}_0(a), \quad 0 \leq a \leq M, \quad \text{such that} \\ \underline{n}_0(a) &\leq n_0(a), \quad 0 \leq a \leq M. \end{aligned}$$

$$\begin{aligned}
\frac{\partial \bar{n}(a, t)}{\partial t} + \frac{\partial \bar{n}(a, t)}{\partial a} &= -(m(a) + \underline{e}h(a))\bar{n}(a, t), \quad 0 < a < M, \quad t > 0, \quad (2.9) \\
\bar{n}(0, t) &= \bar{b}\bar{\beta}_0 \int_0^M \beta(a)\bar{n}(a, t)da, \quad 0 \leq a \leq M, \quad t > 0, \\
\bar{n}(a, 0) &= \bar{n}_0(a), \quad 0 \leq a \leq M, \quad \text{such that} \\
n_0(a) &\leq \bar{n}_0(a), \quad 0 \leq a \leq M.
\end{aligned}$$

The two auxiliary systems constitute the lower and upper solution of the system (2.7). By an upper (lower) solution to (2.7) we define a function  $\bar{n}$  ( $\underline{n}$ ) which satisfies (2.7) by substituting  $\geq$  ( $\leq$ ) for the sign of  $=$ .

Concerning the relationship between the solutions of the three systems (2.7), (2.8) and (2.9), the following theorem holds

**Theorem.** *Let  $\underline{n}(a, t)$ ,  $n(a, t)$  and  $\bar{n}(a, t)$  be the solutions of the systems (2.7), (2.8) and (2.9) respectively. Then,  $\underline{n}$  is a lower solution,  $\bar{n}$  is an upper solution to problem (2.7) and hold:*

$$\underline{n}(a, t) \leq n(a, t) \leq \bar{n}(a, t). \quad (2.10)$$

The proof is a review of the steps proved by Li [18] with slight modifications customized for the present study. For the proof of theorem, see Appendix A.1.

For the study of persistence we search for separate solution of the form  $\underline{n}(a, t) = A(a)T(t)$ , following [4]. Substituting this form into equation (2.8) and dividing by  $A(a)T(t) \neq 0$ , we obtain

$$\frac{T'(t)}{T(t)} = -\frac{A'(a)}{A(a)} - (m(a) + \bar{e}h(a)) = r. \quad (2.11)$$

Because the left hand side of the equation is only a function of  $t$  while the right hand depends only on  $a$ , each side is equal to a constant  $r$ . Using a known result from Hoppensteadt [12], if we solve the two separate differential equations for  $T(t)$  and  $A(t)$ , then the solution  $n(a, t) = A(a)T(t)$  satisfies the boundary condition of problem (2.8) which takes the form

$$\bar{b}\bar{\beta}_0 \int_0^M b(a)e^{-ra} \exp\left(-\int_0^a (m(s) + \bar{e}h(s))ds\right) da = 1. \quad (2.12)$$

If we let

$$\underline{\phi}(r) = \bar{b}\bar{\beta}_0 \int_0^M b(a)e^{-ra} \exp\left(-\int_0^a (m(s) + \bar{e}h(s)) ds\right) da, \quad (2.13)$$

we obtain the following properties:  $\lim_{r \rightarrow \infty} \underline{\phi}(r) = 0$ ,  $\lim_{r \rightarrow -\infty} \underline{\phi}(r) = \infty$  and  $\underline{\phi}(r)$  is decreasing on  $(-\infty, \infty)$  since

$$\underline{\phi}'(r) = -a\bar{b}\bar{\beta}_0 \int_0^M b(a)e^{-ra} \exp\left(-\int_0^a (m(s) + \bar{e}h(s)) ds\right) da < 0.$$

From those properties we derive that the integral equation  $\underline{\phi}(r) = 1$  has a unique solution  $\underline{r}$ . If the solution of (2.12) is  $\underline{r}$  then  $\underline{n}(a, t)$  has a separable solution of the form

$$\underline{n}(a, t) = \underline{C}e^{\underline{r}(t-a)} \exp\left(-\int_0^a (m(s) + \bar{e}h(s)) ds\right). \quad (2.14)$$

In a similar way, we get the integral condition for  $\bar{n}(a, t)$ ,

$$\bar{b}\bar{\beta}_0 \int_0^M b(a)e^{-ra} \exp\left(-\int_0^a (m(s) + \underline{e}h(s)) ds\right) da = 1, \quad (2.15)$$

with upper solution

$$\bar{n}(a, t) = \bar{C} \exp(\bar{r}t) \exp(-\bar{r}a - \int_0^a (m(s) + \underline{e}h(s)) ds), \quad (2.16)$$

and

$$\bar{\phi}(r) = \bar{b} \bar{\beta}_0 \int_0^M b(a) e^{-ra} \exp\left(-\int_0^a (m(s) + \underline{e}h(s)) ds\right) da. \quad (2.17)$$

Combining (2.10) and the two expressions for the lower  $\underline{n}(a, t)$  and upper solutions  $\bar{n}(a, t)$  of (2.7), we obtain

$$\begin{aligned} \underline{C} e^{\underline{r}(t-a)} \exp\left(-\int_0^a (m(s) + \bar{e}h(s)) ds\right) &\leq n(a, t) \leq \\ &\leq \bar{C} e^{\bar{r}(t-a)} \exp\left(-\int_0^a (m(s) + \underline{e}h(s)) ds\right). \end{aligned} \quad (2.18)$$

It is obvious that if  $\underline{r} > 0$  then from the left hand side of the inequality (2.18) it follows that the population  $n(a, t)$  is persistent, while for  $\bar{r} < 0$  the right hand side of inequality tends to zero which means that the population goes to extinction, provided in both cases that  $t \gg 1$ . In section 4, we calculate numerically the values  $\underline{r}$  and  $\bar{r}$ .

## 2.2. Fish growth model

Growth of fish is a complex process that depends on density-dependent (via changes of food availability, vital space) and environmental factors (i.e. temperature, oxygen concentration of the water) [31]. Due to the lack of information of how anchovy weight is affected by these factors, we adopt a simple growth function where the related parameters for anchovy are available and well studied.

The fish growth  $W(a)$  is estimated using a widely applied model to describe growth in length in fishery applications, the Von Bertalanffy growth equation [8]

$$L(a) = L_{\max} - (L_{\max} - L_0) e^{k_n(a-a_0)}, \quad (2.19)$$

where  $L(a)$  is the length of fish age  $a$ ,  $L_{\max}$  is the asymptotic length,  $L_0$  is the length at birth,  $k_n$  a curvature parameter and  $a_0$  is the hypothetical age at birth. Growth in weight - assuming a stochastic variation in order to incorporate environmental effects- can be derived from the power relation between fish weight and length,

$$W(a) = a_w L(a)^{b_w} \cdot e^\varepsilon, \quad (2.20)$$

where  $\varepsilon$  is a multiplicative error with mean 0 and variance  $\sigma^2$  (set 0.01).

Substituting von Bertalanffy's equation (2.19) into equation (2.20) the weight of fish with age  $a$  is represented by the equation

$$W(a) = a_w \left( L_{\max} - (L_{\max} - L_0) e^{-k_n(a-a_b)} \right)^{b_w} \cdot e^\varepsilon. \quad (2.21)$$

The parameters  $L_{\max} = 180$  mm,  $k_n = 0.587$  years<sup>-1</sup>,  $a_0 = -0.846$  years are provided from Stergiou and Karachle [29]. The parameters  $a_w$  and  $b_w$  take the values  $a_w = 0.0000011$  gr cm<sup>-1</sup>,  $b_w = 3.364$  (dimensionless) (unpublished data, 2007),  $L_0 = 3.5$  mm and  $a_b = 0.013$  years. For simplicity and due to no detailed data, we consider the same equation for both sexes.

