

# **Life-history model of sardine-anchovy cycles**

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## **Goal**

To develop a simple life-history model for sardine and anchovy that can explain the mechanisms causing the globally observed cyclic stock fluctuations.

## **Background and motivation**

According to the Food and Agriculture Organization of the United Nations, the catch of anchovy reached its peak in the 1970s, dramatically decreased in the 1980s, and recovered to the previous level in the 1990s. In contrast, the catch of sardine began to grow in the 1970s, reached its peak in the 1980s, and has dropped sharply in the 1990s. This oscillatory phenomenon, known as sardine-anchovy cycles, has been observed in at least four different oceanic regions. Both anchovy and sardine serve as major food resources around the globe, so their cycling strongly impacts seafood supplies, fisheries economics, and coastal communities.

Recent studies discovered that fluctuations in air temperature and ocean temperature were similar, in terms of phase and duration, to the oscillatory catches, suggesting that sardine-anchovy cycles are partly driven by climatic changes. In addition, interactions among these species, and also among cohorts within each species, have been suggested to contribute to the cycles. In general, however, the causal origin of sardine-anchovy cycles remains unknown, and no comprehensive model exists yet to describe these cycles. In this project, we will try to address this gap.

## **Research questions**

The aim of my project is to develop a life-history model that reproduces the observed sardine-anchovy cycles and helps understanding the mechanisms that cause these stock fluctuations. Specifically, I will address the following questions:

- What class of models is best suited for describing sardine-anchovy cycles?
- What equations best describe the growth, maturation, reproduction, and mortality of sardine and anchovy?
- How are these equations reflecting density regulation, trait effects, and interspecific interactions?
- If the developed model can reproduce the observed cycles, what does this tell us about the mechanisms causing this global phenomenon?

## **Methods and work plan**

### ***Work plan***

I will pursue the following steps to complete my research project:

- Develop suitable equations for a sardine-anchovy population dynamics model.
- Find the required parameter values from the literature or through own estimations.

- Refine the model specification until a good match with observations is achieved.
- Analyze the model to understand the causes of cycles.

### Population dynamics

The life cycles of sardine and anchovy can be divided into two stages: first is the immature stage and second is the mature stage. Immature and mature individuals experience growth and mortality. Immature individual become mature through maturation, which may occur at different ages and lengths. Reproduction only occurs at the mature stage and results in the production of immature offspring.

Let  $N_{i,a}(t)$  be the density of species  $i$  at age  $a$  in year  $t$  ( $i = S$ : sardine;  $i = A$ : anchovy),

$$N_{i,a}(t) = N_{i,1,a}(t) + \sum_{a_M=1}^a N_{i,M,a,a_M}(t), \quad \text{for } a = 1, \dots, A_i,$$

where I refers to immature individuals and M to mature individuals,  $a_M$  is an individual's maturation age, and  $A_i$  is the maximum considered age for species  $i$ . We assume that maturation can take place only after the age of immature individuals is greater than 1.

The densities of immature individuals change according to the following equation,

$$N_{i,1,a}(t+1) = \begin{cases} s_{i,1,0}(t) \sum_{a=1}^{A_i} \sum_{a_M=1}^a f_{i,a,a_M}(t) N_{i,M,a,a_M}(t), & \text{if } a = 1, \\ s_{i,1,a-1}(t) [1 - m_{i,a-1}(t)] N_{i,1,a-1}(t), & \text{if } a > 1. \end{cases}$$

where  $f_{i,a,a_M}(t)$  is the fecundity in year  $t$  of an individual of species  $i$  at age  $a$  that has matured at age  $a_M$ ,  $m_{i,a}(t)$  is the maturation probability in year  $t$  of species  $i$  at age  $a$ , and  $s_{i,j,a}(t)$  is the survival probability in year  $t$  in species  $i$  at maturation stage  $j$  from age  $a$  to age  $a+1$ .

The densities of mature individuals change according to the following equation,

$$N_{i,M,a,a_M}(t+1) = \begin{cases} s_{i,1,a-1}(t) m_{i,a-1}(t) N_{i,1,a-1}(t), & \text{if } a = a_M, \\ s_{i,M,a-1,a_M}(t) N_{i,M,a-1,a_M}(t), & \text{if } a > a_M. \end{cases}$$

### Growth

We follow the growth model of Lester et al. (2004),

$$L_{i,1,0}(t) = 0,$$

$$L_{i,1,a}(t) = L_{i,1,a-1}(t-1) + h_i(t),$$

$$L_{i,M,a,a_M}(t) = \frac{3}{k_i g_i + 3} [L_{i,M,a-1,a_M}(t-1) + h_i(t)],$$

where  $g_i$  is the gonadosomatic index of species  $i$ , defined as the ratio of gonad weight and somatic weight, and  $k_i$  is the energy density of gonad tissue relative to somatic tissue of species  $i$ .

