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DIPLOME D'ÉTUDES APPROFONDIES EUROPEEN EN MODELISATION DE L'ENVIRONNEMENT MARIN

SOCRATES/ERASMUS

FISH GROWTH MODELLING

Growth of the European anchovy (*Engraulis encrasicolus*) in the Tagus Estuary, Portugal

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If you can imagine it, you can create it.

If you can dream it, you can become it.

William Arthur Ward

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1 INTRODUCTION

Coastal zones are the most heavily populated and ecologically vulnerable areas worldwide. Here many different and often contradictory interests exist which have to be carefully managed. For this purpose it is absolutely necessary to enhance the forecast capacity regarding the medium to long-term evolution of the coastal marine system in view of human activities and natural changes.

Forecast models for coastal waters, complemented by continuous monitoring systems and supported by efficient databases, can provide this kind of assistance, helping in the development of management concepts compatible with sustainable growing and with the preservation of ecosystems integrity. These integrated systems, if used in a regular basis by local authorities, can help them to achieve important improvements in coastal management practice.

Regarding all the uses that an estuary is submitted to, it is important to assess the required environmental quality for the maintenance of the fish stocks. It is important to know the location of the specific coastal areas chosen by the fish for their spawning and feeding activities, so that decision makers may have the knowledge of the more relevant areas to protect and therefore the measures needed to be implemented at an upper level.

To be able to predict *where is the fish going* one has to gather biological and ecological field data and the results of experiments that provide an estimate of the fish environmental preferences. Oceans, lakes and ponds offer their inhabitants environments that are variable in space and time. Movements in these systems, either vertically or horizontally, impose gradients in growth and survival through the effects of temperature, food concentration, sensory capabilities, predator density and detection risk. All large and commercially important marine fish stocks undertake seasonal horizontal migrations. The extent of these migrations varies with age, size and environmental conditions. Understanding the forces that create spatial distributions is a major challenge to ecology, but also has clear economic benefits to humans, by allowing more precise assessments of managed stocks (Giske *et al*, 1998). While field studies may reveal patterns at a given time and place and laboratory investigations may isolate effects of single causes, models may combine several forces in continuous space and time.

An effective management of the fisheries resources requires an understanding and the ability to predict long-term fluctuations in abundance and biomass production due either to human perturbations or environmental variations. Therefore it is required a detailed study of the life stage specific processes of the fish. Recent study has indicated that very often it is insufficient to study the averaged early-life dynamics of a year class to understand recruitment processes in fish populations. To understand these dynamics it may be necessary to follow diary growth and mortality for a period of time (Cowan Jr *et al*, 1999). Processes that operate during a specific time of the year or during a specific life stage may be critical in determining annual recruitment level. However, examinations of life stage specific processes are difficult to make in the field. Simulation modelling is an attractive alternative that provides a context for evaluating the effects of many interacting factors potentially important affecting recruitment.

This work was developed in the scope of the european DEA (*Diploma Eruditionum Altarum*) in Modelling of the Marine Environment. The goal of this work is the development of a growth model for a fish population in a coastal ecosystem. In the near future, this growth model will provide the basis to build a model of the movement of fish in the marine environment according to their environmental preferences, permitting then to predict the fish preferred areas. These models will be inserted in the already developed ecohydrodynamic system, MOHID2000 (for more information see section A.1).

The Tagus Estuary (Portugal) is selected as the framework to study the growth of the population of european anchovy, *Engraulis encrasicolus*, since there inhabits a considerable population of this species.

1.1 Tagus Estuary

1.1.1 Morphology

The Tagus estuary is the largest estuary of Portugal and one of the largest european estuaries. It is located near Lisbon (38º44’N, 9º08’W), capital of Portugal and the most important city built on its margins (see Fig.1). The metropolitan area has nowadays around 2 million inhabitants, an important harbour and big industrial complexes around the estuary. It covers an area of about 320 km^2, has a length of 80 km from the upstream limit of the dynamic tidal effect (near Muge) to the river mouth (near S. Julião da Barra – Bugio) (Ferreira *et al*, 1994; Costa, 1999). The submerged surface changes from 30000 ha in the neap tide to 34000 ha in the spring tide (Cabrita & Moita, 1995).

Fig.1 Tagus Estuary.

The estuary is composed of a deep, straight and narrow inlet channel and a broad, shallow inner bay. The inlet channel, allowing the entrance of seawater in the estuary, is about 15 km long and 2 km wide (reaching a 40m depth), while the bay is about 25 km long and 15 km wide (with a complex bottom topography that includes channels, tidal flat areas and sand banks). Upstream, a single narrow channel marks the entrance of the Tagus river. The maximum depth is 42 m near the mouth (with an average of 10 m), but a considerable upstream area has 2-3 m. It is a mesotidal estuary with semi-diurnal tides with tidal ranges varying from 1 to 4 m (Costa, 1999).

The main source of fresh water of the estuary is the Tagus river, with smaller contributions from other rivers (Trancão, Sorraia). The discharge pattern of the Tagus river reflects the regularization with Spain, the dry and wet seasons and large inter-annual variations: the average discharge varies between 100 and 2200 $m^3.s^{-1}$ (Pina, 2001; Costa, 1999; Cabrita & Moita, 1995). The residence time of fresh water is highly variable and ranges from 65 days at a discharge of 100 $m^3.s^{-1}$ to 6 days at a discharge of 2200 $m^3.s^{-1}$; the residence time to the modal discharge of 300-400 $m^3.s^{-1}$ is of about 23 days (Martins *et al*, 1984).

1.1.2 Physical and Biological Properties

The estuary is a mixing place of river and oceanic waters. The salinity distribution depends mostly on the river flow and on the mixing imposed by the tidal regime, which is the main mechanism controlling the distribution of aquatic organisms and suspended particulate matter in the estuary. There is a partial two-layer stratification: salinity is higher in the deeper layers because the mixing of fresh and saltwater is slow (Cabrita & Moita, 1995).

Temperature variations influence the estuarine communities, by influencing the dissolved oxygen and several pollutants concentrations. In the Tagus estuary, temperature range is higher upstream, with maximum values at Vila Franca de Xira. There is a considerable thermic homogeneity during winter compared with a pronounced longitudinal gradient during summer.

The Tagus estuary is a highly productive ecosystem, and has considerable conservation value, since it provides an optimum habitat for many crustacean, molluscs, fish and bird species. This has led to the creation of a Natural Reserve in 1976, covering a large surface of estuarine water, mud banks, saltpans, salt marshes, islands and agricultural land (Ferreira *et al*, 2001).

The Tagus estuary presents a high productivity and the most abundant primary producers are the salt marsh vegetation, microphytobenthos, and macrophyte algae; together they provide food for benthic fauna and habitat for many species. The primary producers are responsible for the removal of high amounts of nutrients, which improves the estuarine water quality.

Although the estuary is recognised as a highly productive ecosystem, some of its natural resources have been degraded in the last 30 years due to the increased water and soil pollution. Directly or indirectly the estuary is the final disposal place of the catchment-produced effluents. The implementation of the EU Water Directives is progressively reducing the organic matter and nutrients load in the estuary. The quantification of the maximum admissible loads discharged from each affluent sub-basins (Tagus, Trancão and Sorraia and smaller streams) requires a good understanding of the biological processes inside the estuary and in the coastal zone near the estuary's mouth, which is an important recreational and leisure zone.

All those factors contribute for the need of efficient managing tools that allow the local authorities to make decisions based on the better knowledge that they may have available in each moment. To achieve this knowledge it is necessary to collect information about the different parameters that play an important role in the ecosystem, integrate this information in order to make it representative of the whole estuary and make it available in a comprehensive way to the decision makers.

1.1.3 Fish in the Tagus Estuary

The maintenance of the coastal fisheries stocks is to a large extent dependent on the natural conditions of the estuary, since several fish species use it as a *nursery* area, or migrate through the estuary at different stages in their life cycle. The nursery zones are located in the shallowest upstream part of the estuary, near Vila Franca de Xira, Montijo and Alcochete.

The estuarine community varies throughout the year and is rare the fish that inhabit permanently in the estuary. As the strong currents of the estuary can drag eggs, the majority spawns in the sea. Nevertheless the species whose life cycle develops in the estuarine environment have to arrange mechanisms that hinder this drag of eggs (Costa, 1999).

In 1996 and 1997, Costa (1999) identified 44 fish species in this estuary, including resident species, species that use the estuary as a *nursery*, migrant and occasional species. Some of the most abundant species in this estuary is the european seabass (*Dicentrarchus labrax*), the common sole (*Solea vulgaris*), the gilthead seabream (*Sparus aurata*) with considerable commercial interest, the sand and marbled goby (*Pomatoschistus minutos* and *P. microps*) and the european anchovy (*Engraulis encrasicolus*), this last with commercial interest for fisheries.

The anchovy and the goby live in this estuary throughout their life cycle, while the european seabass, the common sole and the gilthead seabream use it as a *nursery*. These last species spawn in the sea and the juveniles use the estuary as foreground *nursery*, where they find greater amount of food, minor number of predators and good conditions of temperature; they remain during a variable period depending on the species and return to the sea. Some adults enter occasionally in the estuary to feed (Costa, 1999; Monvoisin, 1997).

The survival of the estuarine fish is affected by diverse factors as pollution, overfishing and dams. The overfishing of several species in this estuary causes the decrease of the fish stocks because juveniles are caught, thus preventing the adult population to increase and consequently producing a minor number of eggs.

1.2 European Anchovy, Engraulis encrasicolus

The european anchovy *Engraulis encrasicolus* (family - Engraulidae, order – Clupeiformes) is a very abundant species from Norway to England, all western Europe, Mediterranean, Black and Azov seas, South Africa, Gulf of Suez, western Indian Ocean, Mauritius, Seychelles and upwelling area around Somalia, as shown in Fig.2 (Costa, M.J., 1999; Whitehead, 1990; Whitehead *et al*, 1988).

Fig.2 *Engraulis encrasicolus* distribution (FAO *in* Froese & Pauly, 2000)

It is a pelagic and mainly coastal marine species, forming large schools and feeding on planktonic organisms. It is a eurythermic and euryhaline species that tolerates salinities from 5-41 ppt and in some areas, enters estuaries, lagoons and lakes, especially during spawning activity. Tends to move further north and into surface waters in summer, retreating and descending in winter. This species adult mean weight is of 30 g and a maximum length of 20 cm (see Fig.3).

Fig.3 European anchovy, *Engraulis encrasicolus* (Frose & Pauly, 2000)

The european anchovy presents a short life span (three to four years), seasonal migrations, an intense growth and an age of first maturity with one year (*r* selection strategy, i.e. selection for maximum rate of population reproduction in a fluctuating environment). It spawns from April to November with peaks usually in the warmest months. In the Tagus estuary the European anchovy spawns one time in the April/May period (Ré, 1986). Eggs are ellipsoidal to oval, floating in the upper 50 m and hatching in 24-65 hrs, presenting a biomass of 0,226 mg wet weight (Ré, 1986). Since the eggs are pelagic, their shape prevents their transport through the estuary, because it offers less resistance to the currents. This fish species is a multiple spawner (often more than ten batches within a season). This mechanism is an efficient means of ensuring complete use of food and increases the probability of population survival, as well as being an adaptation for unstable environmental conditions and high mortality in early stages of ontogeny.

Survival of anchovy larvae is determined by the food availability in a period of omnivorous feeding, and there is a close synchrony between key larval abundance and the zooplankton population maximum. The anchovy feeds mainly on copepod nauplii larvae, mollusc larvae, phytoplankton, copepods and cirripeds (Berdnikov *et al*, 1999).

The european anchovy is a highly commercial species, marketed fresh, dried, smoked, canned, frozen, made into fish meal and used as bait (Frimodt, 1995). As a target fisheries' species, the anchovy has received intensive study (Winkler, 2000; Berdnikov, S.V. *et al*, 1999; Costa, 1999; Santos *et* al, 1997; Tudela & Palomera, 1997; Magoulas *et al*, 1996;

Myers *et al*, 1995; Koranteng, 1993; Morales-Nin & Pertierra, 1990; Karacam & Düzgünes, 1990; Palomera & Lleonart, 1989; Spanakis *et al*, 1989; Palomera *et* al, 1988; Erkoyuncu & Ozdamar, 1989; Uriarte & Adtudillo, 1987).

The anchovy fisheries management of the southwestern Europe and of the Mediterranean Sea is difficulted by the large interannual variability in the populations' abundance. The anchovy life cycle seems to be adapted to a highly variable environment, presenting both high growth rate and fecundity and also active migrations to areas that gather better conditions (Palomera *et al*, 1988).

The model built in the framework of this thesis is applied to this fish species, since (1) it has an important role maintaining this ecosystem's trophic web, (2) it is a resident species in the Tagus estuary and (3) because it is highly used in fisheries. The anchovy life cycle is quite similar to the sardine's cycle (Ré, 1986).

2 METHODOLOGY

2.1 State of the Art

Fish simulation models have been developed for assessment on fisheries and environmental quality management, simulating fish population using individual-based models IBMs (Lindholm *et al,* 2001; Cowan Jr *et al*, 1999, 2000; Cowan Jr *et al*, 1999; Monvoisin *et* al, 1999; Rose *et* al, 1999; DeAngelis *et al*, 1991).

Spatial modelling of fish with individual behaviour was initiated by Balchen's group (Balchen, 1976 and Reed & Balchen, 1982 *in* Giske *et al*, 1998). IBMs are created on the recognition that individuals differ in their characteristics and abilities and that such differences may be important in ecology and population dynamics. These models simulate the fish growth in terms of the biomass variations or using an energetic-based approach (Levebvre *et al* 2001; Hanson, 1997). One of the main features of IBMs with regard to spatial distributions has been the recent development of spatially explicit models (Tyler & Rose, 1994), which incorporate spatial heterogeneity, individual variability and individual movement. One of the problems with IBMs is that they are little more than a way of accounting for individuals in a population. If IBMs are to become an important tool for explaining the behaviour of individuals and populations, models that describe why individuals are motivated for actions are needed. This means that individual actions should be viewed in the light of what evolution has found favourable.