### 3. Data function estimates

In this section, we define the data function forms for the population model (2.2): natural mortality  $m(a)$ , fishing mortality  $f(a, t)$ , birth function  $B(a, t; N)$ , initial distribution  $n_0(a)$  and determine their parameters by fitting to the available data. In an effort to handle the data for the period 2003-2008 we decided to work with average values of the biological parameters (e.g fecundity, spawning frequency, natural and fishing mortality) in order to be able to have a easier understanding of the importance of each parameter. In case of incomplete data, parameter values from other areas or related species were imposed.

#### 3.1. Natural mortality function $m(a)$

Natural mortality is a significant factor in fish population dynamics. A qualitative pattern of natural mortality (often called bathtub) indicates that natural mortality is not constant throughout the life cycle of a fish, [5]. According to the bathtub pattern, natural mortality of a fish is extremely high at its early stages. Afterwards, it starts decreasing during the pre-adult stages while a stable death rate is noticed during middle age. An increased death rate comes back at the older fish age. In the present work, we follow the above concept as the available data verify this pattern.

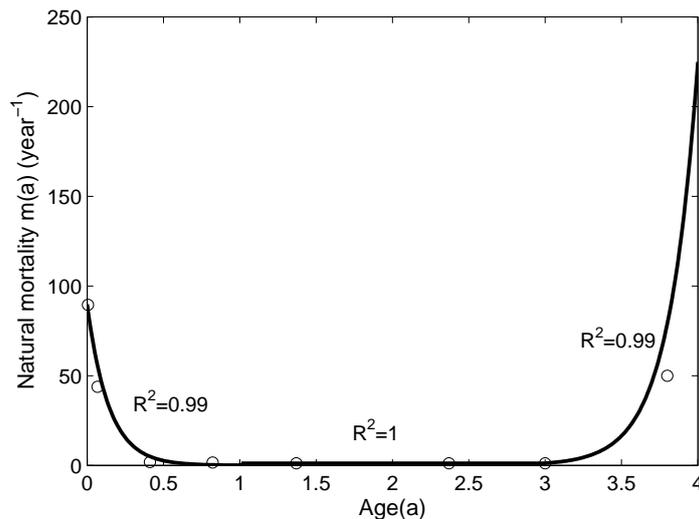


Figure 1: Piecewise fitted natural mortality function  $m(a)$  (continuous line) on the available data (open circles). Age is in units of years.

The piecewise continuous function constructed to describe the natural mortality rate of anchovy,  $m(a)$  as a function of age  $a$  is shown in Figure 1. An exponential fitting using the least square criterion is applied to the data of pre-adult stages: embryonic stage ( $m = 89.49 \text{ year}^{-1}$ ) (Pers. Commun. with S. Somarakis), larval stage ( $m = 43.8 \text{ year}^{-1}$ ) (Somarakis and Nikolioudakis [28]), juvenile stage ( $m = 1.82 \text{ year}^{-1}$ ) (Perterra et al., [23]). For the adult stages from age 1 to 3, we assumed a constant natural mortality rate ( $m = 1.20 \text{ year}^{-1}$ ) (Giannoulaki et al., [11]) and an

exponential fitting for ages 3 to 4 years is implemented. The mathematical formulation of the mortality function  $m(a)$  is as follows,

$$m(a) = \begin{cases} m_1 e^{-\ell_1 a}, & 0 < a < 1, \\ m_2, & 1 \leq a \leq 3, \\ m_3 e^{\ell_3 a}, & 3 < a \leq 4. \end{cases} \quad (3.22)$$

with  $m_1 = 88.91 \text{ year}^{-1}$ ,  $\ell_1 = 7.028 \text{ year}^{-1}$ ,  $m_2 = 1.2045 \text{ year}^{-1}$ ,  $m_3 = 1.833 \cdot 10^{-7} \text{ year}^{-1}$  and  $\ell_3 = 5.232 \text{ year}^{-1}$ .

### 3.2. Fishing mortality function $f(a, t)$

The fishing mortality  $f(a, t)$  is separated into an effect of age  $h(a)$  and time  $e(t)$

$$f(a, t) = h(a) e(t), \quad (3.23)$$

where the function  $h(a)$  represents the variation of fishing mortality due to age and  $e(t)$  a function that incorporates the presence or not of a closed fishing season (set to 0 if the time is closed to fishing, set to 1 if fishing occurs in that time) following the idea of [2].

For the construction of  $h(a)$ , we use average fishing mortality values of the period 2003-2008 for the different age groups: for age-1 ( $d = 0.14 \text{ year}^{-1}$ ), age-2 ( $d = 0.13 \text{ year}^{-1}$ ), age-3 ( $d = 1.15 \text{ year}^{-1}$ ) and a small value for age-3+ ( $d = 0.01 \text{ year}^{-1}$ ) provided by [11]. A quadratic polynomial least square fitting ( $R^2 = 0.96$ ) is applied for these parameter values as shown in Figure 2. Anchovies with age less than 0.9 year are not practically part of fishing stock due to no commercial interest, so harvesting function  $h(a)$  is zero for these ages. Also, fishing mortality has no meaning for fishes more than 4 years, as a maximum life span of  $M = 4$  years is assumed for anchovy [26]. Synoptically,  $h(a)$  has the form,

$$h(a) = \begin{cases} 0, & 0 < a < 0.9, \\ d_1 a^2 + d_2 a + d_3, & 0.9 \leq a \leq 4, \end{cases} \quad (3.24)$$

with  $d_1 = -0.575 \text{ year}^{-3}$ ,  $d_2 = 2.821 \text{ year}^{-2}$  and  $d_3 = -2.09 \text{ year}^{-1}$ .

In anchovy fishery, fishing activity shows a seasonal variation during the year. Particularly, a fishing effort limitation is implemented from December to March for purse seine fleet [26]. This means that the fishing mortality is zero during this period. Thus,  $e(t)$  is set zero for December to March and 1 elsewhere:

$$e(t) = \begin{cases} 0, & 0 < t < t_1, \\ 1, & t_1 \leq t \leq t_2, \\ 0, & t_2 \leq t \leq 1, \end{cases}$$

where  $t_1 = 0.25 \text{ year}$ ,  $t_2 = 0.91 \text{ year}$ .

### 3.3. Birth function $B(a, t; N)$

The birth function  $B(a, t; N)$  is modelled by the product of three functions separable in the variables  $a$ ,  $t$  and  $N$ ,

$$B(a, t; N) = \beta(a)b(t)\beta_0(N), \quad (3.25)$$

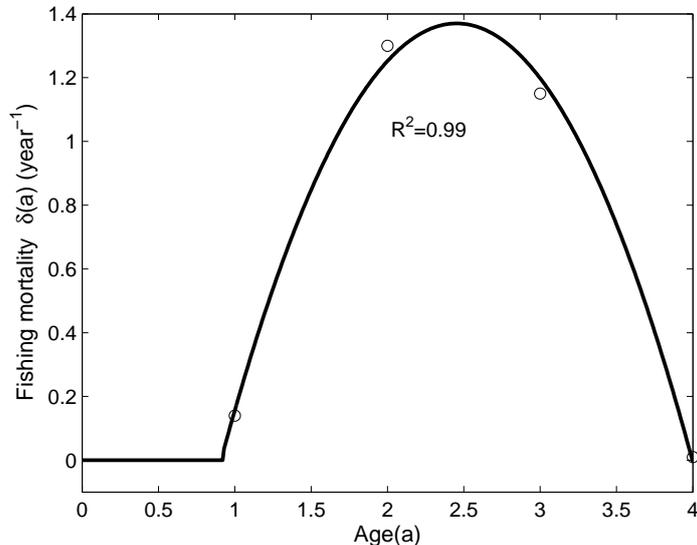


Figure 2: Fitted fishing mortality function  $h(a)$  (continuous line) on the available data (open circles). Age 0 to 0.9 year fish does not lie into fishing pressure due to no commercial interest. Age is in units of years.

where  $\beta(a)$  characterizes the average number of eggs laid by a female during one batch,  $b(t)$  express the daily spawning frequency (the ratio of spawning females to all females) and  $\beta_0(N)$  is a proportional term which describes the effect of the population density on fertility.

