

A Simulation Model of the Dynamics of Peruvian Anchoveta (*Engraulis ringens*)

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Abstract

This contribution — an account of work in progress — describes the key elements of a model simulating the dynamics of the anchoveta (*Engraulis ringens*) in the Peruvian upwelling system (4° to 14°S). This model, based on coupled differential equations, is parametrized mainly using empirical data and functional relationships presented in two volumes issued by ICLARM in 1987 and 1989, and may thus be viewed as test of the hypotheses presented therein. Results to date suggest that present knowledge of mechanisms controlling the anchoveta stock is essentially consistent, and sufficient to build a model reflecting essential features of the stock biomass and recruitment dynamics.

Introduction

The Peruvian upwelling ecosystem is one of the four great eastern boundary current upwelling ecosystems of the world. Strong fluctuations both in physical and biological parameters characterize this system. Foremost among these are those due to El Niño events occurring irregularly every few years, and which result in an occurrence of warm surface waters off the Peruvian coast, and a decrease in transport of nutrients to the surface (Arntz and Fahrbach 1991). Outside of El Niño events, the strong upwelling of nutrient-rich water, induced by steady winds from southeast parallel to the coast, supports a food web with extremely high biomasses, and in which the anchoveta (*Engraulis ringens*) plays a key role. Anchoveta supported in the late 1960s the world's largest single-species fishery, and contributed 20% to the world fish catch before it collapsed in the early 1970s. While a consensus may have emerged that both overfishing and a strong El Niño event contributed to this collapse (Pauly and Tsukayama 1987 and the contributions therein), research on various aspects of anchoveta biology continues and this contribution indicates one approach to integrating the results of this research (see below).

The northern stock of the Peruvian anchoveta population is distributed from 4° to 14° South and up to 75 km offshore, thus populating an area of about 100,000 km² (Pauly and Tsukayama 1987). Anchoveta has always dominated this system (de Vries and Percy 1982) except for some years in the 1970s, when it was replaced by sardine (*Sardinops sagax*) (Muck 1989). Its distribution is mostly limited to cold, plankton-rich upwelled waters. El Niño events strongly affect the population, but if favorable circumstances

follow, the stock is able to recover quickly. Such circumstances appear to have prevailed since the beginning of the 1990s, and anchoveta catches have been increasing steadily, as may have been predicted from Bakun (1990).

Anchoveta feed on a mixed diet of phyto- and zooplankton (Alamo 1989; Pauly et al. 1989; Rojas de Mendiola 1989; Jarre-Teichmann 1992) and grow up to maximum length of about 20 cm (Palomares et al. 1987). They spawn from their twelfth month on with two peaks every year (Senocak et al. 1989): one small peak in late austral summer, February - March, and one stronger peak in spring, September - October.

The objectives of the model presented here are to: i) integrate into a coherent whole all the available information (historical, biological and physical data, species parameters, empirical relations and existing submodels) on the historical stock, the derived recruitment and other data and the parameters and factors determining the development and structure of the anchoveta stock; ii) increase scientific understanding of the system and the mechanisms affecting it; and hopefully iii) predict the development of anchoveta biomass a few months ahead.

Data and Methods

The measured or derived time series data used are sea surface temperatures (SST) data from Pauly and Tsukayama (1987), turbulence data from Bakun (1987), primary production data from Mendo et al. (1989), egg stock data from Santander (1987) and Pauly and Soriano (1989); while the anchoveta egg consumption ("cannibalism") data were taken from the Rojas/Alamo-database (see Rojas de Mendiola (1989), Alamo (1989) and Pauly et al. (1989)). The growth parameter estimates are from Palomares et al. (1987). Recruitment and biomass data are from Pauly et al. (1987) and Pauly and Palomares (1989).

Previous models of the Peruvian upwelling system were published by Walsh (1975), Kremer and Sutinen (1975) and Walsh (1981), all focusing on the lower trophic levels. Krapivin and Aivazyan (1983) and Aivazyan and Krapivin (1984) published a model with more detail on anchoveta. However, only the steady-state models of Jarre-Teichmann (1992) were used for parametrization and calibration of the model presented here.

The modelling approach is based on work by Dr. Peter Muck, Lima, who formalized several of the basic relationships linking anchoveta with its ecosystem (Muck 1991; Muck et al. 1989a, 1989b), and specifically its predators (Muck and Pauly 1987; Muck and Fuentes 1987, Muck et al. 1987, Muck and Sanchez 1987), while the model itself is built on a shell written in Turbo Pascal by Jørgen Salomonsen from the Royal Danish Pharmaceutical Highschool, Department of Environmental Chemistry, in Copenhagen in close cooperation with the author (Jarre-Teichmann et al. 1992 gave a brief description).