It has been ongoing the development of simulation models for fish behaviour (Breitburg *et al*, 1999; Ficksen *et al*, 1998; Heath *et al*, 1998; Sekine *et al*, 1997; Sekine *et al*, 1996; Eckman *et al*, 1993; Sekine *et al*, 1991a; Sekine *et al*, 1991b), including fish movement (McDermot & Rose, 2000; Sutton *et al*, 2000; Railsback *et al*, 1999; Giske *et al*, 1998), to predict the fish distribution and the influences of environmental conditions on fish survival (Lindholm *et* al, 2001; McDermot & Rose, 2000; Lamouroux *et al*, 1999a; Lamouroux *et al*, 1999b; Jaworska *et al*, 1997).

These studies often include a model of the fish biomass growth, dependent on its processes of feeding, respiration and excretion. In fact, environmental conditions affect these processes (directly or indirectly) and so these models consider biological constraints (food quantity and quality, predators of the studied species), system's physical-chemical conditions (bottom material, water temperature, current velocity, depth, dissolved oxygen, salinity, turbidity, ammoniacal nitrogen) and human-related stress (fishing, pollution). Predicting the fish biomass is much more inaccurate compared to predicting the behaviour of a fish. There are so many factors affecting fish growth that modelling 60% of the fish biomass change is in fact a good estimate (Sekine, M. *personal communication*).

Direct Density Dependence

Population processes such as survival, growth, reproduction and movement are said to be density dependent if their rates change as a function of population abundance. Processes that limit population growth at high abundances (e.g. slower growth, increased emigration, lower survival) or increase numerical growth at low population abundances (e.g. faster growth, increased immigration, higher survival) are examples of direct density dependence or **compensation**. Direct density dependent processes operate as a negative feedback and tend to stabilize population abundance. If processes such as survival and growth decrease at low population abundances or increase at high abundances, they are referred to as inverse density dependence or **depensation**. Inverse density dependent processes operate as a positive feedback and tend to destabilize populations.

While compensation is a population-level phenomenon, it is important to note that it is individual responses to abundance changes that cause both compensatory and depensatory density-dependence (Rose & Cowan, 2000; DeAngelis *et al*, 1991). Individuals in a fish population compete with one another for a limited pool of environmental resources vital to their survival and successful reproduction. Examples of these environmental resources are food, refuge from predators and suitable sites for spawning (Berdnikov, 1999). Compensation's principle is that the greater the number of fishes in relation to this pool of vital resources, the more intense the competition. Increased intensity of competition for these resources may then express itself in decreased survival rates, slower growth rates, reduced reproduction or increased emigration from the area of competition. The result is that very dense populations that exceed the available resources decline in numbers until the competitive pressure is reduced. On the other hand, when population abundance is low in relation to the available environmental resources, the intensity of competition is minimized. The result is an increase in survival, growth and reproduction and a decrease in emigration, which operate to increase population abundance.

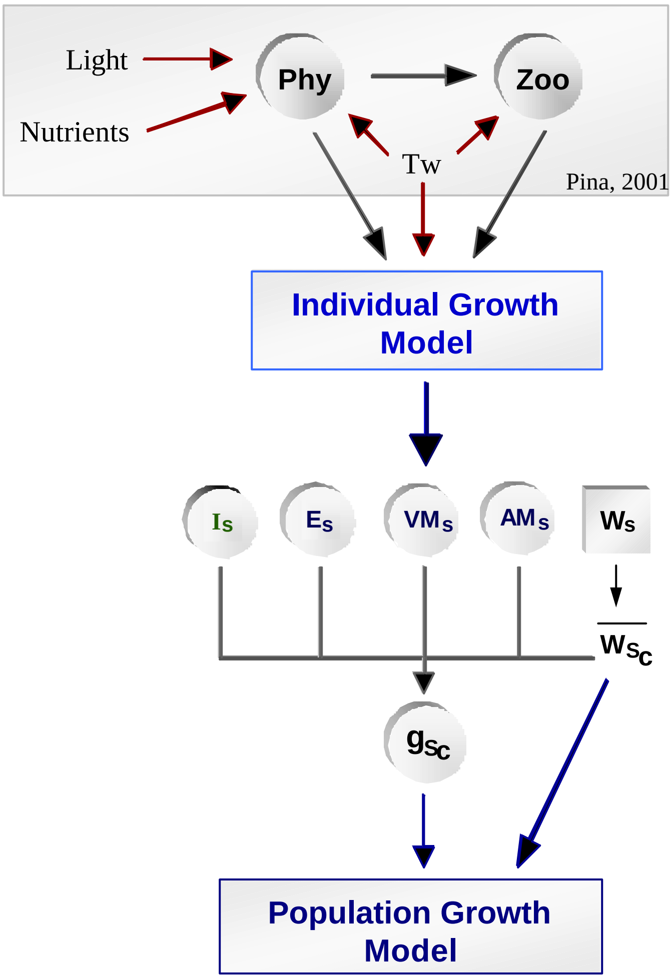
An increment in an existing mortality, or even a new source of mortality, imposed on a fish population will at first tend to diminish the numbers of fish; this decrease in numbers of individuals will cause a population response to compensate the increased mortality. The magnitude of the compensatory response and the life stages in which it operates **vary among species**, depending on their history strategy (survival, growth and reproduction rates), and can **vary among populations** due to site-specific conditions (e.g. environmental resources available, food web arrangement). Rose & Cowan (2000) confirm that the existence of compensation is found in spawner-recruit data, empirical studies and also in fisheries management. Berdnikov *et al* (1999) demonstrated that anchovy recruitment numbers in the Azov Sea usually greatly exceed survivors from the previous generation, presenting a high sustainability of the population in face of unfavourable environmental conditions and heavy fishing.

The question of compensation is important in assessing the effects of anthropogenic stressors on fish populations (Jaworska *et al*, 1997). Harvest levels or entrainment and impingement rates that exceed the compensatory reserve of a population would cause population declines. The consequences of overestimating compensation can be severe: population decline to a severely low abundance. To be protective of the resource, people usually resort to the no compensation hypothesis unless one can demonstrate a clear and unequivocal understanding of the compensation mechanism (Rose & Cowan, 2000). Rarely there is sufficient empirical evidence to comprehend how the various life stages and processes combine to cause the compensatory response of a particular population. Assuming no compensation, or underestimating compensation, is extremely protective of the natural resources but it lowers economic efficiency and causes potentially excessive and unnecessary financial costs. Understanding compensation at the process-level permits to bound the magnitude of compensation appropriate to use in population models.

Individual-based modelling offers a promising approach for modelling population and community dynamics (DeAngelis *et al*, 1991) and has features that should help in quantifying compensatory responses of fish populations. Representing local interactions in space, size-based interactions, episodic effects, movement and stochasticity, all of which are important to realistically simulate fish population dynamics and compensation, is relatively easy in IBMs. Anthropogenic stresses in fish populations can be directly inserted in these models, and then be used to scale the numbers of individuals' loss up to the population level. If one can realistically represent how individuals grow, survive, reproduce and move, then population-level phenomenon such as compensation should be obtained by summing over all of the individuals in the model. Compensation becomes an emergent property of the model, rather than being imposed in relationships used to construct the model (Rose & Cowan, 2000).

2.2 Conceptual Model

The model developed in the framework of this thesis involves two distinct sub-models: the individual growth model (IGM) and the population growth model (PGM). The main goal of this thesis is to build the population growth model, but since there are processes significant at



Pina, 2001

Fig. 4 . Overview of the Growth Model. *Tw* is water temperature; I_S is ingestion of stage *s*, E_S is egestion of stage *s*, excretion due to VM_S (vital metabolism of stage *s*) and AM_S (active metabolism of stage *s*). The IGM produces time series of W_S (biomass of the individual fish in stage *s*) and W_{Sc} is the mean biomass of the individual fish in the class *c* of stage *s*; $g_{S\,c}$ is the scope for growth of the individual fish in the class *c* of stage *s*, calculated in the PGM.

the individual fish scale, the IGM is also developed. In the near future, with the PGM it will be possible to build a model of the fish movement according to the population's environmental preferences. Field observations indicate that fish inhabit different areas according with their life stage. Therefore, fish prefer different environmental conditions in each life stage (Berdnikov *et al*, 1999) and this should be considered in the model of the fish movement.

Fig.4 provides a simplified view of the model. The model considers that the individual growth depends on food availability and water temperature. This model creates series of results of the individual fish's variation of biomass in time, for each of the stages of its life cycle. These results are then treated to estimate a mean biomass for each life stage. In fact, as the PGM is a class transition model, in this phase it is estimated mean biomass values for defined classes of each life stage. With this procedure is then possible to calculate the *scope for growth* for these mean biomass values for each class of the life stages and develop the PGM.

2.3 Individual Growth Model (IGM)

This section explains the basic equations used in the Individual Growth Model (see Fig.5). The IGM model is based on a biomass balance. This model simulates the biomass growth of an individual fish, for each of its life stages, considering the fish's metabolism.

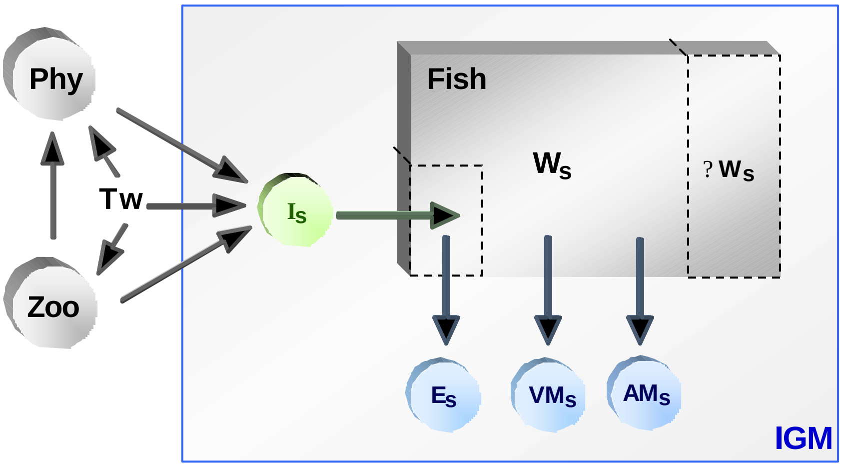


Fig.5 Individual Growth Model. For the life stage *s*, the individual fish's biomass (W_S) is variated by the difference between daily 'production' (ingestion, I_S) and 'destruction' (egestion, E_S, excretion due to the vital metabolism, VM_S and to the active metabolism, AM_S) and this difference is the individual fish's biomass variation ($?W_S$). Ingestion is a function of water temperature (*Tw*) and food availability (phytoplankton, *Phy* and zooplankton, *Zoo*) and the excretion (*VM* and *AM*) is a funcion of the fish's biomass, food availability and water temperature.

This model uses modified equations of the Shallow-Sea Ecological Model (Sekine *et al*, 1991a). The biomass growth is described as follows:

$$\frac{\partial W}{\partial t} = I - E - (VM + AM) \qquad (1)$$

where W is the individual fish's biomass (mgC.individual^{-1}), I is the amount eaten or ingestion (mgC.d^{-1}), E is the egestion, i.e. the amount of ingested food that's not assimilated (mgC.d^{-1}) and $VM+AM$ is the excretion component, i.e. the losses of biomass due to the fish's metabolism, where VM is the vital metabolism (mgC.d^{-1}) and AM is the active metabolism (mgC.d^{-1}). McDermot & Rose (2000) developed an individual-based model to piscivore stocking where the growth function also uses these two metabolic losses of fish biomass. The ingestion is given by:

$$I = \mathrm{Imax}^{Ki}.W^{Ka}.\frac{\mathrm{Wfood}}{\mathrm{Wfood} + Ks} \qquad (2)$$

where $Imax$ is the maximum ingestion rate or maximum growth rate (d^{-1}), Ki is a stage-specific ingestion coefficient, Ka is a stage-specific coefficient that translates the scope of biomass growth in the specific stage, $Wfood$ is the number of available preys or food amount (individuals.L^{-1}) and Ks is the half-saturation constant (individuals.L^{-1}). The maximum ingestion rate is a function of water temperature:

$$\mathrm{Imax} = Kb.\exp(Kc.Tw) \qquad (3)$$

where Kb is the maximum ingestion rate at 0 ºC (d^{-1}), Kc is a temperature constant (ºC^{-1}) and Tw is the water temperature (ºC).

The amount of available food *Wfood*, is calculated as follows by:

$$Wfood = \frac{Z}{wp} + \frac{P ? ? .Z}{wp} \qquad (4)$$

where Z is the prey concentration, wp is the weight of one individual prey (mgC.prey^{-1}), P is the concentration of phytoplankton in the environment (mgC.L^{-1}), Z is the concentration of zooplankton in the environment ($mgC.L^{-1}$) and ? is a coefficient of zooplankton intake by the individual fish, dependent on the fish size.

Destruction processes presented in equation (1) are given by:

$$E = I \,.\, (1 - K_E) \qquad (5)$$

$$VM = W \,.\, K_{VM} \qquad (6)$$

$$AM = I \,.\, K_{AM} \qquad (7)$$

where K_E is the net assimilation efficiency, K_{VM} is the vital metabolism biomass consumption rate (d^{-1}) and K_{AM} is the active metabolism excretion rate.

All the equations are developed for the larvae, juvenile and adult stages. In the egg stage, there is no ingestion and egestion, vital metabolism and active metabolism are considered null, resulting in no growth. Each of the life cycle's stages (egg, larvae, juvenile and adult) presents different characteristics in the physiological processes and so this model contemplates those differences by considering stage-specific coefficients' values for each of the four stages of the fish's life cycle.

2.3.1 Interaction between fish and habitat

The fish interacts with habitat by feeding and excreting. In this model, phytoplankton and zooplankton constitute de fish food (or prey), and it is considered that there is always enough food in the system for this single fish. This model assumes that there is a dependence between the prey size and the fish size, considering that the fish can eat phytoplankton since the beginning of the larval stage, but the amount of zooplankton intake increases with the fish size and hence the fish's age, if one considers that the fish has a growth where higher biomass is equivalent to more age.