Anchovy fecundity (number of eggs produced per female) is usually proportional to its weight [25], i.e., if the eggs are of the same size, bigger fish are usually more fecund than smaller ones. Sexual maturity is accomplished with the completion of its first year of anchovy's life [26]. This means that the age group from 0 to 1 is not a part of the parental population. Therefore, taking into account the biological characteristic of anchovy's reproduction strategy, we assume that the number of eggs produced by an individual female fish is implicitly related to its age  $a$  via its weight,

$$\beta(a) = \begin{cases} 0, & 0 < a < 1, \\ fec \cdot W(a), & 1 \leq a \leq 4, \end{cases} \quad (3.26)$$

where  $fec$  is the batch fecundity (number of eggs produced per gr of female) and  $W(a)$  the weight in gr of a mature female. We imposed the average value  $fec = 320$  for the batch fecundity from estimates in Somarakis et al [27].

Natural birth rates are often markedly seasonal due to several factors. These can be due to such things as exposure to seasonal weather patterns, resource availabilities and population interactions [9]. Anchovy exhibits an extended spawning activity mainly from May to September with a variable reproductive rate which is closely associated with prey-fields and environmental factors [26]. Estimates of spawning frequency in June (the peak of reproductive period) indicated a range from 0.34 to 0.44 [27]. Choosing a value within this range as a peak value for June, we assumed a normal

distributed function form to represent the proportion of active spawning population that reproduces during a year,

$$b_0(T) = k_1 \left( 1 - \frac{(T - k_2)^2}{(T - k_2)^2 + k_3} \right), \quad T \in [0, 1], \quad (3.27)$$

where  $k_1 = 0.42$ ,  $k_2 = 0.5$  year,  $k_3 = 0.04$  year<sup>-2</sup> and  $b_0(0) = b_0(1)$ . The fertility function  $b(t)$  in (2.2b) is a continuous function composed by the function  $b_0(t) \in C^1([0, 1])$ . Particularly,  $b(t) = b_0(t - k)$ ,  $k = 0, 1, 2, \dots$ . So,  $\underline{b} \leq b(t) \leq \bar{b}$ ,  $t > 0$ . For the needs of the numerical simulation the time dependent part of birth function is also calculated as  $b(t) = b_0(t)$ ,  $t = \text{mod}(T, 1)$ . The graph form of  $b_0(t)$  is represented in Figure 3.

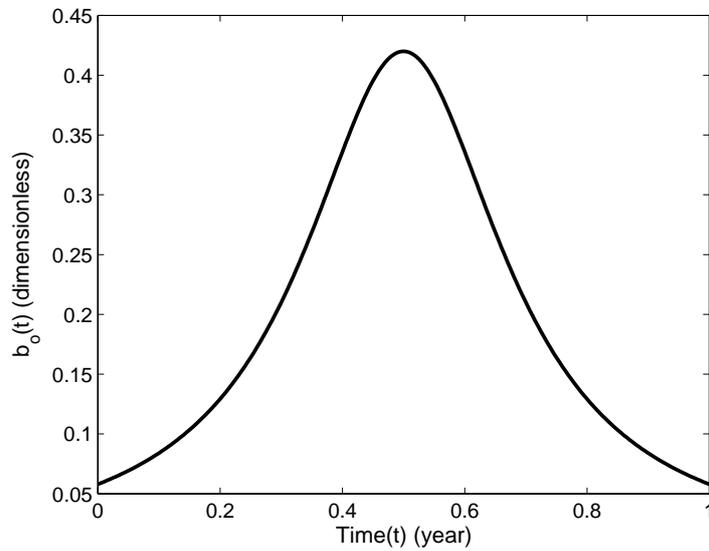


Figure 3: The time dependent part of birth function during a year,  $b_0(t)$ .

Finally, we chose a decreasing function  $\beta_0(N)$  of the total population density  $N(t)$  inspired by Kostova and Chihev [16], to represent the proportion of birth rate variation due to the density effects. More precisely,

$$\beta_0(N) = \frac{W^*}{k_0 + (1 - k_0)e^{-k_c N}}, \quad (3.28)$$

where  $k_0, k_c, W^* > 0$  constants. Obviously as  $N \rightarrow \infty$ ,  $\beta_0(N)$  saturates at  $W^*/k_0$ .

We allowed a variation of fertility by 10% due to population density interactions. For this reason we set  $W^* = 1$  and  $k_0 = 1.1$ . The choice of parameter  $k_c$  which describes the convexity of the curve was manually chosen,  $k_c = 0.2$ .

#### 3.4. Initial distribution $n_0(a)$

The determination of initial distribution  $n_0(a)$  is based on population abundance estimates for age-1, age-2 and age-3 groups during summer season as given in [11].

By age-1 group, we define fish of age within 1-2 years old, age-2 group includes fishes with age 2-3 years old and fish with age 3-4 years old are included in the age-3 group. For reducing the great uncertainty on estimation of the initial values for age-0 group (fish with age 0-1 years old) during June, we start the model run in January. Because of no significant reproduction activity during winter, it is acceptable to impose an indicative number of individuals for age 0-0.5 years old ( $n_1$ ) in January without great error. Assuming a 6-month shift of the summer data, the age-1 group will shift to age range 0.5-1.5 years old ( $n_2$ ), age-2 group to age range 1.5-2.5 years old ( $n_3$ ) and age-3 to age range 2.5-3.5 years old ( $n_4$ ). For age 3.5-4.0 years ( $n_5$ ) we assumed an indicative value as this group is considered negligible. Keeping a constant average ratio of the most abundant population abundance ( $n_2$ ) with each other age range:  $\frac{n_1}{n_2} = n_{1,2}$ ,  $\frac{n_2}{n_2} = n_{2,2}$ ,  $\frac{n_3}{n_2} = n_{3,2}$ ,  $\frac{n_4}{n_2} = n_{4,2}$ ,  $\frac{n_5}{n_2} = n_{5,2}$  as estimated from the available data (Giannoulaki et al. [11]), we calibrated the initial value of ( $n_2$ ) to fit with the biomass estimates. The values of  $n_{1,2}$ ,  $n_{2,2}$ ,  $n_{3,2}$ ,  $n_{4,2}$ ,  $n_{5,2}$  are estimated  $n_{1,2} = 0.05$ ,  $n_{2,2} = 1$ ,  $n_{3,2} = 0.46$ ,  $n_{4,2} = 0.07$ ,  $n_{5,2} = 0.0145$ , see [11].

We must note that one possible choice of determining the initial distribution could be done by using the values of one year. This assumption would lead to misleading. The reason is that there is great variability of available data from year to year. For example, estimates for age-1 group range between  $1148.1 \cdot 10^6$  for 2002 to  $5524.9 \cdot 10^6$  individuals for 2006. The initial distribution for the problem is represented in Figure 4.