A standard fourth-order Runge-Kutta algorithm with step size control was used as integration method. Definition of the state variables and processes (=elements included in the model, i.e., thought to be important in the system) and their parametrization relies largely on the contributions in the books edited by Pauly and Tsukayama (1987) and Pauly et al. (1989), and on Jarre-Teichmann et al. (1991).

For the single species version of the model (the multispecies version, including anchoveta predators, is not presented here), the number of individuals and their mean weights, in eight distinct age-classes, were selected as state variables. The age classes are: eggs and yolk-sac larvae, feeding larvae, small juveniles, juveniles and four successive classes for adults. Eggs and yolk-sac larvae have been united in one age class as it was assumed that their parameters, especially their (instantaneous) mortality rate, are approximately equal for both groups. The model output are data files of the development in time of these state variables number and mean weight in each age class.

For each of these 16 state variables, one differential equation was derived representing the processes affecting it (except for the mean weight of the eggs and yolk-sac larvae, which was assumed constant). The resulting set of 15 (coupled, ordinary, deterministic, partly nonlinear) differential equations forms the core of the model, and is solved numerically on a personal computer.

An overview of the anchoveta age classes included in the model, and of the processes affecting their numbers and weight is given in Table 1; an overview of the parametrization of these processes is given in Table 2.

The following three fluxes (or "transitions") between age classes are modeled as continuous processes: from egg and yolk-sac larvae-class to the (feeding) larvae-class, from larvae to small-juvenile ("metamorphosis"), and from small-juveniles to juveniles ("recruitment"). The fluxes between the juveniles and the first adult class, and among adult classes, are modeled as discontinuous processes with a complete transfer, every six months, of the content of each class into the next class.

Whenever possible, model parameters pertain to standardized conditions for the years 1966 to 1970. A standardized year, derived from data for the years 1966 to 1970, was calculated to obtain standardized SST, turbulence and primary production data. These are included into the model as forcing functions, i.e., functions not themselves influenced by model outputs.

From data in Pauly and Soriano (1987), a relation between mean individual gonad weight, and subsequently reproductive output, and total anchoveta biomass was established. The duration of the larval stage was set at 18 days, corresponding to a maximum length of about 1 cm and a maximum weight of about 1.4 mg. The mortality rates for yolk-sac larvae, feeding larvae and small juveniles are assumed to be seasonally varying as was the mortality rate of eggs, with high rates during times when high numbers normally occur.

Starvation was assumed as dominant cause of baseline mortality ("M0") and therefore linked, using an inverted Michaelis-Menten relationship, with primary production (and assuming that primary production is approximately proportional to plankton biomass).

Murphy (1977) suggested a lack of density-dependence in clupeoids such as anchoveta. This is still reflected in the literature, i.e., as well-documented density-dependent feedback mechanisms for fish such as anchoveta are rare. Still, this model includes three feedback mechanisms. The first of these relates feeding and metabolism to biomass such that increasing biomass leads, via a reduction of the parameters of the von Bertalanffy growth formula, to poorer growth. The second feedback mechanism is biomass-dependent egg production, derived from the relation between individual gonad weight and total biomass in Pauly and Soriano (1987). Evidence for egg cannibalism in anchoveta, the third feedback mechanism considered here,

Table 1. Parametrization of the various age classes of Peruvian anchoveta included in simulation model (see also text).

Age class	Processes affecting number of individuals	Processes affecting their mean weight
Eggs and yolk-sac larvae	(+) Spawning, (-) cannibalism, (-) other mortalities, (-) transitional ^a)	Constant, not affected
Larvae (feeding)	(+) Transitional, (-) starvation, (-) other mortality, (-) metamorphosis	(+) Gompertz growth
Small juveniles	(+) Metamorphosis, (-) baseline natural mortality, (-) other mortality, (-) recruitment	(+) Feeding, (-) metabolism
Juveniles	(+) Recruitment, (-) baseline natural mortality, (-) other mortality	(+) Feeding, (-) metabolism
Adults (4 classes)	For each: (-) baseline natural mortality, (-) other mortalities	For each: (+) feeding, (-) metabolism

^a Transition from yolk-sac stage to feeding larvae stage.

Table 2. Simplified overview of the processes included in the model and their representation. FOP = first order process, i.e., a flux out of a source is proportional to the source.