In the IGM model, the "destruction" processes are egestion (E) and excretion due to vital and active metabolisms (VM an AM). Both egestion and active metabolism are simulated as partial losses of the ingested prey biomass. The ammonia production may be predicted from the vital metabolism consumption of fish biomass. Organic matter inputs to the environment may be calculated from the non-assimilated food (egestion) and the active metabolism consumption of biomass.

2.4 Population Growth Model

The population dynamics is simulated through a modification of a class transition model (Ferreira *et al*, 1998 in Simas *et al*, 2001; Berdnikov *et al*, 1999). This model considers the fish's four stages of its life cycle: eggs, larvae, juveniles and adults, taking into account the individual stage-specific biological processes. In each stage there are several classes and so the model considers:

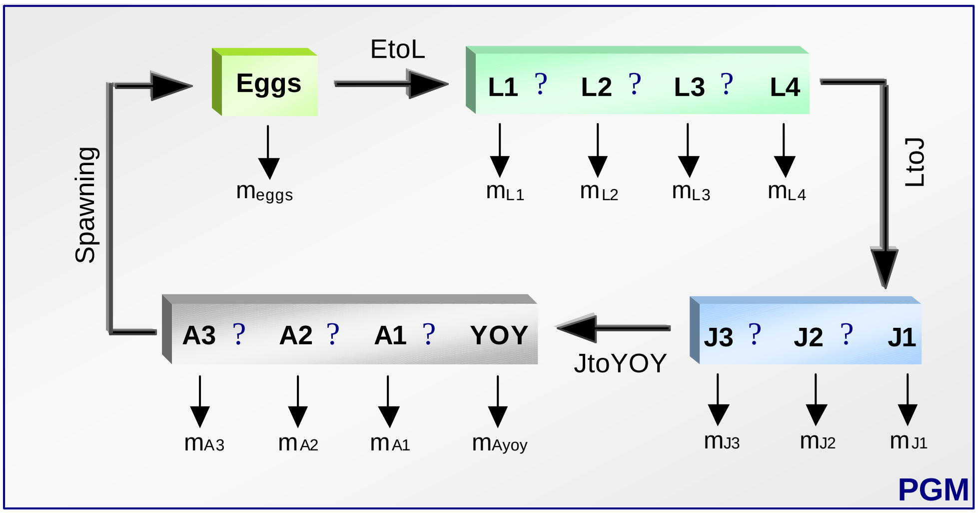


Fig. 6. Population Growth Model's classes for each stage (one class for the eggs, four classes for larvae stage, *L*, three classes for the juvenile stage, *J* and four classes in the adult stage, *A*, being *YOY* the Young-of-the-Year individuals), with characteristic mortality for each class, *m* and transition of stages' rates (*EtoL*, *LtoJ* and *JtoYOY*, transition of eggs to larvae, larvae to juveniles and juveniles to adults' young-of-the-year, respectively).

The transition of the number of individuals of the fish population **between classes** in each of the stages of the life cycle is given by:

$$\frac{?n_{sC}}{?t} ? \frac{? ?n_{sC} ?t ?g_{sC} ?}{?s} ? m_{sC}.n_{sC} \qquad (8)$$

where *n* is the number of individuals of stage *s* and class *c*, *g* is the scope for growth of stage *s* and class *c* (d^{-1}), *m* is the mortality rate of stage *s* and class *c* (d^{-1}) and *t* is time (d). Therefore, the number of individuals in each class depends on the individual *scope for growth* and on a natural mortality rate. Fig.7 illustrates how the number of individuals varies along the life stage according to Equation (8). This model considers only the natural mortality rate, but in the future it will develop to consider human pressure on the population (e.g. fishing, pollution).

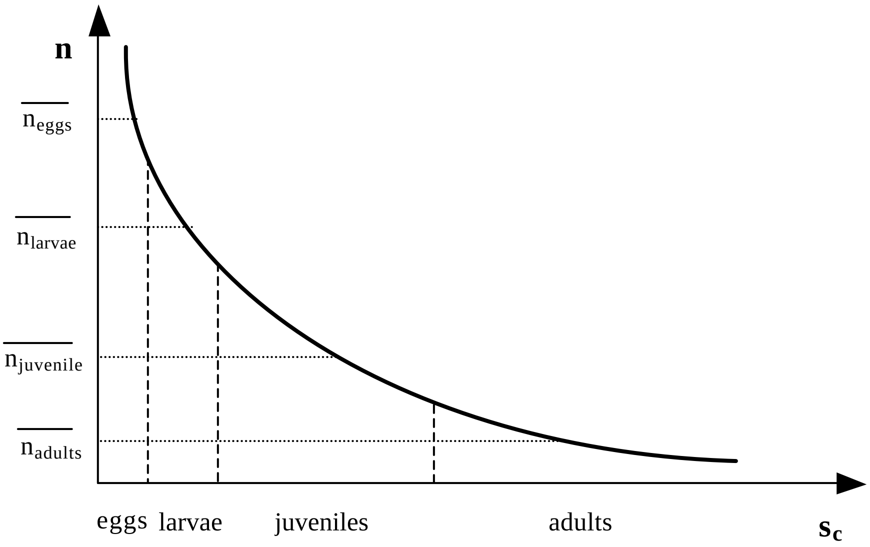


Fig.7 Variation of the number of individuals per stage of the fish life cycle. In each stage there is a mean number of individuals. One of the reasons for considering several classes per stage is that it greatly diminishes the error in the estimate of these numbers of individuals.

The scope for growth, *g* is described as:

$$g_{s_C} = \frac{I_{s_C} - E_S - \left(VM_{s_C} + AM_{s_C}\right)}{ws_{C+1} - ws_C} \qquad (9)$$

where I_S, is ingestion (mgC.d^{-1}), E_S is egestion (mgC.d^{-1}), VM_S is vital metabolism (mgC.d^{-1}) and AM_S is active metabolism (mgC.d^{-1}) in the class c of stage s; ws_c and ws_{c+1} are the mean weights of the individual fish (mgC) in the class c and $c+1$, respectively. Mean weights of each class are estimated from the time series of the biomass results simulated by IGM and ingestion, vital metabolism and active metabolism are calculated as in IGM but using mean biomass values in each class.

The transition **between stages** is simulated considering that it is required a period of time for the development of the fish in each stage. Fish need a period of time in the stage of larvae before being juveniles and so on. Nevertheless, as this is a population growth model, fish aren't all in the same stage in a given moment in time, existing eggs, larvae, juveniles and adults at the same moment and in each stage there are individuals more developed than others. Therefore it is reasonable to consider a transition rate ($stos+1$), as follows:

$$s \text{ to } s+1 = \frac{s_f}{t_s} \qquad (10)$$

with s_f being the last class of stage s (eggs, larvae or juveniles; never the stage *adults*, since this is the last stage of the life cycle) and t_s the characteristic duration of the specific stage (t_{eggs}=2 d, t_{larvae}=31 d, $t_{juveniles}$=330 d). As seen in Fig.6 there is a transition of eggs to larvae, *EtoL*, larvae to juveniles, *LtoJ* and juveniles to adults, *JtoYOY*.

Spawning is a function of the number of individuals in each class of the adult stage, n_{Ac}: young-of-the-year, A1year, A2years and A3years (number of adults) and of each class's effective spawners (not all fish are able to spawn), provided there is a specific batch size for each fish species. Effective spawners of class *c* is the percentage of fish in the class *c* that are actually able to spawn (the ability to spawn depends on the fish's sex and reproductive maturity):

$$Spawning = BS.\sum S_{Ec}.n_{Ac} \qquad (11)$$

where *BS* is the batch size (eggs.individual^{-1}), S_{Ec} is the number of effective spawners in the class *c* and n_{Ac} is the number of individuals in class *c* of the adult stage. In the PGM spawning period occurs in April/May and hence the spawning is of 1 time per year.

Mortality fluctuates along the life cycle. In fact, eggs and larvae present the highest natural mortalities (Lindholm *et al*, 2001; Jaworska *et al*, 1997; DeAngelis *et al*, 1991). In this model each class of each stage presents a characteristic mortality, so that in the overall population there is a mortality rate curve as described by Fig. 10.

2.4.1 Interaction between fish population and habitat

The fish population interacts with habitat by feeding and excreting. Concerning the dynamics of the fish population predation over the phytoplankton and zooplankton in the ecosystem this model considers variations of the prey concentration throughout the year and how it affects the population's growth. In fact, this influence is included in the individual growth model, that produces the results from which it is then calculated each stage's mean biomass and also in the population growth model, in the ingestion and destruction processes calculus. This model assumes that the fish population is not able to reduce extensively the phytoplankton and zooplankton's concentrations in the system and therefore the starvation-induced mortality is not measured.

The organic matter and ammonia production by the fish population is easily estimated from the PGM results for the egestion and active metabolism (organic matter) and vital metabolism (ammonia) partial consumption of fish's biomass, multiplied by the number of individuals in the population. As this model will be integrated in the MOHID system (for more information see section A.1) in the near future, it is important to include the fish population's input of ammonia and organic matter in the environment.

2.5 Fish movement

Movement rules are a critical component of spatially explicit IBMs because movement is an essential process used by fish to adapt to changing environment and competitive conditions. In fact, fish move to improve food intake and growth, to reduce vulnerability to predation risks that vary with fish size and environmental conditions, to seek shelter during high flows and avoid stranding as flows decrease, and to avoid competition with dominant fish. Models must be able to simulate these movements correctly if they are to be useful for predicting population responses to changes in habitat, mortality rates or competition (Railsback *et al*, 1999). Furthermore, verifying that movement rules produce realistic movement decisions is one of the model evaluation steps needed for IBMs to be accepted for decision-making and research.

Railsback *et al* (1999) studied fitness measures and movement rules, in stream fish IBMs. Spatially explicit IBMs use movement rules to determine when an animal departs its current location and also to determine its movement destination. These rules generally compare locations using some measures of a fish's expected fitness and assume that fish make movement decisions at least in part to increase their fitness. Movement rules are critical to realistic simulation of how individuals, and therefore populations, respond to changes in habitat and population density. Recent research shows that many fish move quickly in response to changes in physical and biological conditions, so movement rules should allow fish to rapidly select the best location that is accessible. Regarding movement rules, Railsback *et al* (1999) concluded that (1) IBMs should assume that the fish are familiar with their surroundings over an area greater than their current location (models should let fish move any time that better habitat is available within the area they are familiar with) and (2) models should let fish select the best habitat available instead of moving randomly. If routine non-exploratory movement is simulated as partially random, it should occur over a considerably smaller time scale than habitat variation.

Fitness measures are used in movement rules to rate alternative destinations. The theory that minimizing the ratio of mortality risk to food intake maximizes a fish's fitness is not applicable to typical IBM movement decisions and can cause serious errors in common situations. Instead, Railsback *et al* (1999) developed fitness measures from unified foraging theory that are theoretically compatible with IBMs. This fitness causes fish to select habitat that maximizes its expected probability of survival over a specified time horizon, considering both starvation and other risks. This fitness measure is dependent on the fish's current state, making fish with low energy reserves more willing to accept risks in exchange of higher food intake. Another measure represents the expectation of reaching reproductive maturity by multiplying expected survival by a factor indicating how close to the size of first reproduction the fish grows within the time horizon.

Sekine *et al* (1991a, 1991b, 1997) studied fish movements according to their environmental factors. Using an object-oriented programming language, they developed the Shallow-Sea Ecological Model (SSEM), which simulated fish movement according to their preference for environmental conditions as well as competition among species. The movement component considered advection and diffusion and also the movement by swimming. The swimming of living organisms was caused by their preferences and the criteria to decide the movement were food amount, depth, water temperature and the nature of the sea bottom.

Later, Sekine *et al* (1997) developed a model of fish distribution according to the fish preference for environmental factors such as water temperature, depth, cover, shade, current velocity, turbidity, food amount, biomass, stem of aquatic plants and composite conditions. In this model the parameter values for the environmental preference and the weight values of the environmental factors could be introduced without calibrating the preference parameters again. This model's calibration depended on experimental simulations. In these experiments, a determined number of fish was placed in tanks and several environmental conditions were tested to measure fish preferences (in terms of their distribution in the tank).

Lindholm *et al* (2001) modelled fish movement according to habitat complexity, using a simple population model with a modified Beverton-Holt equation to simulate the effects of habitat-mediated processes on population responses at the landscape scale. It considers a population subdivided into *n* regions, where each region is represented by a particular level of habitat complexity. Habitat complexity is interpreted as a measure of the vertical relief and cover from predation provided by a particular substratum (e.g. pebble-coble, sand, boulder) and any associated emergent epifauna (e.g. sponges, amphipod tubes, cerianthid anemones, shell deposits, biogenic depressions). It also considers that habitat complexity is uniform within any region and that each region is either a marine protected area in which no fishing disturbance occurs or that it is outside a marine protected area and altered by fishing activity. In Lindholm *et al* model net per-month movement between regions is a function of the percentages of individuals moving between regions and it is specified that movement rates are the inverse of a habitat complexity score. Lindholm *et al* (2001) concluded, among other things, that movement rates were critical for predicting the effects of marine protected-area size on fish survival.

3 MODEL IMPLEMENTATION

3.1 Individual Growth Model

The conceptual model of the Individual Growth (IGM) uses the Tagus estuary as the case study and *Engraulis encrasicolus* as the studied fish species. The model was implemented using the Powersim^{TM} software. A first sensitivity analysis is done, considering the environmental variables (phytoplankton, zooplankton and temperature) constants in space and time.

This model uses temporal series of phytoplankton and zooplankton calculated by Pina (2001) for a central area in the Tagus estuary and these results are in good agreement with field measurements. Pina's results indicated that the daily mean concentrations of phytoplankton and zooplankton were described throughout the year as shown in the curves of Fig.8.