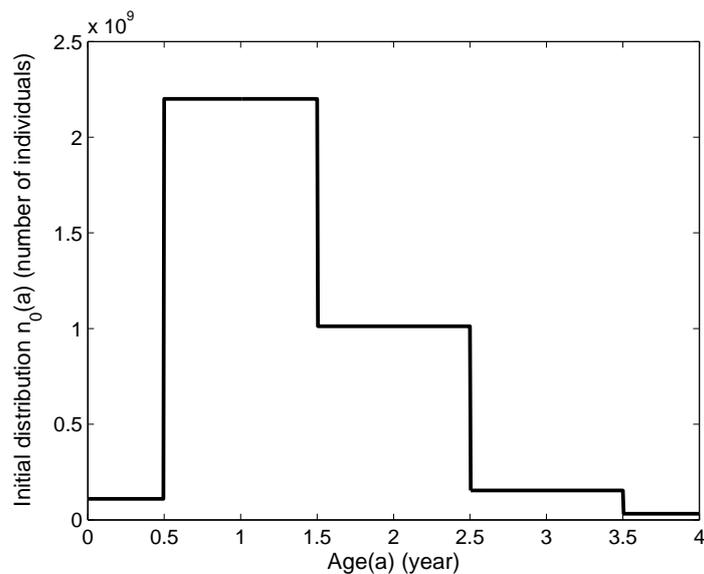


Figure 4: Initial distribution  $n_0(a)$ .

#### 4. Design of simulations

*Biomass and catch.* The total biomass of anchovy  $B(t)$  at time  $t$  is calculated by the product of weight  $W(a)$  and population abundance  $n(a, t)$  through the integral

$$B(t) = \int_{M_0}^M W(a)n(a, t)da, \quad a \geq M_0. \quad (4.29)$$

For comparison with the available biomass data we eliminate the first stages of anchovy and the lower part of the integral starts from a middle-adult fish age, namely  $M_0 = 0.5$  year.

Also, a generalized Baranov equation is used to simulate the anchovy catches in number, see [24],

$$c_n(a, t; \Delta t) = \frac{f(a, t)}{m(a) + f(a, t)} n(a, t) \times (1 - \exp(-(m(a) + f(a, t))\Delta t)), \quad (4.30)$$

where  $c_n(a, t; \Delta t)$  is the catch in number of fish of age  $a$  at time  $t$  effected in a small time interval  $[t, t + \Delta t]$  of length  $\Delta t$ .

Yield (mass) for each age  $a$  at the time interval  $[t, t + \Delta t]$  can be determined as a product of the catch in numbers from equation (4.30) and the weight mass (2.20),  $Y(a, t; \Delta t) = c_n(a, t; \Delta t) W(a)$ . The total yield  $Y(t; \Delta t)$  at the time interval  $[t, t + \Delta t]$  is estimated by integrating the equation (4.30) with respect to  $a$ ,

$$Y(t; \Delta t) = \int_{a_0}^M c_n(a, t; \Delta t) W(a)da. \quad (4.31)$$

*Normalization.* In order to solve numerically the problem we proceed initially in the nondimensionalization of it. We scale the variables of problem (2.2a) in the following way: we normalize  $n$ , by setting  $u = \frac{n}{n_c}$ , for  $n_c = \max\{n_0(a), 0 < a < M\}$ . Also we set  $\alpha = \frac{a}{a_c}$  and  $\tau = \frac{t}{t_c}$  where  $\alpha, \tau$  are the dimensionless age and time respectively. Then, problem (2.2) for  $\tau > 0$  takes the form

$$\frac{\partial u(\alpha, \tau)}{\partial \tau} + c \frac{\partial u(\alpha, \tau)}{\partial \alpha} = -\mu(\alpha)u(\alpha, \tau) - \psi(\alpha, \tau)u(\alpha, \tau), 0 < \alpha < \bar{M}, \quad (4.32a)$$

$$u(0, \tau) = \int_0^{\bar{M}} \gamma(\alpha, \tau, \bar{N}(\tau))u(\alpha, \tau)d\alpha, \quad (4.32b)$$

$$u(\alpha, 0) = u_0(\alpha), \quad 0 < \alpha < \bar{M}, \quad (4.32c)$$

$$\bar{N}(\tau) = \int_0^{\bar{M}} u(\alpha, \tau)d\alpha, \quad (4.32d)$$

where  $\mu, \psi$  are the dimensionless natural and fishing mortality respectively,  $c = t_c/a_c$ ,  $\gamma$  is the birth rate,  $\bar{N} = N/(n_0 \cdot \bar{M})$  the normalized total population and  $\bar{M} = M/a_c$  the scaled upper age limit. Choosing  $a_c = t_c = 1$  year we have that  $c = 1$  which we will use in the rest of our analysis.

More specifically we have that

$$\mu(\alpha) = \begin{cases} \mu_1 e^{-\lambda_1 \alpha}, & 0 < \alpha < 1, \\ \mu_2, & 1 \leq \alpha \leq 3, \\ \mu_3 e^{\lambda_3 \alpha}, & 3 < \alpha \leq 4, \end{cases} \quad (4.33)$$

with  $\mu_1 = t_c \cdot m_1$ ,  $\mu_2 = t_c \cdot m_2$ ,  $\mu_3 = t_c \cdot m_3$ ,  $\lambda_1 = a_c \cdot \ell_1$ ,  $\lambda_3 = a_c \cdot \ell_3$ . Also regarding the fishing mortality  $\psi(\alpha, \tau) = \delta(\alpha) \cdot \varepsilon_0(\tau)$  we have

$$\delta(\alpha) = \begin{cases} 0, & 0 < \alpha < 1, \\ -\delta_1 a^2 + \delta_2 a - \delta_3, & 1 \leq \alpha \leq 4, \end{cases} \quad (4.34)$$

with  $\delta_1 = t_c \cdot d_1 \cdot a_c^2$ ,  $\delta_2 = t_c \cdot d_2 \cdot a_c$  and  $\delta_3 = t_c \cdot d_3$  and

$$\varepsilon_0(\tau) = \begin{cases} 0, & 0 \leq \tau \leq \tau_1, \\ 1, & \tau_1 \leq \tau \leq \tau_2, \\ 0, & \tau_2 \leq \tau \leq 1, \end{cases} \quad (4.35)$$

with  $\tau_1 = t_1/t_c$  and  $\tau_2 = t_2/t_c$ . Regarding the dimensionless birth rate,  $\Gamma(\alpha, \tau; \bar{N}) = \gamma_1(\alpha)\gamma_2(\tau)\gamma_3(\bar{N})$ , we have

$$\gamma_1(a) = \begin{cases} 0, & 0 < \alpha < 1, \\ \beta_0 \cdot w(\alpha), & 1 \leq \alpha \leq 4, \end{cases}$$

with  $\beta_0 = fec$  and

$$w(\alpha) = a_w \left( L_{\max} - (L_{\max} - L_0) e^{-\kappa_n(\alpha - \alpha_0)} \right)^{b_w} \cdot e^\varepsilon,$$

for  $\kappa_n = k_n \cdot a_c$ ,  $\alpha_0 = a_0/a_c$ . Note also that

$$\gamma_2(\tau) = \beta_1 \left( 1 - \frac{(T - \beta_2)^2}{(T - \beta_2)^2 + \beta_3} \right),$$

with  $\beta_1 = k_1$ ,  $\beta_2 = k_2/t_c$ ,  $\beta_3 = k_3/t_c^2$  and  $T = \text{mod}(\tau, 1)$ . In addition,

$$\gamma_3(\bar{N}) = \frac{W^*}{k_0 + (1 - k_0) e^{-(k_c \cdot n_0) \bar{N}}}.$$

*Numerical scheme.* We will apply an upwind scheme in order to obtain a numerical solution for the problem. We introduce a spatial grid  $\alpha_j = j\Delta\alpha$ ,  $j = 0, 1, \dots, J$ , where  $\Delta\alpha = \bar{M}/J$  is the mesh size and  $J$  is a positive integer. We also consider a fixed time interval  $0 \leq \tau \leq T_f$ . The step length in time is denoted by  $\Delta\tau$  and  $t_i = i\Delta\tau$ ,  $i = 0, 1, 2, \dots, N_f$ , with  $N_f = \lceil T_f/\Delta\tau \rceil$ , are the discrete time levels. Also  $\sigma = \frac{\Delta\tau}{\Delta\alpha}$ .