Process	Modelling approach and remarks	Sources
Spawning	Reproductive output depending on season and mean adult weight, adult biomass, fraction of mature adults (itself depending on SST) and fraction female	Pauly and Soriano (1987); Pauly and Soriano (1989)
Egg and yolk-sac larvae cannibalism	FOP, with a mean (seasonally varying) rate of 0.0078 day ⁻¹ and g-1 adult biomass.	Pauly and Soriano (1989)
Egg and yolk-sac larvae mortality (other sources)	FOP with mean (seasonally varying) rate of 1.29 day ⁻¹ .	Pauly and Tsukayama (1987); Pauly and Soriano (1989)
Transition to feeding larvae	FOP	Equation (2) in Pauly (1987)
Gompertz growth of larvae	From 0.042 mg (or 3 mm) on, with $a = 0.034$ and $A_0 = 0.0895$.	Lasker et al. (1970); Jørgensen et al. (1991)
Starvation of larvae	Inverted Michaelis-Menten-shaped dependency from turbulence. Starvation rate is 0.14 at most.	Rojas de Mendiola and Gómez (1981); Cury and Roy (1989)
Metamorphosis from larvae to small juveniles	FOP with rate itself rising with the average weight of the larvae.	Palomares et al. (1987)
Feeding, metabolism and baseline mortality of small juveniles	Identical with feeding, metabolism and baseline mortality of adults.	Smith (1985)
Mortality of small juveniles (other sources)	FOP with an average (seasonally varying) rate of 0.03 day ⁻¹ .	Smith (1985)
Recruitment	FOP; rate assumed to increase linearly, with mean weight; development time: 75 days, derived from VBGF parameters for 1969.	Pauly et al. (1987); Pauly and Palomares (1989); Pauly et al. (1989)
Feeding of adults	Proportional to weight ² / ₃ , with a Michaelis-Menten-shaped dependence on primary production, and related to biomass: biomass and growth are inversely related.	Palomares et al. (1987) Pauly et al. (1987); Mendo et al. (1989); Jarre-Teichmann (1992)
Metabolism of adults	FOP (proportionate to weight), depending on biomass, and on temperature (seasonal growth)	Palomares et al. (1987); Pauly et al. (1987); Tsukayama (1989)
Baseline natural mortality (M ₀)	FOP, related to primary production + 0.00385 day ⁻¹ .	Pauly and Palomares (1989)
Adult mortality (other sources), (Z-M ₀)	FOP, constant rates for each class; class 2: 0.0043; classes 3-6: 0.0038 day ⁻¹ .	Pauly and Palomares (1989)

was presented by Pauly and Soriano (1989); this was assumed proportional to the number of eggs and proportional to stock biomass. As yolk-sac larvae appear incapable of escaping being eaten, it was assumed that cannibalism affects them in the same way as the eggs. All three feedback-mechanisms are formulated such that above or below the average biomass for 1966-1970, of 145 gm⁻², the feedbacks act to decrease or to increase biomass, respectively.

Results and Discussion

Fig. 1 presents selected results, illustrating different key aspects of the models, while Table 3 provides quantitative details on the fit between model runs and observations.

Overall, there seems to be a good correspondence between simulated and system data, especially for the evolution of biomass.

Output data for recruitment and mean weights in particular age classes are nonetheless not yet satisfactory.

Only few of the parameters used differ markedly from values in the literature. These are egg production, which had to be increased by 40% and total mortality rates of larvae and small juveniles, which were increased by about 90% and 50%, respectively. On the other hand, the feeding rate of small juveniles was about 16% lower than in the other classes. Such deviations appear acceptable.

Parameters which turned out very sensitive to changes are the half-saturation constants in the (inverted) Michaelis-Menten, relating primary production and starvation of larvae (and M₀ juvenile or adult fish). The duration of the yolk-sac, and feeding stages also turned out to be quite important, requiring finely-tuned calibration.

Earlier versions of the model exhibited a wide range of behavior, ranging from extreme annual and biannual oscillations to chaotic sensitivity to initial values. This is now largely overcome, and the

Table 3. Comparison of observed data with outputs of model for simulating the dynamics of Peruvian anchoveta.