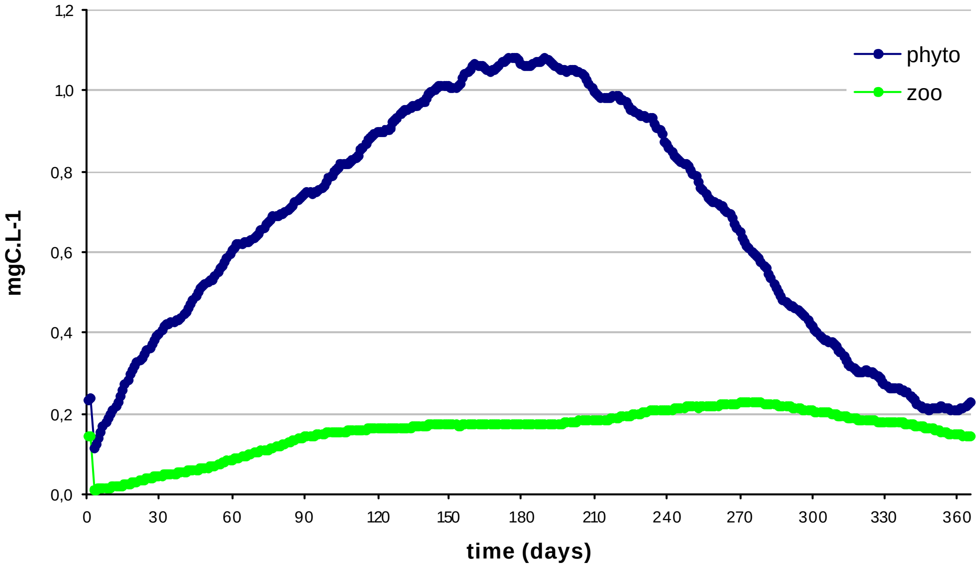


Fig. 8. Daily mean concentration (mgC.L^{-1}) of phytoplankton and zooplankton for the year 1999 in a central box of the Tagus estuary (Pina, 2001).

The IGM simulates the growth of the individual fish in each of its life stages. The parameters used in the individual growth models are presented in Table.1, resulting from the calibration of the model after introducing some typical values presented by Sekine (1991b) and Gypens *et al* (2001).

Table .1 Parameter values used in the IGM.

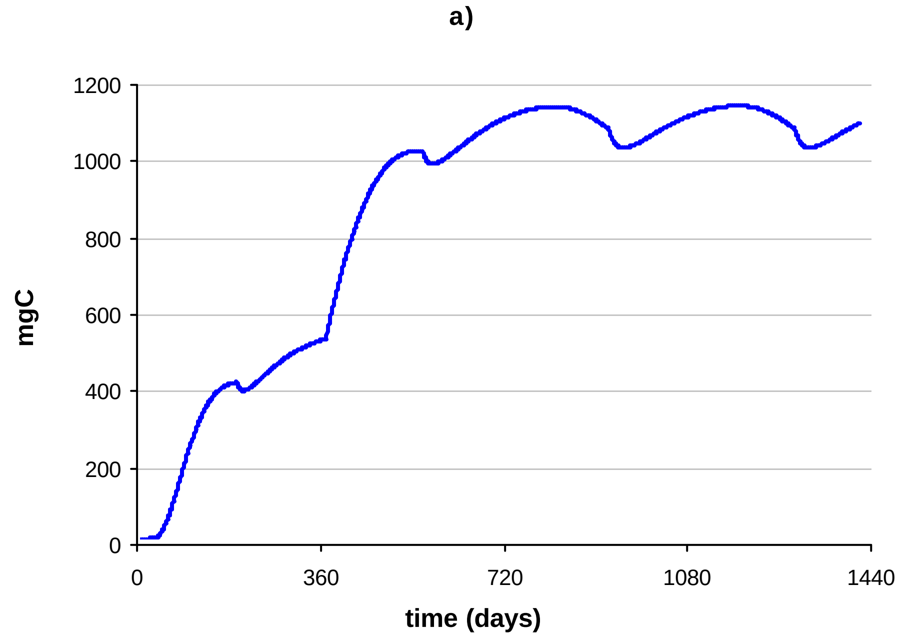
Name	Units	Meaning	Larvae	Juvenile	Adult
Ki	-	Ingestion coefficient	0,3	-0,25	-0,25
Ka	-	scope of biomass growth in the specific stage	0,7	0,68	0,64
Kb	d^{-1}	maximum ingestion rate at 0 ºC	0,1210	0,0339	0,0146
Kc	$ºC^{-1}$	temperature constant	0,0693	0,0693	0,0693
Tw	ºC	water temperature	18	18	18
?	-	coefficient of zooplankton intake by the individual fish	0,5	1	1,5
Wp	mgC. $prey^{-1}$	weight of one individual prey	0,01	0,01	0,01
Ks	$individuals.L^{-1}$	half-saturation constant	4	4	3
K_E	-	net assimilation efficiency	0,7	0,8	0,8
K_{AM}	-	active metabolism excretion rate	0,2	0,1	0,2
K_{VM}	d^{-1}	vital metabolism biomass consumption rate	0,1780	0,0670	0,037

3.2 Population Growth Model

The conceptual model of the Population Growth (PGM) uses the Tagus estuary as the case study and *Engraulis encrasicolus* as the studied fish species. The model was implemented using the Powersim^{TM} software. First, the PGM was tested with several simulations with different initial conditions for the number of individuals in each class of the fish population and no irregularities were found in the results. For that reason it is chosen that the population initial number of individuals is of 150.000 eggs (the same number of eggs as in an individual batch; this value is confirmed by Melo, 1994).

In the population growth model, individual mean weights necessary for the *scope for growth* estimate in each class of each life stage, are given by the IGM results (see Fig.9b for individual mean weights – the mean values are calculated upon the biomass curve throughout the life cycle illustrated in Fig.9a). Ingestion and destruction processes are estimated as in the IGM (using the values presented in Table.1), but using the mean biomass values.

The PGM uses a characteristic mortality rate for each class. The PGM simulations consider the curve of Fig.10 and plus two different situations of higher mortality rates in the adult stage (see Table.2, scenarios 3 and 4). In the first few days of life, fish face an intense mortality, either because they are driven by the currents and therefore may end up in places too adverse (in the stage of egg and the L_1 and L_2 classes of the larvae stage), either because they are too young and don't know how to find food or how to escape from predators (larvae stage). In the egg stage only 10% of the eggs survive and in the larvae stage there is a total mortality of 59% in one-month period. According to Ré (1986) in the first period of life fish may present 60-100% mortality rates. At the end of their life cycle, fish present a higher mortality rate because they present a higher risk of dying of age and/or diseases (in the class A_3).



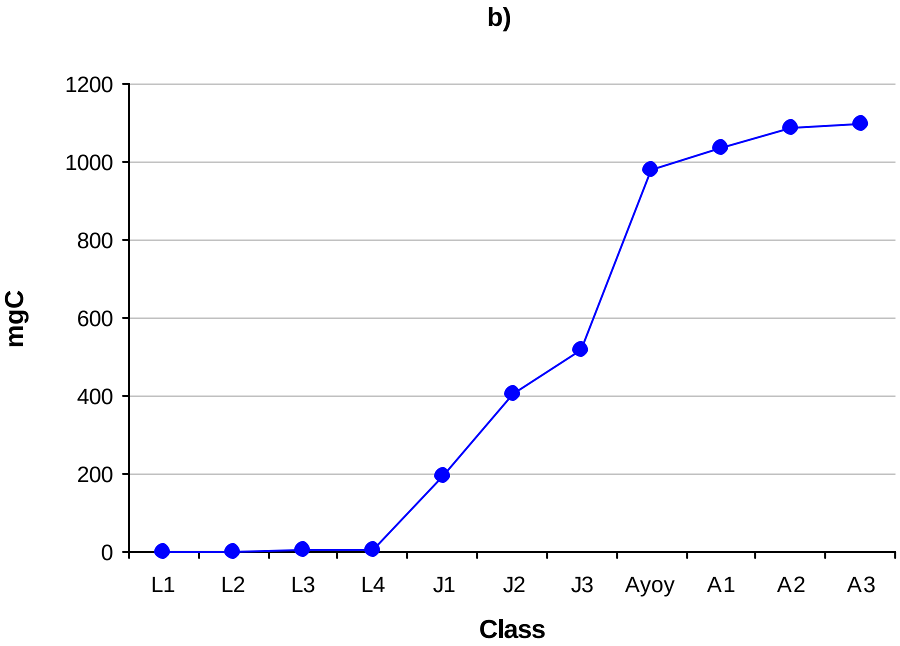


Fig. 9 a) IGM results for a simulation of the anchovy's biomass growth in the Tagus estuary for 4 years, providing the individual fish biomass (mgC). From these results it is possible to calculate the b) mean individual weight of an individual fish in each class of the stages of larvae, juvenile and adult used in the PGM. Comparing curves a) and b) it is concluded that b) represents the biomass mean values throughout all the fish's life stages.

Four different scenarios are developed to test the PGM model (see Table.2). Scenario 1 is an ideal situation without environmental or anthropogenic stresses; scenario 2 is a situation with a less reproductive population (due to environmental stress), where the number of spawners in the adults' stage is less significant; scenario 3 is a situation considering anthropogenic stresses (e.g. fishing) over all the classes of the adult stage, represented by a mortality 10 times higher than in scenario 1; scenario 4 is a modification of scenario 3, considering fishing stress over the adult classes except for the young-of-the-year individuals.

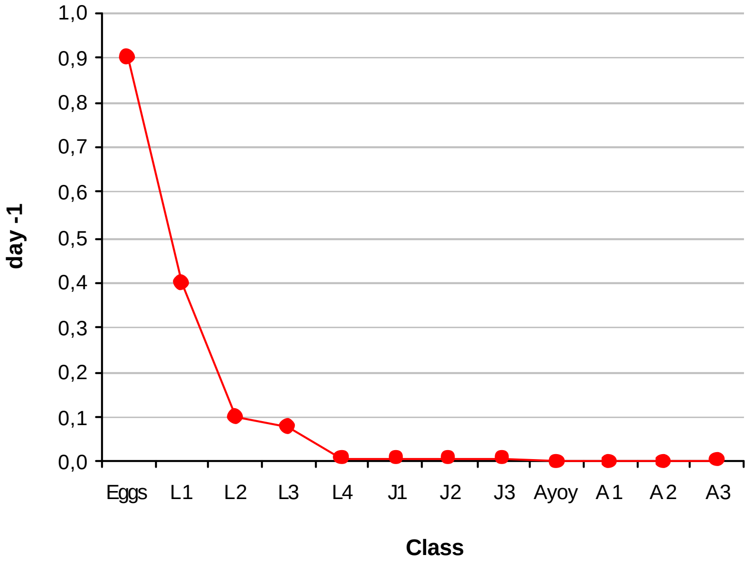


Fig. 10. Mortality rates used in the PGM for each class.

Table.2 PGM parameters' values and state variables initial values. These values result from the calibration of the model after introducing some typical values presented by Melo (1994), Ré (1986) and Henrique Cabral (*pers.com*).

Name	Units	Meaning	Scenario			
			1	2	3	4
BS	eggs.individual^{-1}	batch size (per individual fish)	150000	150000	150000	150000
S_{Eyoy}	-	percentage of spawners in class A_{YOY}	0,2	**0,1**	0,2	0,2
$S_{E\ A1}$	-	percentage of spawners in class A_1	0,4	**0,2**	0,4	0,4
$S_{E\ A2}$	-	percentage of spawners in class A_2	0,3	**0,2**	0,3	0,3
$S_{E\ A3}$	-	percentage of spawners in class A_3	0,3	**0,2**	0,3	0,3
m_E	d^{-1}	characteristic mortality in class Eggs	0,9	0,9	0,9	0,9
m_{L1}	d^{-1}	characteristic mortality in class L_1	0,4	0,4	0,4	0,4
m_{L2}	d^{-1}	characteristic mortality in class L_2	0,1	0,1	0,1	0,1
m_{L3}	d^{-1}	characteristic mortality in class L_3	0,08	0,08	0,08	0,08
m_{L4}	d^{-1}	characteristic mortality in class L_4	0,01	0,01	0,01	0,01
m_{J1}	d^{-1}	characteristic mortality in class J_1	0,008	0,008	0,008	0,008
m_{J2}	d^{-1}	characteristic mortality in class J_2	0,008	0,008	0,008	0,008
m_{J3}	d^{-1}	characteristic mortality in class J_3	0,008	0,008	0,008	0,008
m_{Ayoy}	d^{-1}	characteristic mortality in class A_{yoy}	0,001	0,001	**0,01**	0,001
m_{A1}	d^{-1}	characteristic mortality in class A_1	0,001	0,001	**0,01**	**0,01**
m_{A2}	d^{-1}	characteristic mortality in class A_2	0,001	0,001	**0,01**	**0,01**
m_{A3}	d^{-1}	characteristic mortality in class A_3	0,005	0,005	**0,05**	**0,05**

4 RESULTS AND DISCUSSION

4.1 Individual Growth Model

The IGM was calibrated and simulations starting in April with the parameters' values presented in Table.1 provide the results discussed in this section.

This model produces the individual fish's biomass throughout its life cycle (Fig.9a) in accordance with the expected. Before the adult stage (first 360 days) fish present an exponential growth - a considerable part of the ingested food allows the increase of the individual's biomass and not only the individual's survival. In addition, this exponential growth presents scope variations due to the seasonal variations in food availability. In the adult stage (after 360 days) the ingested food tends to be completely consumed by the fish's vital and active metabolisms and therefore the oscillations in the biomass result from seasonal variations in food availability. There is the exception of the young-of-the-year adults (the first semester of the second year (i.e. days 360 to 540) that present an extensive growth, which is in accordance to what it is usually observed in the field.

Considering that carbon biomass (mgC) represents 40% of the fish's dry weight (mg dw) and that fish's dry weight is 10% of its wet weight (mg ww), multiplying the IGM individual's biomass results by a factor of 25 provides the fish's wet weight. Therefore, according to the IGM results (see Fig.9a), an adult fish weights 27,4 g ww (1095 mgC), which is in agreement with field observations (25 to 30 g ww - Dr. Henrique Cabral *pers. com.*).

Concerning the larval growth the model considers the larvae metabolism as shown in Fig.11. The area between the IngestionL and DestructionL curves gives the larvae biomass growth. Destruction processes are discriminated with rectangular unfilled marks (egestion, active metabolism and vital metabolism). The vital metabolism consume of biomass is the highest, after half of the larval stage's period. However, in the first 17 days, egestion plays the main role of the destruction processes.