For a time step  $\Delta\tau$  and a spatial step  $\Delta\alpha$  we consider the element:  $u^i = (u_0^i, u_1^i, \dots, u_J^i) \in \mathbb{R}^{J+1}$  and  $u_j^i \simeq u(\alpha_j, t_i)$  is the approximation to the exact solution  $u(\alpha_j, t_i)$  of the problem (2.2) at the point  $(\alpha_j, t_i)$ . Also we use the notations  $I(u^i) := \int_0^{\bar{M}} \gamma(\alpha, t_i) u(\alpha, t_i) d\alpha$ . By  $I_h$  we denote the numerical approximation of  $I$ , that is  $I_h(u^i) = \sum_{j=0}^{J''} \Delta\alpha \gamma(\alpha_j, t_i, N_i) u_j^i$  where the '' means that the first and last terms of the sum are halved, i.e. the trapezoidal rule is used. An upwind scheme

applied to problem (2.2a-2.2d), for  $i = 0, 1, 2, \dots, N_f$  and  $j = 1, \dots, J$  gives:

$$u_j^{i+1} = u_j^i - \sigma c \left( u_j^i - u_{j-1}^i \right) + (\Delta\tau) (\mu(\alpha_j) + \delta(\alpha_j)\varepsilon(\tau_i)) u_j^i, \quad (4.36a)$$

$$u_0^{i+1} = I_h(u^i), \quad (4.36b)$$

$$u^0 = (u_0(\alpha_1), \dots, u_0(\alpha_j)), \quad (4.36c)$$

$$\bar{N}^i = \sum_{j=0}^{J''} (\Delta\alpha) u_j^{i-1}, \quad (4.36d)$$

$$\bar{B}^i = \sum_{j=0}^{J''} (\Delta\alpha) u_j^{i-1} w(a_j), \quad (4.36e)$$

$$C_{\Delta\tau}^i = C_{\Delta\tau}^{i-1} + \sum_{j=0}^{J''} \Delta\alpha \frac{\delta(\alpha_j)\varepsilon(\tau_i)}{\delta(\alpha_j)\varepsilon(\tau_i) + \mu(\alpha_j)} u_j^{i-1} \times \\ (1 - \exp(-\delta(\alpha_j)\varepsilon(\tau_i) - \mu(\alpha_j))\Delta\tau). \quad (4.36f)$$

*Numerical Simulations.* In the next section we present the results of numerical experiments by means of the upwind method. The method was implemented in Matlab programs using double precision arithmetic. The parameters for the various constants appearing in the model are evaluated in the following way:  $\mu_1 = 88.91$ ,  $\mu_2 = 1.2045$ ,  $\mu_3 = 1.833 \cdot 10^{-7}$ ,  $\lambda_1 = 7.028$ ,  $\lambda_2 = 5.232$ ,  $\delta_1 = -0.575$ ,  $\delta_2 = 2.821$ ,  $\delta_3 = -2.09$ ,  $t_1 = 0.25$ ,  $t_2 = 0.91$ ,  $\beta_1 = 0.42$ ,  $\beta_2 = 0.5$ ,  $\beta_3 = 0.04$ ,  $\kappa_0 = 0.5870$ ,  $\alpha_0 = -0.8460$ ,  $b_w = 3.364$ ,  $W^* = 1$ ,  $k_0 = 1.1$ ,  $k_c = 0.2$ ,  $\bar{M} = 4$ . Also it is taken that the normalized initial distribution of the population is  $u_0(\alpha) = u_c = 1$  where  $u_c$  is some constant, i.e. we have initially a uniform distribution of the population regarding its age. The upper age limit is taken to be  $\bar{M} = 4$ . Additionally, it is taken  $p = \frac{d\alpha}{d\tau} = .1$ ,  $c = 1$ ,  $T_f = 8$ ,  $\Delta\alpha = 0.1$ ,  $\Delta\tau = 0.01$ .

#### 4.1. Results

##### 4.1.1. Base run

Figure 5 (upper panel) exhibits the simulated anchovy biomass of relationship (4.29) compared to acoustic biomass estimates ( $\bullet$ ) during June of 2003, 2004, 2005, 2006 and 2008 [27]. The simulations demonstrated generally a satisfactory agreement being within the estimate ranges with an exception for the year 2003 where we have an overestimation.

The yearly additive estimated catches obtained from the model run are also compared with the reported catches as shown in Figure 5 (lower panel). The model output is close to the mean catches for the period 2003-2008 (dot line in Figure 5). The interannual discrepancies between model and data can be imputed to the year to year variations of the fishing mortality  $h(a)$  that it does not be accounted in this model study as we adopted average values over years for each age group.

##### 4.1.2. Numerical consideration of persistence-Calculation of $\underline{r}$ and $\bar{r}$

The value  $\underline{r}$  in which equation (2.12) holds, is calculated (for the calculus part see Appendix (A.2)) taking the value  $\underline{r} = 3.45 > 0$ , which means that the population is persistent according to the left hand of inequality (2.18). Also, the corresponding value  $\bar{r} = 4.59 > 0$  as solution of (2.15) is also positive which implies that the population does not go to extinction following the right hand of inequality (2.18). The numerical

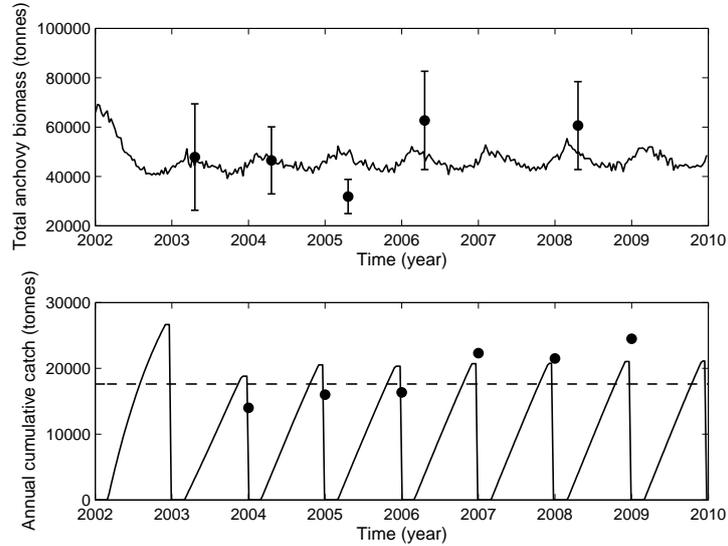


Figure 5: Upper panel: simulated total anchovy biomass with correspondence to acoustic biomass estimates ( $\bullet$ ) obtained in June of 2003, 2004, 2005, 2006 and 2008 [27]. Bars are approximate 95% confidence intervals. Lower panel: simulated annual cumulative catches are compared with the annual reported catches (anchovy biomass caught per year,  $\bullet$ ) [11]. Dot line is the average catch level for the period 2003-2008.

approximations of  $r$  and  $\bar{r}$  verify the theoretical consideration of persistence through the double inequality (2.18). Graphically, the values  $r$  and  $\bar{r}$  can be represented as the intersections of the functions  $\phi(r)$  (see 2.13) and  $\bar{\phi}(r)$  (see 2.17) with the line  $y = 1$ , respectively. The corresponding graphs are shown in Figure 6.