Time span of run: 10 years	Source	Observations	Fit	Model outputs
Spawning	Pauly and Soriano (1989)	Feb: 313 Sep/Oct: ≤ 1555	☺	Feb: 450 Sep/Oct: 1700
Egg + yolk-sac larvae	Pauly and Soriano (1989)	Feb: 332: Sep/Oct: ≤ 2086	☹	Feb: 350 Sep/Oct: 420
Transition (of yolk-sac to feeding larvae)	Pauly (1987)	0.144 day ⁻¹	☺	0.14 day ⁻¹
Larvae/egg ratio	Walsh et al. (1980); Sandoval de Castillo (1979)	$\approx 1:1$, \geq Sep: 1:2	☺	+ 1:2
Recruitment rate	Palomares et al. (1987); Pauly and Palomares (1989)	0.009 day ⁻¹	☹	0.0032 day ⁻¹
Recruitment	Pauly et al. (1987); Pauly and Palomares (1989)	≈ 4.23 ind. m ⁻² (mean 1966-1970)	☹	3.64 day ⁻¹
Seasonality of recruitment	Data for 1966-1970 from Pauly and Palomares (1989)	Max: Dec/Jan Min: Sep	☹	irregular behavior
Metabolic rate of adults	Pauly et al. (1987); Palomares et al. (1987)	0.008 day ⁻¹	☹	0.005 day ⁻¹
Weight of larvae (age class 0)	Lasker et al. (1970); Palomares et al. (1987)	0.042 - 2.3 mg, Mean ≈ 0.15 mg	☺	0.13 mg
Weight of small juveniles (age class 1)	Palomares et al. (1987)	0.00139 - 0.356 g, Mean ≈ 0.1 g	☺	0.05 g
Weight of juveniles (age class 2)	Palomares et al. (1987)	Min: 0.36 g	☹	0.6 g
Weight in age class 3	Palomares et al. (1987)	5.1 g	☹	2.7 g
Weight in age class 4	Palomares et al. (1987)	14.4 g	☹	8.1 g
Weight in age class 5	Palomares et al. (1987)	25 g	☹	14.2 g
Weight in age class 6	Palomares et al. (1987)	34 g	☹	24.3 g
Mean weight (through all age classes)	Calculated from data of Tsukayama and Palomares (1987);	5 g	☹	3.6 g
Seasonality of mean weight	Palomares et al. (1987); and Pauly and Palomares (1989)	Max: Dec/Jan Min: May/Aug	☺	Max: Dec/Jan Min: May/Aug
Daily weight increment	Palomares et al. (1987); Jurte-Teichmann (1992)	0.28- 0.65%	☺	0.27 - 0.56% (-1.05% for juveniles)
Total mortality rate of larvae (age class 0)	Walsh et al. (1980)	0.13 day ⁻¹	☹	0.25 day ⁻¹
Total mortality rate of small juveniles (age class 1)	Smith (1985)	0.02 day ⁻¹	☺	0.03 day ⁻¹
Total mortality rate of juveniles (age class 2)	Pauly and Palomares (1989)	0.0066 day ⁻¹	☺	0.0056 day ⁻¹
Total mortality rate in age class 3	Pauly and Palomares (1989)	0.0066 day ⁻¹	☺	0.0056 day ⁻¹
Total mortality rate in age class 4	Pauly and Palomares (1989)	0.0066 day ⁻¹	☺	0.0056 day ⁻¹
Total biomass	Pauly and Palomares (1989), mean of 1966-1970	Mean: 145.3 g m ⁻² range: 130-160 g m ⁻²	☺	Mean: 160 g m ⁻² range: 130-160 g m ⁻²
Seasonality of biomass	Palomares et al. (1987)	Max: Dec Min: June/July	☺	Max: Dec Min: June/July
K of VBGF	Palomares et al. (1987)	Mean 1966-1970 0.884 (year ⁻¹)	☹	0.6 year ⁻¹
L _∞ of VBGF	Palomares et al. (1987)	Mean 1966-1970 20.7 cm	☹	18.2 cm