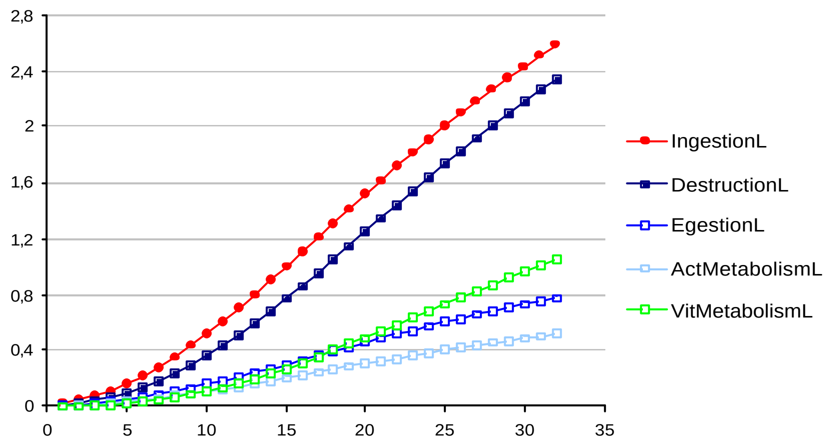


Fig.11 Larvae Metabolism.

In the juvenile stage there is an important biomass growth - at the end of this stage the fish's biomass is about 80 times higher than at the end of the larval stage (see Fig.9a,b). As this stage presents a characteristic time higher than that of the larvae, seasonal variations in phytoplankton and zooplankton are relevant as observed in Fig.12 - there is a period during winter when ingested food is not enough to supply the fish's destruction processes and therefore forcing a consumption of the fish's biomass.

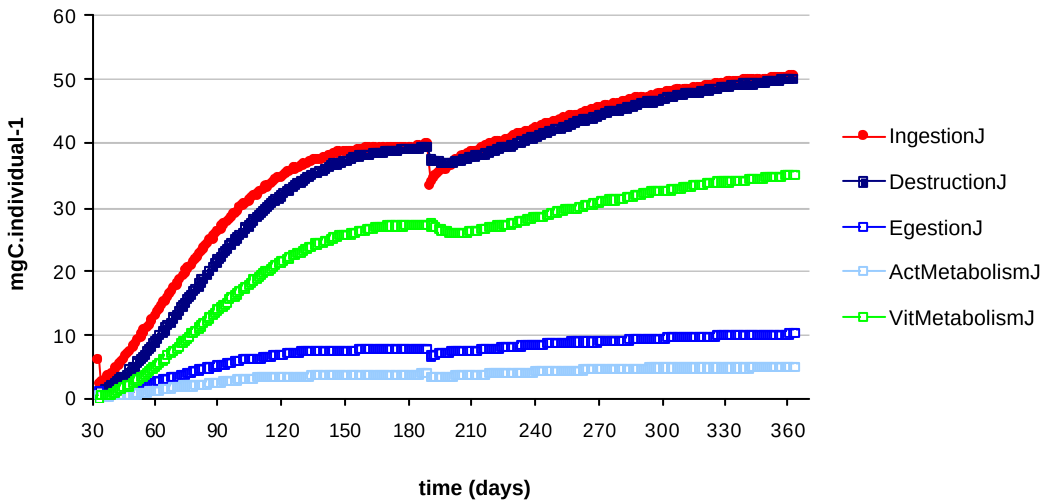


Fig.12 Juvenile metabolism.

As explained earlier, the adult metabolism is somewhat different of that observed in the previous stages (see Fig.13). In the first six months of the adult stage (the Young-Of-the-Year class in the population growth model) there is a significant biomass growth when the fish attains its first maturity age. At the same time there is an important increase in the individual's vital metabolism's consumption of biomass, thus preventing further growth with the same scope.

The adult stage lasts for about three years and consequently the winter collapses of food availability is very evident (compare Fig.13 with Fig.14). In these periods, ingestion decreases to a point where destruction processes are higher, which causes the individual's biomass to decrease in those periods (as observed in Fig.9a).

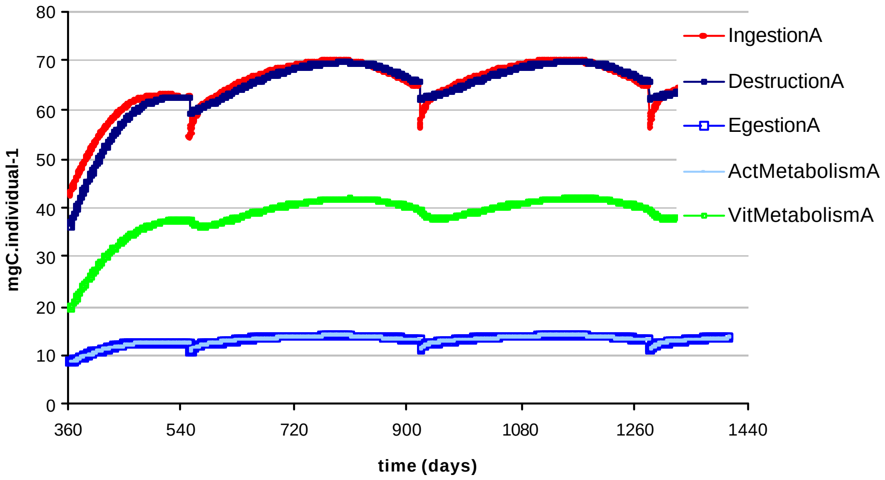


Fig.13 Adult metabolism.

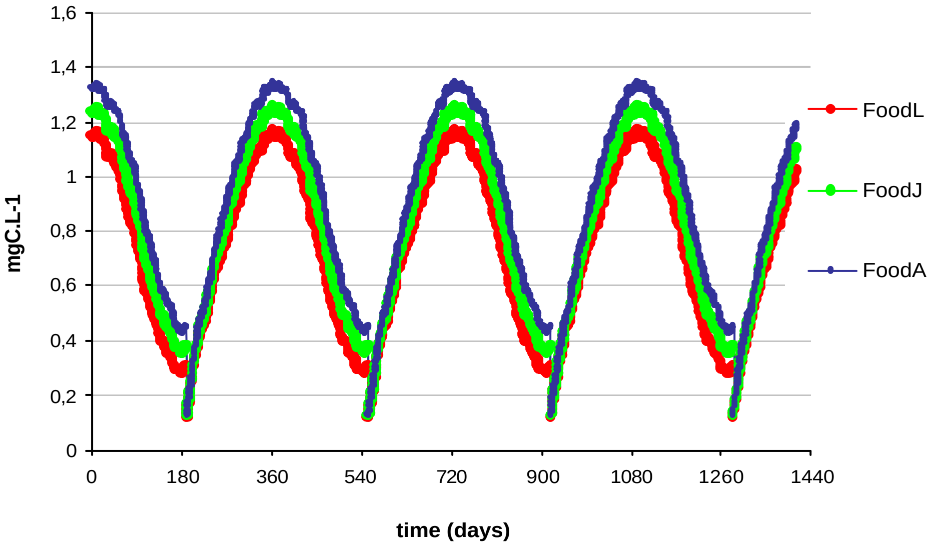


Fig.14 Available food for larvae (FoodL), juvenile (FoodJ) and adult (FoodA).

Running the IGM model with the parameters' values presented in Table.1 but using a series of food amount in the environment of **five times smaller** of that shown by Fig.8 (daily mean concentrations of phytoplankton and zooplankton) causes a smaller individual biomass growth, as illustrated in Fig.15, which is in agreement with what it would be expected. Here it is clear the model constrain of the fish's growth with the available food amount: less food availability causes lower growth.

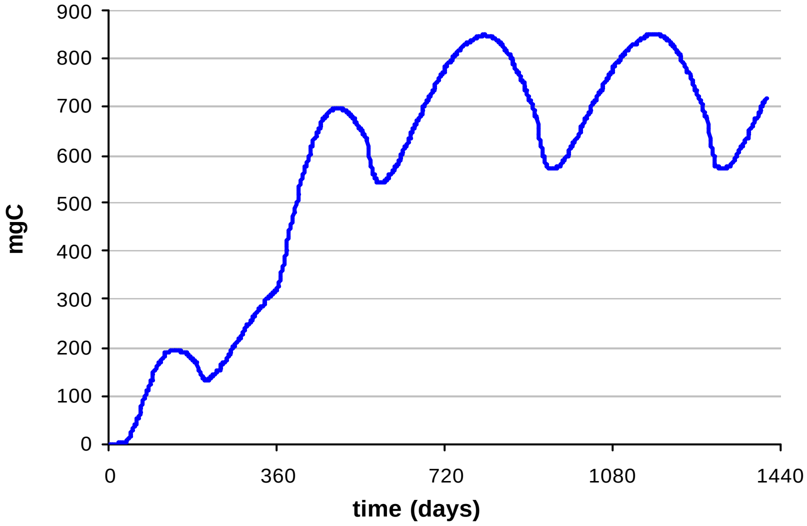


Fig. 15 Individual fish biomass (mgC) - IGM results for a simulation of the anchovy's biomass growth in the Tagus estuary for 4 years, using series of food amount five times smaller than that shown by Fig.8.

Another environmental factor considered by the IGM model is the water temperature (*Tw*), also of great importance to the fish's growth. The european anchovy withstands temperatures ranging from 6 to 29ºC. Comparing the IGM results of the individual biomass growth considering a ***Tw* of 10ºC** (Fig.16), with the results obtained with a *Tw* of 18ºC (Fig.9a), and all the other parameters remaining the same (Table.1), it is evident that when the water temperature gets closer to the limit, the fish's growth is lower.

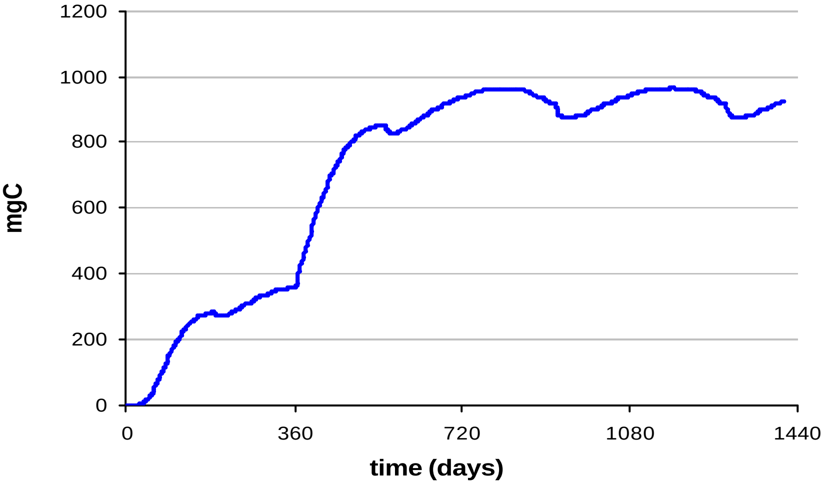


Fig. 16 Individual fish biomass (mgC) - IGM results for a simulation of the anchovy's biomass growth in the Tagus estuary for 4 years, with water temperature of 10ºC.

4.2 Population Growth Model

The PGM was simulated for five years to develop different scenarios, starting with a population of 150.000 eggs (the equivalent to one individual batch – Melo, 1994 -, not representative of real life systems, but it facilitates the interpretation of the results). In the PGM, ingestion and destruction processes are considered as in the IGM, but using the mean biomass values calculated from the individual biomass IGM results (see Fig.9b). The defined characteristic mortality rates (see Fig.10) are a key element in the model, as it would be expected.

4.2.1 Life Cycle in the Fish Population

There is an input of 150.000 eggs and the number of eggs rapidly decreases to zero because mortality in this stage is very high (m_E=0,9) and because the characteristic time of this stage is of 2 days – the survivors shift to the larvae stage (Fig.17a, Fig.18a, Fig.19a, Fig.20a). These results may be very useful when modelling fish movements according to their environmental preferences in time scales smaller than 1 year. When modelling fish movement it is possible to observe the importance of currents' variations throughout the year, since fish in the egg stage move with the water currents. Month-to-month currents variations cause different larvae settlement and consequently lead to different levels of survival.

In the larvae stage the characteristic mortality rates decrease from L_1 to L_4 (from 0,4 to 0,01 – see Fig.10) and therefore the number of individuals in class L_1 is considerably higher than that of classes L_2, L_3 and L_4, as illustrated in Fig.17b, Fig.18b, Fig.19b and Fig.20b.

When moving up to the juveniles' and adults' stage, the food availability constraint plays an important role (see Fig.17c,d, Fig.18c,d, Fig.19c,d, Fig.20c,d). In fact, the seasonal variations in the amount of available food, determined by the phytoplankton and zooplankton concentrations in the system, force variations in the scope for growth, and thus the number of fish in each class. From stages J_1 to J_3 the number of individuals decreases due to each class's characteristic mortality and the shifts to the next class. In the adult stage however, depending on the characteristic mortality (reference scenario or anthropogenic stress scenario, both presented in the next section 4.2.2) the number of individuals may increase or decrease (Fig.17d, Fig.18d, Fig.19d, Fig.20d).

4.2.2 Scenarios

In this section are presented the results obtained in four different scenarios (see Table.2), thus permitting an efficient analysis of the PGM parameters.

Scenario 1 is an ideal situation without environmental or anthropogenic stresses. When comparing the different scenarios, scenario 1 is the reference scenario.

Scenario 2 is a situation with a less fertile population, considering a less significant number of spawners per class in the adult stage. This second scenario represents a situation where the fish population experience environmental stress (other than food availability and water temperature, already included in the model), consequently declining the reproduction activity, therefore being less *fit* (Railsback *et al*, 1999).

Scenario 3 is a situation considering anthropogenic stresses (e.g. fishing) over all the classes of the adult stage, represented by an increase in the characteristic mortality 10 times higher than in the reference scenario.

Scenario 4 is a modification of scenario 3, considering fishing stress over the adult classes except for the young-of-the-year individuals (to simulate the result of fisheries' law restriction in fishing mesh size). In this fourth scenario it is assumed that the present mesh size limit imposed by the law is so that it forbids catches of fish in the young-of-the-year adults class.