#### 4.1.3. Fishing closing periods

There is evidence that an appropriate fishing time closing period in which harvesting is reduced or prohibited can be an effective means of assisting a depleted fishery to recover [32]. Closed seasons are often imposed during the spawning period hoping that this will increase the reproductive abundance [2]. In Aegean anchovy fishery, a fishing restriction period is applied as mentioned from December to March. To test whether the timing of closed fishing period is crucial for anchovy variability, we impose a closed season of the same length (3 months) during and outside the spawning period. The resultant runs are compared with the base run and the scenario of no closed fishing season.

The change of anchovy biomass and annual catches under different monthly fishing closing periods is shown in Figure 7. Firstly, the simulation results showed that fishing restriction period is a favoring management measure for the protection of the anchovy resources. Base run simulation (black line) show a notable differentiation especially concerning biomass compared to simulation without imposed closing period (cyan line). In case of the other three month closures, although there are no significant variation in catches, the closing period from March to May seems to favor conditions

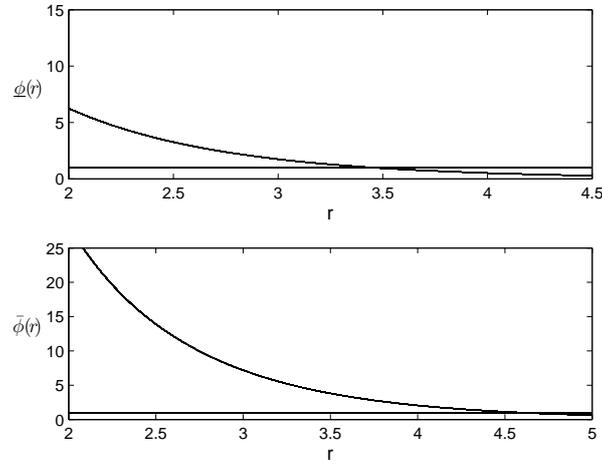


Figure 6: The values  $\underline{r}$  and  $\bar{r}$  represented graphically as intersections of  $\underline{\phi}(r)$  (see 2.13) (upper panel) and  $\bar{\phi}(r)$  (see 2.17) (lower panel) plots with the line,  $y=1$ .

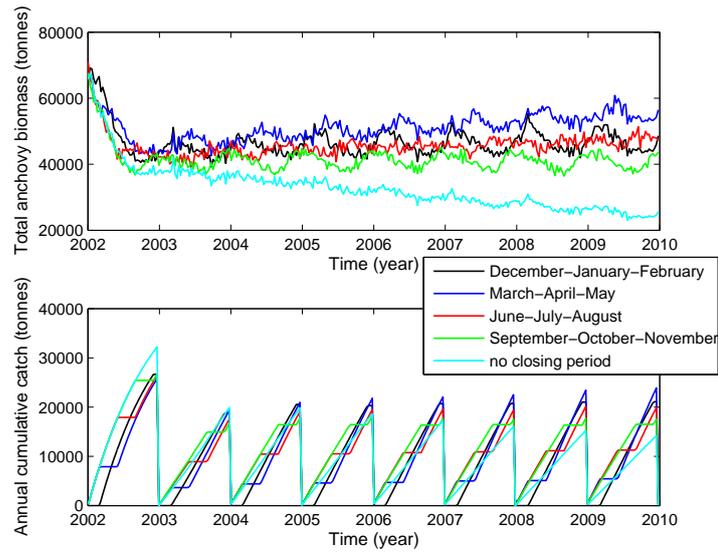


Figure 7: Simulated anchovy biomass (upper panel) and annual additive catches (lower panel) under different fishing closing periods. Baseline run: black line, March to May closing period: blue line, June to August closing period: red line, September to November closing period: green line and no closing period: cyan line.

of increase on anchovy biomass. Furthermore, the closing period inside the spawning activity (red line) did not have a strong impact on positive increase of biomass.

A second experiment examined the significance of duration of closing period on

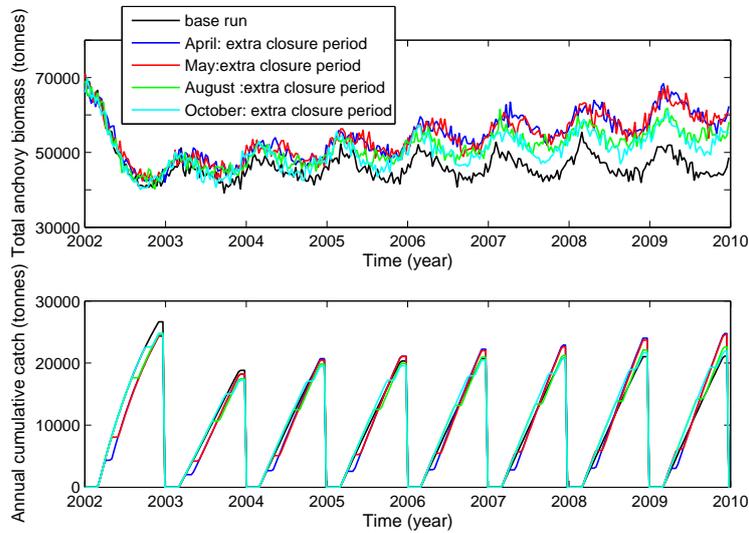


Figure 8: The simulated biomass in dimensionless form under extra monthly fishing closing periods: black line: base run, red line: extra one month closure during summer, blue line: extra two months closure during summer, green line: extra three month closures during summer.

anchovy biomass, by imposing an extra month closure. From the sensitivity runs, it seems that the duration of closing period is more effective instead of the month selection (Figure 8). Overall, this measure seems to have important positive results after the 4th year of implementation. In case of spring closure (April or May) the recovery of the stock in terms of biomass was quite effective. Of course such a management scenario would have to face the problem of law enforcement a controversial point between policy makers and fishermen. Actually, industry members will not “follow the rules” if those rules seem to much of the time to violate their economical needs.

#### 4.1.4. Selective fishing

Typically, the human predation is designed to harvest individuals that are larger size and indirectly older and heavier [17]. Targeting large fish, which are more valuable, modifies the structure and functioning of fish population with consequences for productivity and resilience of the stocks. For this reason, very often fishing regulation based on mesh size thresholds because selective fishing results in increase in the mean length and weight of fish landed. For the case of anchovy, length frequency distribution records in Aegean anchovies, indicate that majority catches range from 122.5mm to 142.5mm [27]. As the length of a fish is directly connected with age via length equation (2.19) we design some sensitivity runs based on fish length in order to investigate the hypothesis of how the reduction of fishing mortality for specific length ranges contribute to the variation of anchovy biomass. Some indicative length-age range values that we are going to use are based on the length equation (2.19). Particularly, the sensitivity runs are implemented following the pairs: (length, age): (115mm, 1.27), (120mm, 1.37 year), (125mm, 1.48 year), (130mm, 1.6 year), (135mm, 1.74 year), (140mm, 1.89 year), (145mm, 2.08 year), (150mm, 2.27 year) and (155mm,