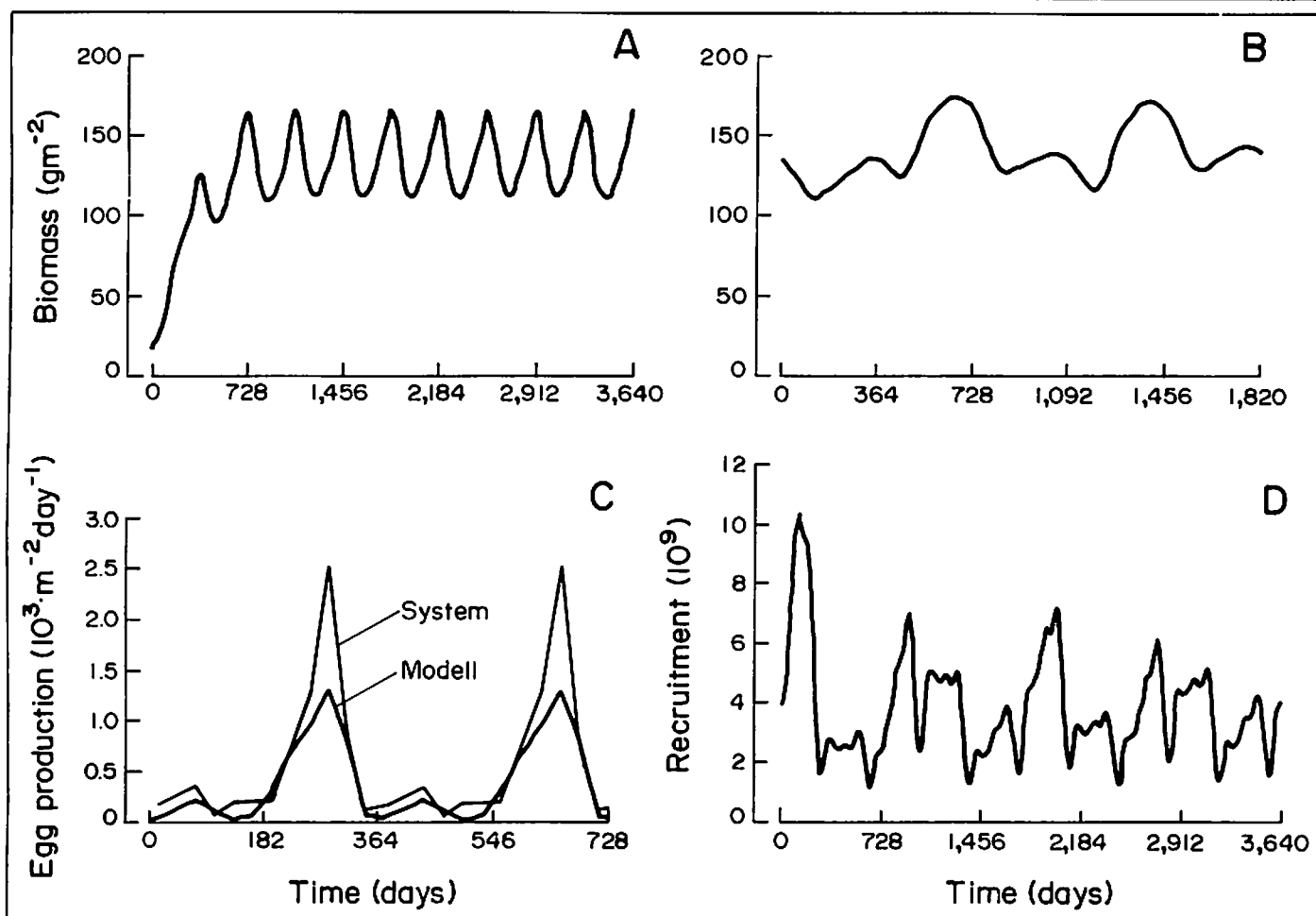


Fig. 1. Simulated dynamics of anchoveta: A. Increase of biomass from a depleted stock, following e.g., an El Niño event. B. Variation of biomass in the absence of El Niño events (note 2-year cycles, earlier noted in Pauly 1987); C. Egg production: match between simulated and observed data; D. Simulated time series of monthly recruitment, showing two peaks per year, as actually observed (see also Table 3).

present parametrization appears sufficient to reproduce all observed behavior of the available anchoveta time series, as well as second order effects, such as the observed reduction of growth performance at high stock sizes (Pauly and Palomares 1989).

The results of this model suggest that the present knowledge of mechanisms controlling the anchoveta stock is for the most part internally consistent and sufficient to build a model reflecting essential features of the stock, such as its biomass and recruitment dynamics. Considering that the model does not yet include several important factors impacting on anchoveta stock dynamics in detail, e.g., predation, these results show surprising correspondence with the system data. The model can thus be called, in a first step, verified in the sense of Jørgensen (1988).

Incorporation of predation, and further calibration, and sensitivity analysis are obvious next steps for the development of this model. It may already be concluded, however, that simulating the dynamics of recruitment and biomass elaboration of fish stocks is an achievable goal, at least when species such as anchoveta are considered, whose habitat seems strongly affected by a few strong, easily modelled environmental factors.

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