Although the PGM differentiates individuals in each class using biomass values, there is a relationship between the fish's biomass and fish's length, hence permitting to compare this value with the limit imposed by the law. Froese & Pauly (2000) developed a database with *a* and *b* values of the following linear regression:

$$W = a.L^{b} \qquad (12)$$

where W is the fish's biomass (g ww) and L is the fish's length (cm total length). Using Pereda and Villamor (1991) *a* and *b* values (0,001 and 3,448 respectively) for *Engraulis* *encrasicolus*, for an adult's biomass of 1095 mgC (27,4 g ww), the correspondent total length is of 19,4 cm. This length value is consistent with field observations (Ré, 1986; Froese & Pauly, 2000; Dr. Henrique Cabral, *pers. com.*).

In the reference scenario (Fig.17), although the population starts with a single batch, its evolution is quite productive – in five years the population increases from zero to 1100 adult fish (Fig.21a). In this scenario the number of individuals in the fish population varies according with seasonal variations in food (Fig.8), provided that there is no other stress to the population.

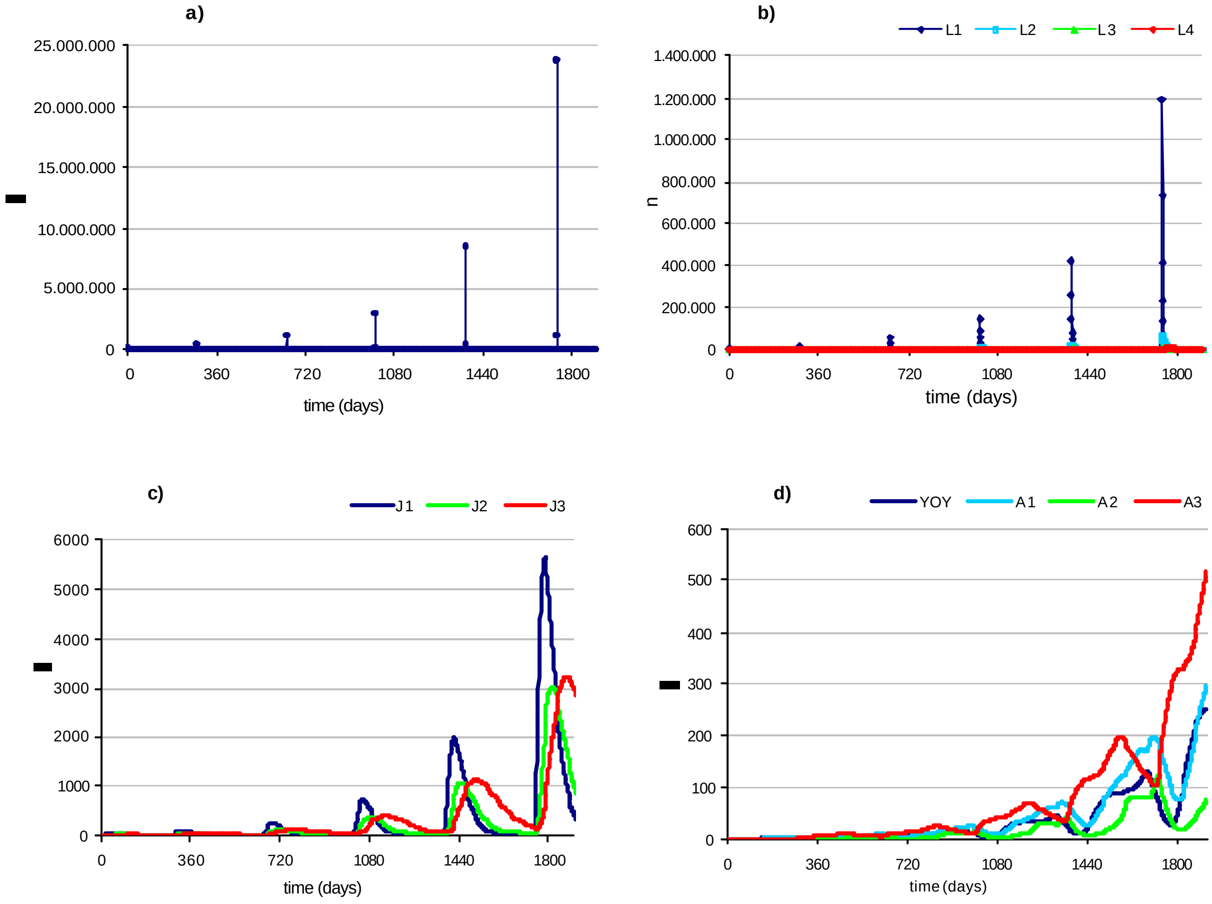


Fig.17 PGM results for the simulation of Scenario 1 or "reference scenario" for 5 years (day 0 corresponds to the beginning of April). a) Number of eggs in the fish population; b) number of fish in each class of the larvae stage; c) number of fish in the classes of the juvenile stage; d) number of individuals in each class of the adult stage (see Section 2.4 for more information about these classes).

When considering environmental stress (other than food availability and water temperature), fish react by decreasing their reproduction activity, due to being less *fit* (Railsback *et al*, 1999). This is the situation simulated in scenario 2. The comparison of scenario 2 (Fig.18) with the reference scenario (Fig.17) puts in evidence the consequences of a lower number of spawners to the total number of fish in the population. In fact, after five years, the population presents an increase of 350 adult fish (Fig.21b). Therefore, diminishing the percentage of spawners in scenario 2 to half or higher than that of scenario 1 (as shown in Table.2) causes an evolution in the adults population 64 % weaker (almost 2/3 less).

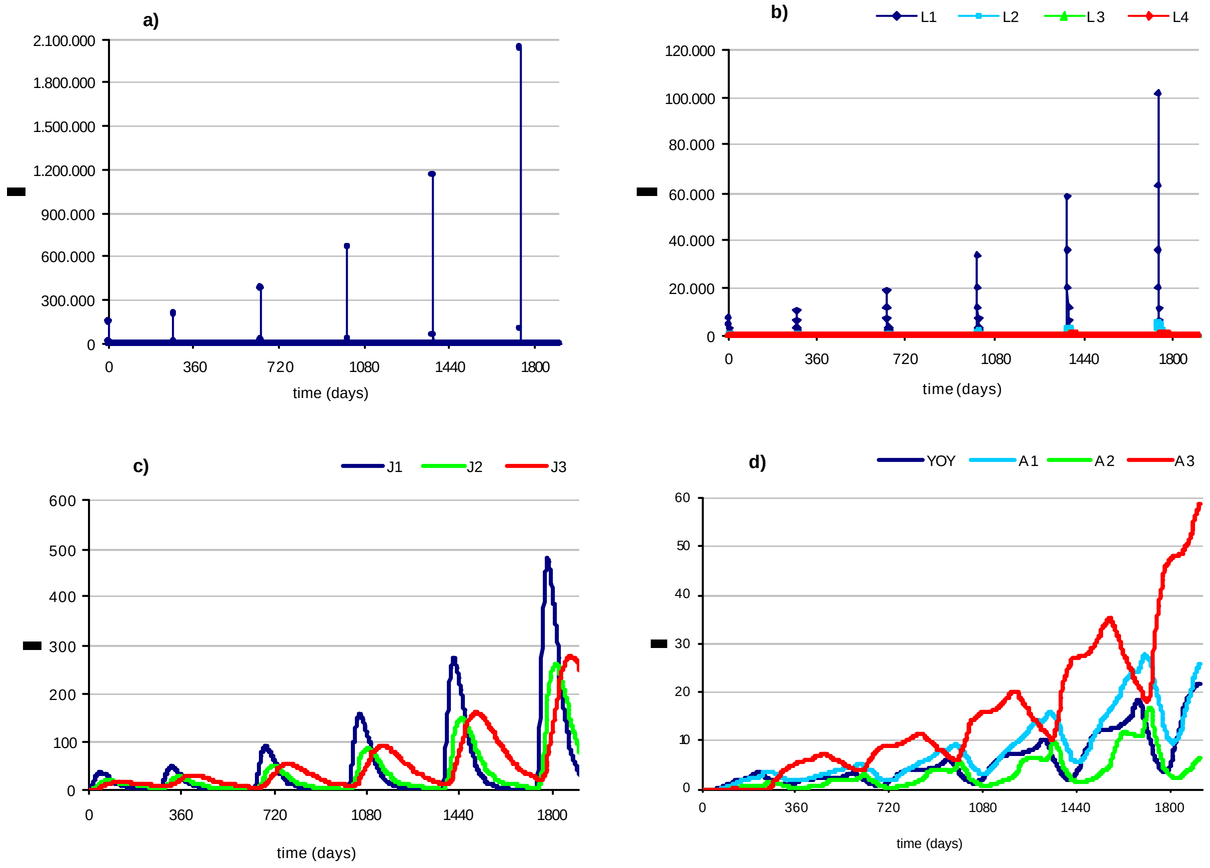


Fig.18 PGM results for the simulation of Scenario 2 or "less *fit* scenario" for 5 years (day 0 corresponds to the beginning of April). a) Number of eggs in the fish population; b) number of fish in each class of the larvae stage; c) number of fish in the classes of the juvenile stage; d) number of individuals in each class of the adult stage (see Section 2.4 for more information about these classes).

Regarding scenarios 1 and 2 (Fig.21a,b), it is clearly identifiable the consequences of a less *fit* population (scenario 2) with the same food availability and same water temperature: the population grows exponentially in both scenarios, but more rapidly if the population is more *fit*. Therefore the “percentage of spawners” parameter S_{Ec} is an important parameter in the PGM model.

If one considers anthropogenic stress on the fish population in the PGM model, the results are quite different from those presented above, as it would be expected. However this is an important scenario to assess the consistency of the PGM results, since anthropogenic stresses are an ever-growing reality in nearly all real aquatic systems.

In scenario 3, anthropogenic stress is incorporated in the PGM model, affecting the four classes of the adult stage, as explained above. This is a scenario that represents the situation of an aquatic system where fishing activity takes place with no rules (no law restriction). The consequence of a higher mortality in the adult stage results in the diminishing of the number of individuals in each class and after few years, in the disappearance of the fish population (Fig.19).

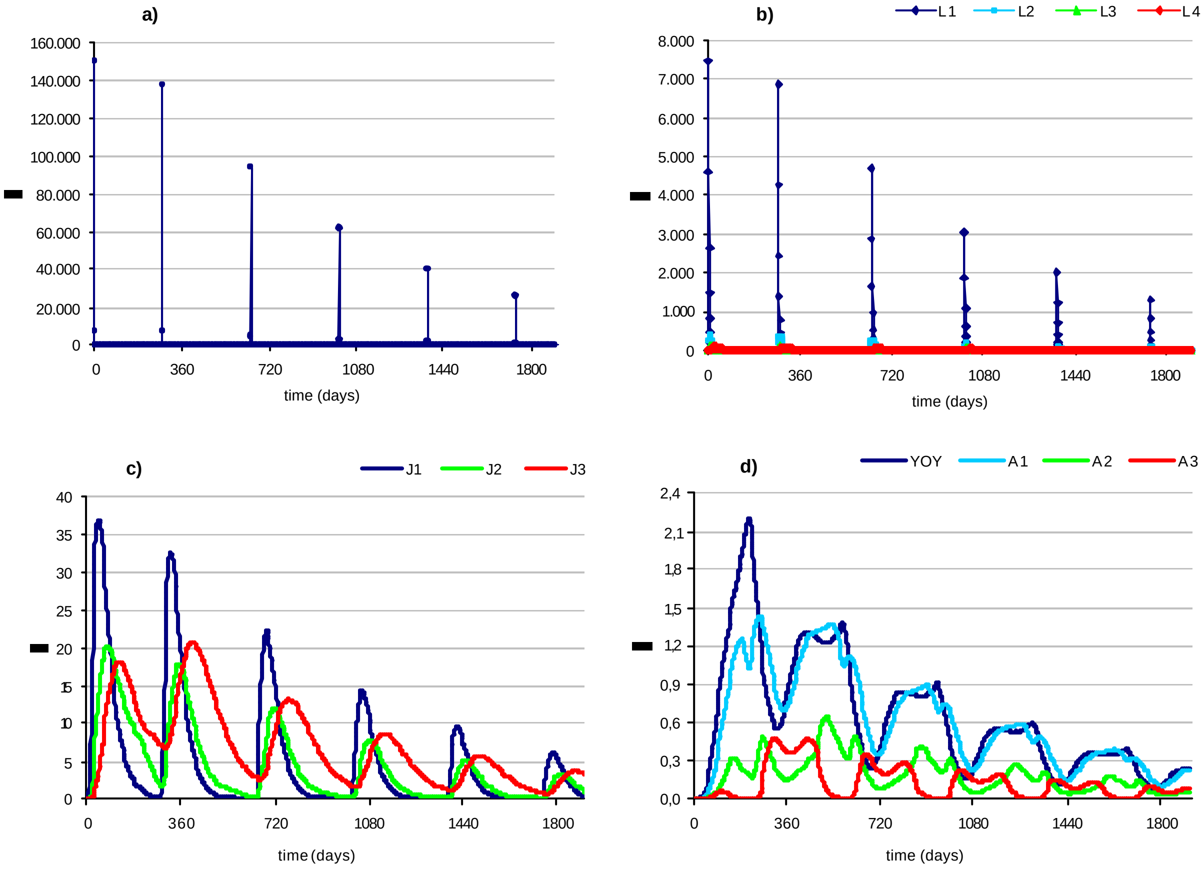


Fig.19 PGM results for the simulation of Scenario 3 or anthropogenic stress scenario for 5 years (day 0 corresponds to the beginning of April). a) Number of eggs in the fish population; b) number of fish in each class of the larvae stage; c) number of fish in the classes of the juvenile stage; d) number of individuals in each class of the adult stage (see Section 2.4 for more information about these classes).

When changing this third scenario to consider fisheries' law restriction in fishing mesh size – resulting in the fourth scenario - only by keeping the young-of-the-year fish mortality as in the reference scenario, the results do not lead to the extinction of the fish population, but to a steady population with short growth (Fig.20).