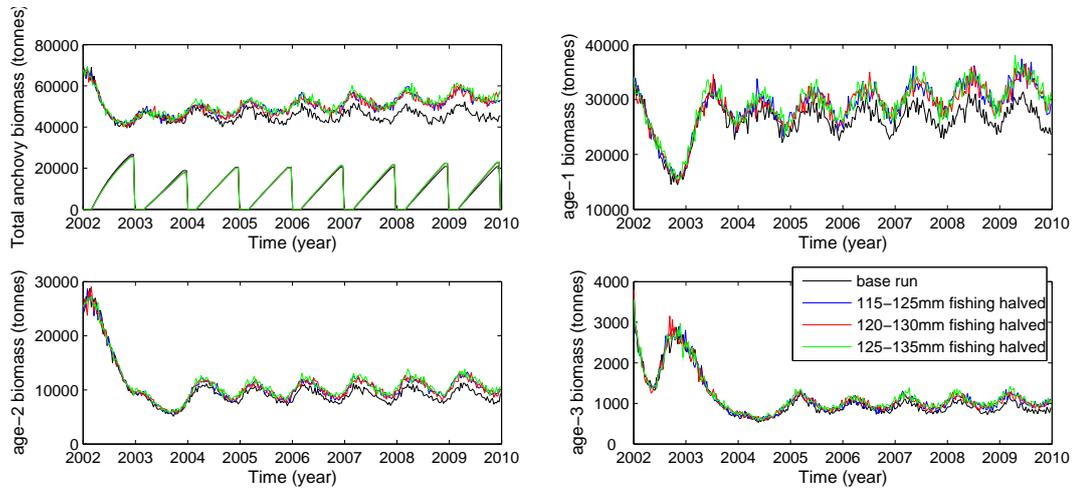


Figure 9: The change of total biomass and biomass per age group under different management strategies on younger individuals; black line: base run, blue line: fishing halved for individuals of 115-125mm, red line: fishing halved for individuals 120-130mm and green line: fishing halved for individuals 125-135mm.

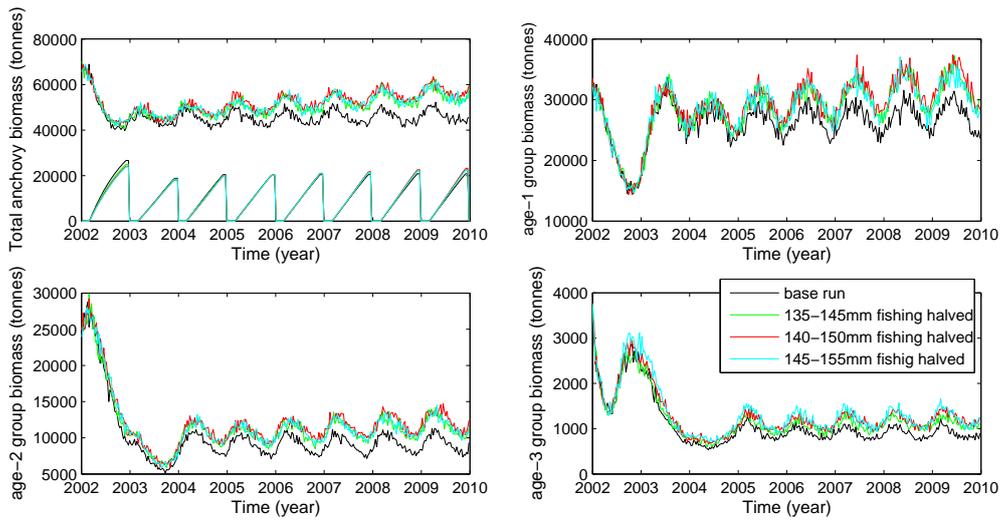


Figure 10: The change of total biomass and biomass per age group under different management strategies on older individuals; black line: base run, green line: fishing halved for individuals 135-145mm, red line: fishing halved for individuals 140-150mm and cyan line: fishing halved for individuals 145-155mm.

2.51 year). For each sensitivity run we reduced the fishing mortality in half. The sensitivity results suggest that reducing the fishing mortality in half on younger age groups (1-1.5 years) a considerable increase on the available anchovy biomass can be

achieved after the fifth year of implementation (Figure 9). Furthermore, although the management measure applies to smaller age-1 group, the effect is slightly positive for age-2 abundance but negligible for older fish (age-3 group).

A worthy aspect that proposed by Hsieh et al. [13] is the possibility - contrary to the traditional selectivity - of saving larger fish at the expense of smaller and indirectly younger ones, part of which could be fished out. Testing this hypotheses we performed sensitivity runs where the fishing on larger fish groups 135mm-145mm, 140mm-150mm and 145-155mm is halved keeping the younger fishes vulnerable to standard fishing. The corresponding results are illustrated in Figure 10. The results indicate that the scenario of keeping the fishing pressure low on older fish can be also an effective measure on the increase of older age groups. The positive effect on both age-1 and age-2 group is visible. Comparing the two Figures 9 and 10, we notice that similar results concerning the anchovy biomass are achieved, but in Figure 10 the presence of older and consequently heavier fish in stock is more possible. We emphasize that the selective fishing measure should be regarded as testable hypotheses monitoring the length distribution of anchovy catches rather than prescribed decisions forced to be implemented. Besides, the adaptive management can be a tool which can increase the chance success in fisheries management [14].

## 5. Discussion

The overall study of the age-structured model indicated that model's base run is adequately consistent within the biomass data ranges. Model simulations lead to the conclusion that the imposition of closed fishing season during the spawning activity would not have an additional benefit on anchovy variability. On the contrary, we propose to the managers the test the scenario of fishing closing period from March to May.

We also recommend that an extra 1-2 month closure, especially during spring season, would have a positive effect on the partial recovery of the stock. We recognize that these kind of measures will have to face the local fisher's objections but at least can be tested every 1-2 years. Actually, every management scheme is measured not only by its internal consistency and potential success but the extent to which fisheries managers and fishermen keeping in mind to work together and share knowledge.

Also, we propose that it is worth to be studied a different approach concerning the size-selective harvesting through the protection of older fish which is possible to contribute on heavier fish as it is shown from the model sensitivity runs. Of course, we emphasize that this management measure is time-consuming and need the incorporation of managers and fishermen for several years.

We emphasize the necessity to develop an improved model which would look for an optimal pattern of the existing measures, as this could help to establish a more effective management strategy. For this reason, the set of an optimal control problem that would take into account these factors together would be a very useful task for future work.

The theoretical and numerical consideration of population sustainability through persistence is included in this study. The importance of considering the persistence and extinction of populations has been recognized [18, 19]. Persistence study for anchovy population demonstrated that the anchovy population does not face the risk of extinction. Of course, it is important to note that the above argument is valid under the specific model framework applied in this work. The incorporation of further assumptions would demand a reassessment of this aspect.

The model study indicated that also natural mortality especially for the first two months of anchovy is an important component of the model having an effect on change of biomass. Anchovy recruitment is characterized by important inter-annual variability which can be attributed except to human-induced effects (fishery), also to environmental factors (temperature, salinity, etc.), physical processes and intrinsic biological attributes [20]. More realism could be added to this study by including real environmental factors (e.g. temperature data series) and exploring information how these factors affect reproduction, the survivability of newborn fishes and in extension the dynamics of anchovy population.

Model fitting was exposed to several uncertainties. These uncertainties included best fit to mortality and fertility functions, data accuracy and adequacy and proper model equations. To avoid inaccuracies and obtain a reliable fitting we used the period with the most updated and completed available data [27]. Average data were used in order to avoid the complexity and potential of best fitting estimates. Despite all these difficulties, the model fitting appeared to be fairly good as a first step in understanding the population dynamics of anchovy integrating the available ecological knowledge. It is profound that the inclusion of extra data information is needed in order to reduce subjective uncertainties in parameter estimation and have more reliable and informative model results.