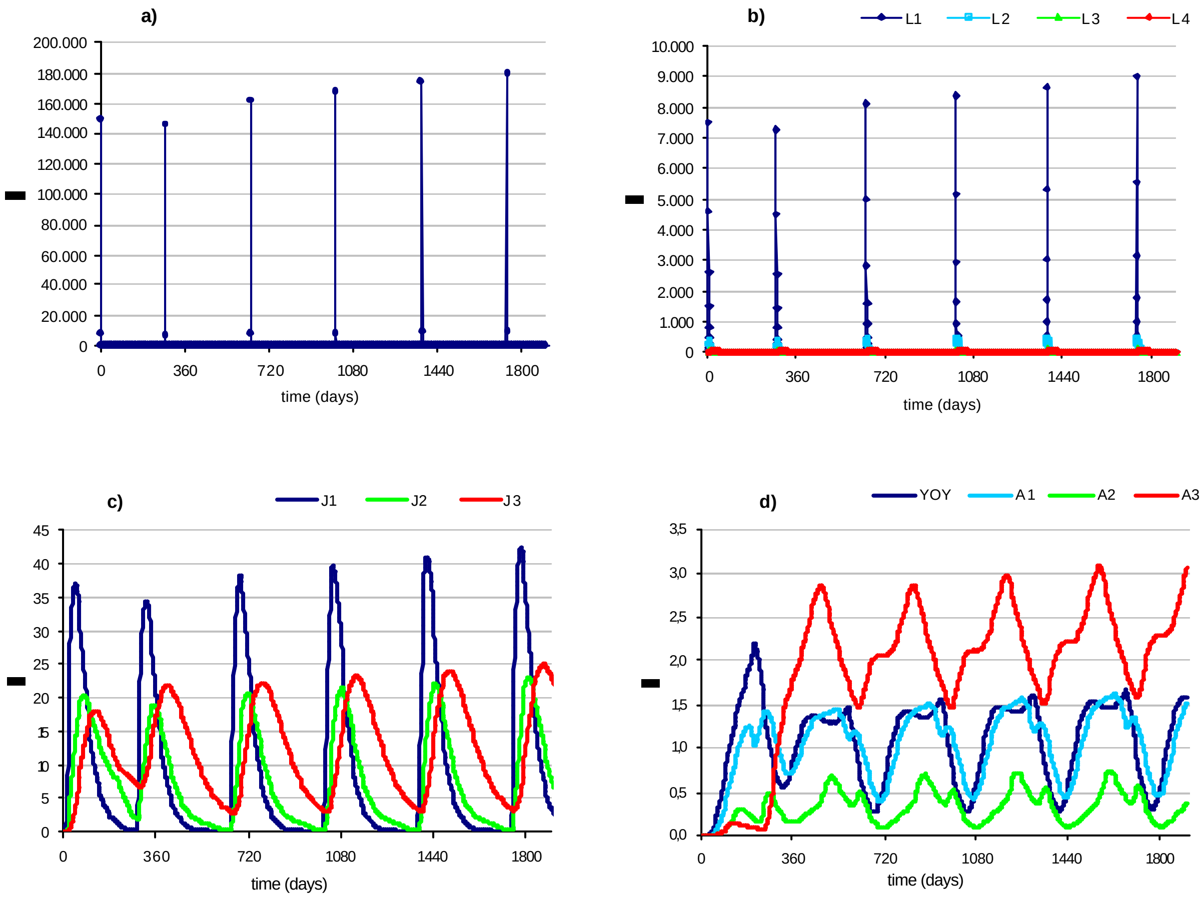


Fig.20 PGM results for the simulation of Scenario 4 or anthropogenic stress with law restriction scenario, for 5 years (day 0 corresponds to the beginning of April). a) Number of eggs in the fish population; b) number of fish in each class of the larvae stage; c) number of fish in the classes of the juvenile stage; d) number of individuals in each class of the adult stage (see Section 2.4 for more information about these classes).

Comparing the results of scenarios 3 and 4 permits to evaluate the effect of the fisheries' law restriction. By catching only the fish with 19 cm or bigger - which by Froese & Pauly's (2000) length-weight relationship is a fish with 25 g ww (1000 mgC) the fish population is saved from extinction (see Fig.21c,d).

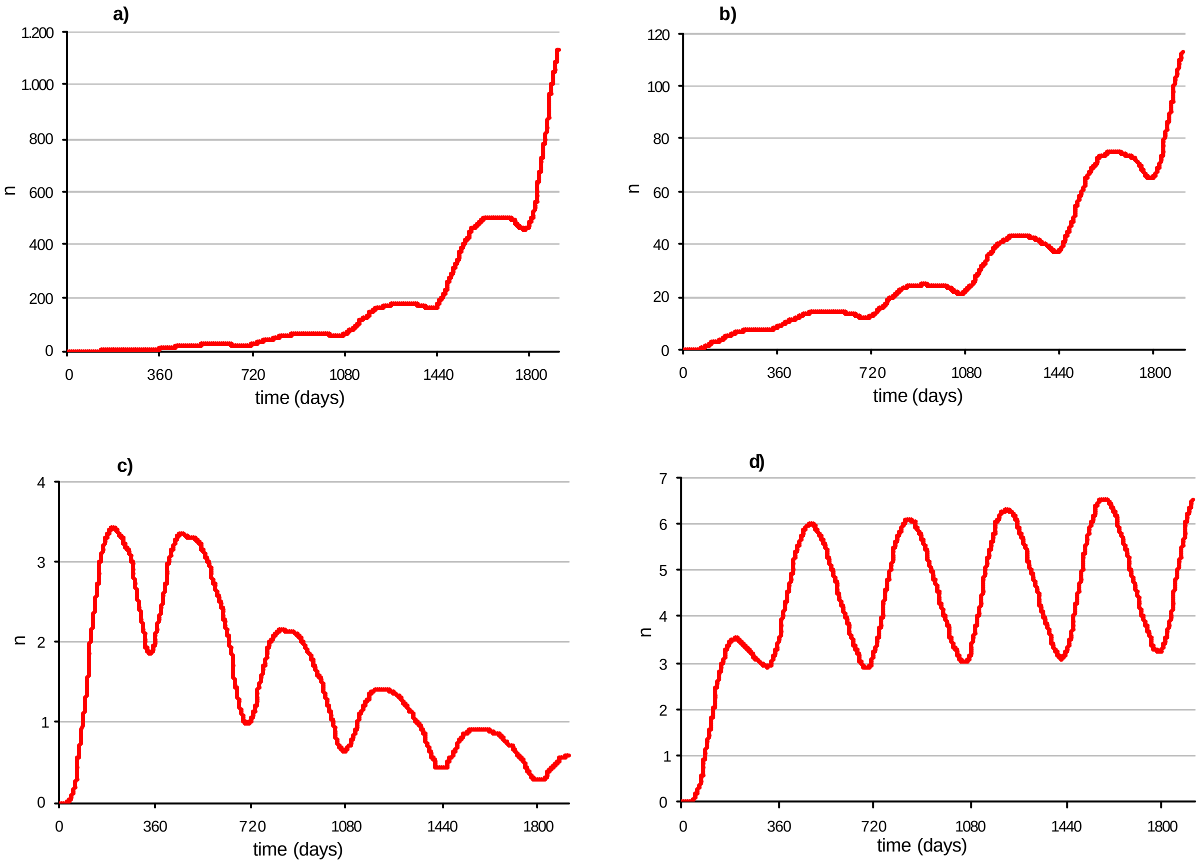
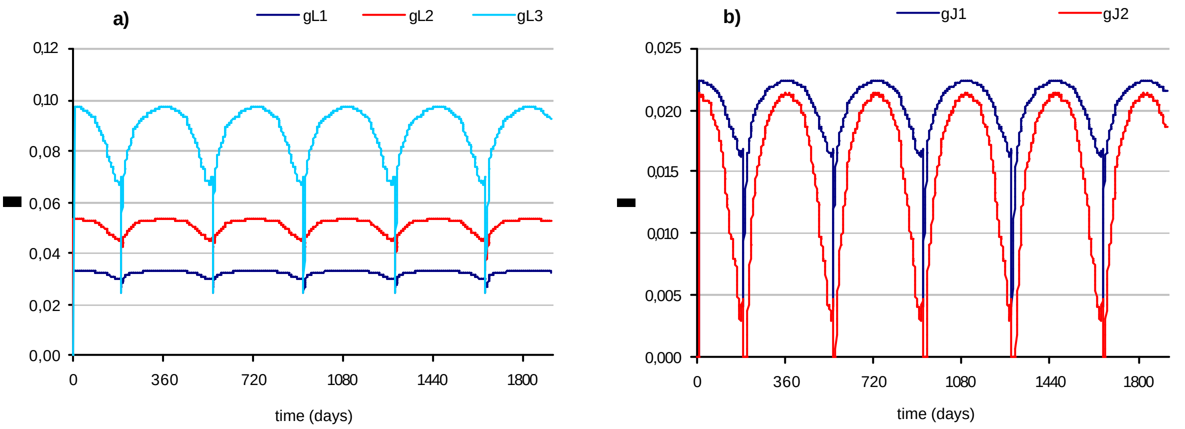


Fig.21 PGM results for the total number of individuals in the adult stage, in the fish population: a) scenario 1, or reference scenario, b) scenario 2 or "less *fit*" scenario, c) scenario 3 or anthropogenic stress scenario and d) scenario 4 or anthropogenic stress with law restriction scenario.

The *scope for growth* function determining the variation of the number of individuals in the population (see Equation 8) depends on the fish's individual metabolic characteristics (see Equation 9). Although several simulations were made with different ingestion, egestion, vital metabolism and active metabolism to test the PGM model, the one presented here is the one that characterizes the anchovy's growth. But it is unmistakable that if one changes the metabolic rates then the individual's mean biomass in each class would be different and so would be the *scope for growth* and consequently the population's growth.

In all the scenarios developed above, scope for growth, *g*, fluctuates as illustrated in Fig.22 in each class of each stage.



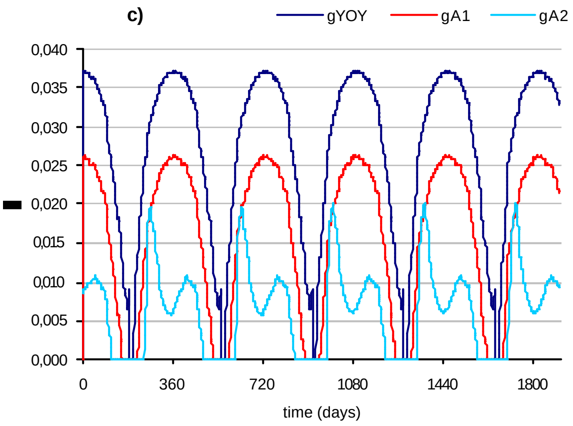


Fig.22 Scope for Growth, g (d^{-1}), for each class of the a) larvae stage, b) juvenile stage and c) adult stage, considered in the simulations of the scenarios presented in this section.

The scenarios were developed without changing the scope for growth, since this function translates the species metabolic characteristics and environmental conditions for food and water temperature, hence permitting to analyse the parameters of the PGM and not those of the IGM. The curve of g function has a mean value for each class as illustrated by Fig.23. The mean value of g increases in the YOY and A_2 classes of the adult stage are due to the small variation in the mean individual biomass, characteristic of this life stage.

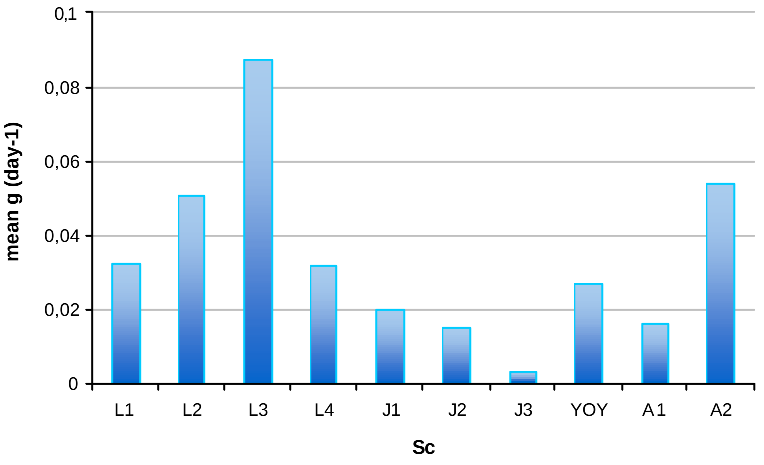


Fig.23 Mean g (scope for growth) in each class of each stage of the life cycle.

5 CONCLUSIONS

The results obtained by the model developed in this thesis are in conformity with field measurements to what it concerns biomass values of the individual fish and growth responses to changes in the environment (the IGM model evaluated water temperature and food availability).

Results of the individual growth model indicate that the growth of the european anchovy throughout the four years of the life cycle culminates in an adult biomass of 27,4 g ww (1095 mgC), which is in agreement with field observations. This biomass value corresponds to a 19,4 cm length fish (also consistent with field measurements).

Concerning the IGM parameters, if one considers a five times smaller food amount (*Wfood*) in the environment (with all the rest of the IGM parameters remaining the same), the adult biomass is smaller (17,5 g ww). Comparing this result with the first simulation, it is concluded from the IGM model that less food availability causes lower growth.

A test was made to analyse the influence of the water temperature (*Tw*). Decreasing this parameter from 18 to 10 ºC, with all the other parameters remaining as in the first simulation (Table.1) the model result for the adult biomass is of 23 g ww. Comparing this result with the first simulation it is concluded that when the water temperature gets closer to the limit supported by the european anchovy, the fish's growth is lower.

Also the results of the population growth model are in agreement with what is expected in each of the four scenarios presented in section 4.2.2. In all the scenarios the population starts with a single batch (150.000 eggs) and the eggs mortality was considered constant and equal to 0,9 (i.e. 10% survival). The mortality rates play a crucial role in the evolution of the number of fish in the population.

Scenario 1 is an ideal situation without environmental or anthropogenic stresses. In the first scenario there is a reasonably productive evolution and in five years the population increases from zero to 1100 adult fish. Scenario 2 considers a less significant number of spawners per class in the adult stage (S_{Ec}), representing a situation where the fish population experience environmental stress that declines the reproduction activity. When considering environmental stress fish react by decreasing their reproduction activity, being less *fit*; in a five years' simulation the population presents an increase of 350 adult fish. Comparing scenarios 1 and 2, it is concluded that a decrease in the percentage of spawners in the population to half or higher, causes an evolution in the adults' population 64 % weaker (almost 2/3 less). Therefore, the consequences of a less *fit* population are very clear: the population grows exponentially in both scenarios, but more rapidly if the population is more *fit*. Therefore the S_{Ec} parameter is very important in the PGM model.

Scenario 3 considers the existence of anthropogenic stresses (e.g. fishing) over all the classes of the adult stage, with an increase in the characteristic mortality 10 times higher than in the first scenario. In this scenario, the results are quite different from those in scenarios 1 and 2. A higher mortality in the adult stage results in the declining of the number of individuals in each class and after few years, in the disappearance of the fish population Scenario 4 is a variation of the third scenario, considering fishing stress over the adult classes except for the young-of-the-year individuals (to simulate the result of fisheries' law restriction in fishing mesh size). In this fourth scenario the results do not lead to the extinction of the fish population, but to a steady population with a small growth. The comparison of the results of scenarios 3 and 4 evaluates the effect of the fisheries' law restriction. By catching only the fish with 19 cm or bigger (with 25 g ww or more) the fish population is saved from extinction.

The scope for growth function translates the species metabolic characteristics and responses to environmental conditions for food and water temperature. If one changes the metabolic rates then the individual's mean biomass in each class is different and so it is the *scope for growth* and consequently the population's growth.

6 RECOMMENDATIONS FOR FUTURE WORK

Despite the growth of the individual fish is modelled here as a function of its metabolic characteristics and environmental conditions water temperature and food availability, the evolution of the population growth model to include movement rules according to the fish's environmental preferences is crucial to get closer to the *real world*. Therefore, the model developed in this thesis will gain by introducing (1) an individual growth model dependent of a higher number of relevant environmental variables and (2) a space concept in the population growth model, not only with advection-diffusion variables, but also with a spatial grid of the fish's environmental preferences. In this case, the individual growth will be dependent of the location of the fish in the estuary, since its fitness is not the same throughout the system. One good example is that of the eggs. Eggs are driven by the water currents, not being able to chose where to swim. Therefore, depending on the water currents in an estuary, eggs may end up in the sea (with zero recruitment to the population in the estuary), or in more protected areas hence permitting them to survive and develop to the larvae stage.

After gathering the knowledge of what as been done so far in the modelling of fish populations area it is in theory somewhat easy to predict the pathway that this model should follow in the near future. However, this pathway is dependent on empirical knowledge gained in field data processing. For instances, to model the fish's environmental preferences it's essential to study the fish's responses to changing environmental variables (as studied by Breitburg *et al*, 1999; Cowan Jr *et al*, 1999; Jaworska *et al*, 1997; Lindholm *et al*, 2001; McDermot & Rose, 2000; Rose & Cowan Jr, 2000; Rose *et al*, 1999a, 1999b; Sekine *et al*, 1991a, 1991b, 1996, 1997; Tyler & Rose, 1994).

In the Tagus estuary it is necessary to gather the complete information about each species location according to the life stage, since fish inhabit different areas of the estuary depending on the stage of the life cycle. In fact, to be capable to accomplish an efficient management of this living resources in Portugal, it is necessary an intensive study in all the portuguese estuaries and coastal zones, since fishing activity is of such a great importance to the Portuguese economy. Therefore, to a sustainable practice of the fishing activity, the processing of field data will permit the development of a *more close to the reality* model that includes each site characteristics and their influence on the evolution of the fish populations.

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Lisbon, 18th of December, 2001

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A APPENDIX

A.1 MOHID2000

The model developed in the scope of this thesis is to be inserted in the System MOHID in the near future. The development of this system was initiated in the decade of 80, but its application to different scientific and technological projects has permitted its successive perfectionings.

MOHID2000 is a full 3D-baroclinic model and has been developed using an object-oriented programming philosophy, using the ANSI Fortran 95. The object-oriented programming has proven to be a very useful methodology in the development of complex programs, especially for those that simulate *real world* problems, of which the modelling of marine or estuarine processes are good examples. The use of the ANSI Fortran 95 guarantees the independence of system MOHID face to the operative system in which the model is executed (Windows, Linux, Unix, etc.) and permits an easy implementation of the code in any environment. The option of running several modules (hydrodynamics, turbulence, drift, etc.) with different time steps allows an optimisation of the required calculation time for the execution of the simulations. The system uses the dynamic allocation of the memory, optimising the use of the computer features and allowing the use of a single executable file.

The model is based on a finite volume concept. Finite volumes' technique consists in applying the physical, chemical and biological laws that conduct the processes intended to simulate, directly to a control volume as a flux divergence. As a consequence, this method automatically guarantees the conservation of transported properties.

The system has two main modules: one manages the **hydrodynamic properties** (ex: velocity, elevation, water fluxes, turbulent viscosity, etc.) and the other manages the **water properties** (e.g. salinity, temperature, density, SPM, nutrients, phytoplankton, coliforms). Both modules solve the equations in the real domain without any space transformation. The geometry information is carried in the areas and volumes needed to calculate the fluxes. The cells may have any initial shape and be subjected to any time deformation, allowing several vertical discretizations, which can be used simultaneously in different regions of the domain. This architecture is equivalent to a generic vertical coordinate.

The hydrodynamic properties evolution is computed solving the three-dimensional primitive equations in rectangular coordinates for incompressible flows. Hydrostatic equilibrium is assumed as well as Boussinesq approximation. The turbulent viscosity can be computed using several models. In the horizontal plan the options are: constant value or Smagorinsky models. In the vertical plan the models that can be used are: a constant value, a mixing length model (Nihoul, 1984), a one-equation (K) model or a two-equations (K-L) model. The water properties evolution is computed solving the advection-diffusion equation explicitly in the horizontal and implicitly in the vertical. The sinks are computed forward in time and the sources are computed backwards to avoid negative values of mass.

The system uses five different types of boundary conditions: free surface, bottom, lateral closed boundary, moving boundary and lateral opened boundary (Neves & Santos, 1991). Moving boundaries are closed boundaries with a position that varies in time. For the lateral and moving boundaries the conditions are always null flux. Any exchange between land and the sea is computed as a discharge (for example a river or an outfall). The discharge module can compute the discharges of hydrodynamic properties (e.g. momentum) and also of water properties (e.g. SPM, salinity). For each of the other three boundary conditions, bottom, surface and open boundary, there are specific modules. The bottom module is responsible for the fluxes between the bottom and the water column (e.g. shear friction, erosion/deposition of sediments). The surface module is responsible for the fluxes between the atmosphere and the water column (e.g. wind forcing, gas emission, solar radiation).

To avoid chaotic growth of the MOHID2000 it is necessary to implement program techniques together with a set of rules that ensure reliability and maintainability. The object-oriented programming is the more powerful technique to achieve these goals. This issue is especially important for large software systems like the MOHID2000. These systems are usually developed by several collaborators separated in time and in space and for this reason a model must be able to incorporate new contributions everyday without any difficulties.

Another very important issue is the input data (pre-processing) of complex models. It is essential to develop graphical interfaces to help users to give the model basic data in a systematic way. If the user is not a member of the development team, the probability of introducing input data errors is somehow high if the input data methodology is for example Ascii files. Output data (post-processing) analysis is also an important issue especially when one’s talking of a 4D numerical tool (3 spatial dimension plus time) that is able to compute the evolution of almost 30 properties. If the users do not have access to tools that allow them to see the output data in an intuitive way this task can lead to a non-profitable time consuming. A graphical interface has been developed to allow the user to explore the data using 2D images (3D slices) animated in time.

A.1.1 Lagrangean Tracers Module

MOHID2000 Lagrangean Tracers Module can be coupled upstream to a finite-differences (sigma, double-sigma, Cartesian) 3D hydrodynamic model and downstream to a zero-dimensional water quality model, an oil dispersion model and a sediment model. This model has been used in a wide number of study cases: impact of organic effluents in estuarine environments, hydrodynamic model calibration comparing tracer trajectories with real drifter trajectories, exchanges between different areas in an estuary, exchanges between the deep ocean and the continental shelf, primary productivity in the ocean, sediment transport, oil dispersion, etc.

The variety of applications enumerated shows that a Lagrangean dispersion model is a privileged tool for coupling physics, biology, chemistry and geology in the marine environment.

A.1.2 Eulerean Transport Module

This module allows calculation of a property characterised by a soft gradient. It solves explicitly the advective and diffusive horizontal terms and implicitly the advective and diffusive vertical terms. The advective term can be solved using one of the following discretization schemes: centred differences, upwind and QUICK.

This module can be coupled both to two and three-dimensional hydrodynamic modules. In the three-dimensional baroclinic module it is used to calculate the spatial and temporal evolution of salinity and temperature since these values are used in determining the density value in each model point.

A.1.3 Cohesive Sediment Transport Module

The simulation of cohesive sediment transport processes is performed solving the 3D-conservative advection-diffusion equation. For the representation of the processes of flocculation and erosion and deposition of bottom sediments refined empirical formulations based on data field was adopted. The models have been calibrated and tested by simulating tidal flows and suspended sediment transport in different estuaries. Results show a good agreement between the numerical predictions and corresponding field measurements.

A.1.4 Water Quality Module

This is a non-dimensional model, which allows easy coupling to a transport module, both in the Lagrangean and Eulerean formulations. This model simulates the main biochemical processes of phytoplankton, zooplankton, phosphorus, nitrogen and oxygen in the pelagic zone. The nitrogen cycle species are modelled separately and include its three main inorganic forms - ammonia, nitrate and nitrite - along with three organic forms of nitrogen - refractory and non-refractory fractions of dissolved organic nitrogen and particulate nitrogen. The phosphorus cycle species simulated by this model include inorganic dissolved forms of which the main group is the orthophosphates (PO43-, HPO42-, and HPO4-), as well as organic dissolved and particulate phosphorus. In relation to oxygen, calculations are made for dissolved oxygen and CBO. For each property the model calculates the sink and source term, due to the main biological and chemical processes occurring in the water column.

ABSTRACT

An effective management of the fisheries resources requires an understanding and the ability to predict fluctuations in abundance and biomass production. In this work it is developed a growth model for individual fish and correspondent fish population in a coastal ecosystem, using the european anchovy (*Engraulis encrasicolus*) in the Tagus estuary (Lisbon, Portugal). The model involves two distinct sub-models: the individual growth model (IGM) and the population growth model (PGM). Individual fish biomass varies in each life stage as a function of its metabolic characteristics, food availability in the environment and water temperature. In the PGM the number of fish in each class of the four life-stages is calculated taking into account the individual stage-specific biological processes, percentage of spawners in the population, class-specific characteristic mortalities and class-specific scope for growth. The IGM simulations give an adult individual biomass of 27,4 g ww with normal food concentration in the Tagus estuary and a mean water temperature of 18ºC. Additionally, the biomass value decreases when either the food amount either the water temperature are decreased. The PGM is simulated in four different scenarios. After a five-year simulation, the total number of adults in the population is higher in the 'reference' scenario (> 'less *fit*/environmental stress' > 'fishing stress with fishing law restrictions' > 'anthropogenic stress'). From the comparison of the scenarios' results it is concluded that: (1) when a population is less *fit* (due to environmental stress), its growth is exponential as in an ideal situation, but with a wicker growth; (2) the application of fishing law restrictions that save juveniles and young-of-the-year adults (<19cm) builds a fish population that tends to stabilization. The evolution of the population growth model to include movement rules according to the fish's environmental preferences is crucial to get closer to the *real world*. To manage the fishing activity in a more sustainable way, it is recommended gathering and the processing of field data that permits the development of a *more close to the reality* model that includes each site characteristics and their influence on the evolution of the fish populations.

RESUMÉ

Une gestion soutenable des ressources de la pêche exige la compréhension et la capacité de prévoir des fluctuations de l'abondance et production de biomasse. Dans le cadre de cet travail c'est développé un modèle de croissance individuelle d'un poisson et aussi de la croissance de la population des poissons correspondants dans un écosystème côtier, en utilisant l'anchois européen (*Engraulis encrasicolus*) dans l'estuaire de Tagus (Lisbonne, Portugal). Le modèle contient deux sous-modèles distincts: le modèle de croissance du poisson individuel (IGM) et le modèle de croissance de la population des poissons (PGM). La biomasse individuelle des poissons change dans chaque étape de la vie en fonction de ses caractéristiques métaboliques, de la disponibilité de nourriture dans l'environnement et de la température de l'eau. Dans le PGM, le nombre de poissons dans chaque classe des quatre étapes de vie est calculé en tenant compte des différents processus biologiques spécifiques de chaque étape, du pourcentage des *spawners* dans la population, des mortalités caractéristiques spécifiques de chaque classe et de la *scope for growth* spécifique de chaque classe. Les simulations du modèle IGM résultent en une biomasse individuelle de l'adulte de 27,4 g ww avec une concentration normale de nourriture dans l'estuaire de Tagus et avec une température moyenne de l'eau de 18ºC. En outre, la valeur de biomasse diminue quand la quantité de nourriture ou la température de l'eau diminue. Le modèle PGM est simulé sur quatre scénarios différents. Après cinq ans, le nombre d'adultes totales dans la population est plus élevé dans le scénario de référence (> 'moins adaptée /pression environnementale' > 'pression de la pêche avec des restrictions de la loi de pêche' > 'pression anthropogène'). De la comparaison des résultats des quatre scénarios on conclut le suivant: (1) quand une population est moins adaptée (en raison de la pression environnementale), sa croissance est exponentielle comme dans une situation idéale, mais plus faible; (2) l'application des restrictions de la loi de pêche qu'économise des juvéniles et des adultes *young-of-the-year* (< 19cm) construit une population des poissons qui tend à la stabilisation. L'évolution du modèle de croissance de la population pour inclure des règles de mouvement selon les préférences environnementales des poissons est cruciale pour devenir plus près du monde réel. Pour faire la gestion de l'activité de pêche d'une façon plus soutenable, il est recommandé d'assembler et de faire le traitement des données du terrain qui permettent le développement d'un modèle plus près de la réalité, qui inclut des caractéristiques de chaque endroit et leur influence sur l'évolution des populations de poissons.

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