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## Appendix A

### A.1 Proof of Theorem

Initially, we are going to use the following lemma which has been proved by Li [18]:

**Lemma.** (see Li [18]). Let  $\beta(a)$  and  $u(a)$  be nonnegative functions satisfying

$$u(0) = \lambda \int_0^{\infty} \beta(a)u(a)da$$

where  $\lambda > 0$ . Then, for any  $\theta \geq \lambda$ , there exists a continuous function  $v(a)$  such that

$$v(0) = \theta \int_0^\infty \beta(a)v(a)da$$

and

$$v(a) \geq u(a), \quad a \geq 0.$$

**Proof of Theorem** Applying the methods of characteristics for the system (2.7) we obtain

$$n(a, t) = \begin{cases} n(t-a, 0) \exp\left(-\int_0^t (m(s+t) + e(s)h(s+a-t)) ds\right), & a \geq t, \\ n(0, t-a) \exp\left(-\int_0^a (m(s+t-a) + e(s+a-t)h(s)) ds\right), & a \leq t, \end{cases} \quad (5.37)$$

and the integral equation

$$n(0, t) = b(t) \beta_0(N) \int_0^t \beta(a)n(0, t-a)G(a, t)da + b(t) \beta_0(N) \int_t^M \beta(a)n(t-a, 0)F(a, t)da. \quad (5.38)$$

The lower solution  $\underline{n}(a, t)$  of (2.7) which satisfies (2.8) is written as

$$\underline{n}(a, t) = \begin{cases} \underline{n}(t-a, 0) \exp\left(-\int_0^t (m(s+t) + \bar{e}h(s+a-t)) ds\right), & a \geq t, \\ \underline{n}(0, t-a) \exp\left(-\int_0^a (m(s+t-a) + \bar{e}h(s)) ds\right), & a \leq t, \end{cases} \quad (5.39)$$

and the integral equation is formulated as follows

$$\underline{n}(0, t) = \underline{b}\underline{\beta}_0 \int_0^t \beta(a)\underline{n}(0, t-a)\underline{G}(a, t)da + \underline{b}\underline{\beta}_0 \int_t^M \beta(a)\underline{n}(t-a, 0)\underline{F}(a, t)da. \quad (5.40)$$

The upper solution  $\bar{n}(a, t)$  of (2.7) which satisfies (2.9) is represented by

$$\bar{n}(a, t) = \begin{cases} \bar{n}(t-a, 0) \exp\left(-\int_0^t (m(s+t) + \underline{e}h(s+a-t)) ds\right), & a \geq t, \\ \bar{n}(0, t-a) \exp\left(-\int_0^a (m(s+t-a) + \underline{e}h(s)) ds\right), & a \leq t, \end{cases} \quad (5.41)$$

and the integral equation

$$\bar{n}(0, t) = \bar{b}\bar{\beta}_0 \int_0^t \beta(a)\bar{n}(0, t-a)\bar{G}(a, t)da + \bar{b}\bar{\beta}_0 \int_t^M \beta(a)\bar{n}(t-a, 0)\bar{F}(a, t)da. \quad (5.42)$$

By the previous lemma and because of the inequalities  $\underline{F}(a, t) \leq F(a, t) \leq \bar{F}(a, t)$  and  $\underline{G}(a, t) \leq G(a, t) \leq \bar{G}(a, t)$ , where  $G(a, t)$ ,  $F(a, t)$  were defined in (2.5) and (2.6) and

$$\underline{F}(a, t) = \exp\left(-\int_0^t (m(s+t) + \bar{e}h(s+a-t)) ds\right),$$

$$\bar{F}(a, t) = \exp\left(-\int_0^t (m(s+t) + \underline{e}h(s+a-t)) ds\right),$$

$$\underline{G}(a, t) = \exp\left(-\int_0^a (m(s+t-a) + \bar{e}h(s)) ds\right),$$

$$\bar{G}(a, t) = \exp\left(-\int_0^a (m(s+t-a) + \underline{e}h(s)) ds\right),$$

we conclude that

$$\underline{n}(0, t) \leq n(0, t) \leq \bar{n}(0, t). \quad (5.43)$$

From the presentation of the solutions (5.37), (5.39), (5.41) and the inequality (5.43) we get our result.

### A.2 Calculation of $\underline{r}$ and $\bar{r}$ from integral equations (2.12) and (2.15).

Because of the piecewise form of the data functions  $m(a)$  and  $h(a)$  as expressed in the equations (3.22) and (3.24) for the calculation of the left hand integral equation (2.12), we need to split it into two other integrals as follows

$$\begin{aligned} \underline{\phi}(r) &= \underline{b} \underline{\beta}_0 \int_0^M b(a) e^{-ra} \exp\left\{-\int_0^a (m(s) + \bar{e} h(s)) ds\right\} da = \underline{b} \underline{\beta}_0 \int_1^3 fec W_\infty \times \\ &(1 - e^{k_n(a-a_0)})^{b_w} e^{-ra} \times \exp\left\{-(m_2 a + \bar{e}(d_1 \frac{a^3}{3} + d_2 \frac{a^2}{2} + d_3 a))\right\} da + \underline{b} \underline{\beta}_0 \int_3^4 fec W_\infty \times \\ &(1 - e^{k_n(a-a_0)})^{b_w} e^{-ra} \times \exp\left\{-\left(\frac{m_3}{l_3}(e^{l_3 a} - 1) + \bar{e}(d_1 \frac{a^3}{3} + d_2 \frac{a^2}{2} + d_3 a)\right)\right\} da = 1. \end{aligned} \quad (5.44)$$

The part of the integral for  $0 \leq a \leq 1$  has not been incorporated in the calculation, as  $b(a)$  is zero in this interval. For our problem,  $\bar{b} = 0.42$ ,  $\bar{\beta}_0 = 0.9808$ ,  $\underline{b} = 0.057$ ,  $\underline{\beta}_0 = 0.9742$ ,  $\underline{e} = 0.2$  and  $\bar{e} = 1$ . The numerical calculations of  $\underline{r}$  and  $\bar{r}$  where made by using the Matlab program (specifically the commands are: `[quad` and `fzero]`). In a similar way the upper solution  $\bar{r}$  of (2.15) will satisfy

$$\begin{aligned} \bar{\phi}(r) &= \bar{b} \bar{\beta}_0 \int_0^M b(a) e^{-ra} \exp\left(-\int_0^a (m(s) + \underline{e} h(s)) ds\right) da = \bar{b} \bar{\beta}_0 \int_1^3 fec W_\infty \times \\ &(1 - e^{k_n(a-a_0)})^{b_w} \times e^{-ra} \exp\left\{-(m_2 + \underline{e}(d_1 \frac{a^3}{3} + d_2 \frac{a^2}{2} + d_3 a))\right\} da + \bar{b} \bar{\beta}_0 \int_3^4 fec W_\infty \times \\ &(1 - e^{k_n(a-a_0)})^{b_w} e^{-ra} \times \exp\left\{-\left[\left(\frac{m_3}{l_3}(e^{l_3 a} - 1) + \underline{e}(d_1 \frac{a^3}{3} + d_2 \frac{a^2}{2} + d_3 a)\right)\right]\right\} da = 1. \end{aligned} \quad (5.45)$$

$$(1 - e^{k_n(a-a_0)})^{b_w} e^{-ra} \times \exp\left\{-\left[\left(\frac{m_3}{l_3}(e^{l_3 a} - 1) + \underline{e}(d_1 \frac{a^3}{3} + d_2 \frac{a^2}{2} + d_3 a)\right)\right]\right\} da = 1. \quad (5.46)$$