For conversion from length to weight, we use allometric relationships

$$W_{i,1,a}(t) = \alpha_i L_{i,1,a}^{\beta_i}(t),$$

$$W_{i,M,a,a_M}(t) = \alpha_i L_{i,M,a,a_M}^{\beta_i}(t),$$

where  $\alpha_i$  and  $\beta_i$  are empirical parameters defining the allometric relationship for species  $i$ . The total biomass density  $B_i$  of species  $i$  in year  $t$  is given by

$$B_i(t) = \sum_{a=1}^{A_i} W_{i,1,a}(t)N_{i,1,a}(t) + \sum_{a=1}^{A_i} \sum_{a_M=1}^a W_{i,M,a,a_M}(t)N_{i,M,a,a_M}(t).$$

The average immature annual length increment  $h_i(t)$  in year  $t$  is a function of the annual temperature  $T_{G,i}(t)$  during the growth season of species  $i$  in year  $t$  and of the total biomass density  $B(t) = B_S(t) + B_A(t)$  of sardine and anchovy in that year. We assume that growth diminishes with  $B(t)$ ,

$$h_i(t) = h_{\max,i} R_{G,i}(T_{G,i}(t)) [1 + \gamma_i B(t)^{\delta_i}]^{-1},$$

where  $h_{\max,i}$  is the maximum immature annual length increment in species  $i$ ,  $\gamma_i$  and  $\delta_i$  specify the density dependence of growth in species  $i$ , and  $R_{G,i}(T_{G,i}(t))$  specifies the temperature dependence of growth in species  $i$ ,

$$R_{G,i}(T_{G,i}(t)) = \exp\left(-\frac{1}{2}(T_{G,i}(t) - T_{\text{opt},G,i})^2 / \sigma_{G,i}^2\right),$$

where  $T_{\text{opt},G,i}$  is the optimal temperature for the growth of species  $i$  and  $T_{G,i}(t)$  is given by

$$T_{G,i}(t) = \int w_{G,i}(\tau) T_i(\tau) d\tau,$$

where  $w_{G,i}$  is the seasonal probability density of growth in species  $i$  and  $T_i(\tau)$  is the temperature at time  $\tau$  in year  $t$ .

### Maturation

We assume that the maturation probability  $m_{i,a}(t)$  depends on age  $a$  and length  $L_{i,1,a}(t)$ ,

$$\text{logit}(m_{i,a}(t)) = c_{i,0} + c_{i,1} L_{i,1,a}(t) + c_{i,2} a,$$

where  $c_{i,a}$  are constants specifying a linear probabilistic maturation reaction norm with constant width, and the logit function is defined as  $\text{logit}(m) = \ln(m / (1 - m))$ .

### Reproduction

We assume that the per capita fecundity  $f_{i,a,a_M}(t)$  diminishes with the total biomass density  $B(t)$  of sardine and anchovy. High biomass density will raise food competition, which reduces surplus energy and thus energy invested in gonad development,

$$f_{i,a,a_M}(t) = \frac{g_i W_{i,M,a,a_M}(t)}{2W_{E,i}} e^{-B(t)/B_{0,i}},$$

where  $W_{E,i}$  is the mean egg weight in species  $i$  and  $B_{0,i}$  specifies the biomass density at which larval survival is reduced to  $1/e = 36.8\%$ .

### Mortality

When we calculate the annual survival rates  $s_{i,j,a}(t)$ , we consider two mortality rates, one describing natural mortality and the other fishing mortality,

$$s_{i,1,a}(t) = \exp(-M_{i,1,a}(t) - F_{i,1,a}(t)),$$

$$s_{i,M,a,a_M}(t) = \exp(-M_{i,M,a,a_M}(t) - F_{i,M,a,a_M}(t)),$$

where  $M_{i,1,a}(t)$  and  $F_{i,1,a}(t)$ , respectively, are the natural mortality rate and fishing mortality rate of immature individuals in species  $i$  at age  $a$  in year  $t$ , and  $M_{i,M,a,a_M}(t)$  and  $F_{i,M,a,a_M}(t)$ , respectively, are the natural mortality rate and fishing mortality rate of mature individuals in species  $i$  at age  $a$  in year  $t$  that have matured at age  $a_M$ .

According to Stearns (1992) and Hirshfield (1980), investments into growth and reproduction reduce an individual's survival,

$$M_{i,1,a}(t) = M_{b,i}(t) + \xi_i h_{\max,i},$$

$$M_{i,M,a,a_M}(t) = M_{b,i}(t) + \xi_i h_{\max,i} + \zeta_i k_i g_i,$$

where  $M_{b,i}(t)$  is the baseline mortality rate for species  $i$  in year  $t$  and  $\xi_i$  and  $\zeta_i$  are fixed constants for species  $i$ . The extra mortality rate  $\xi_i h_{\max,i}$  is assumed to describe the trade-off between growth and survival in species  $i$ , while the extra mortality rate  $\zeta_i k_i g_i$  is assumed to describe the trade-off between reproductive investment and survival in species  $i$ .

The ocean temperature might affect the baseline mortality rate. We assume that there is an optimal temperature for the survival of fish, so that if the ocean temperature is warmer or colder, the natural mortality rate will be increased,

$$M_{b,i}(t) = M_{\min,i} + (M_{\max,i} - M_{\min,i})(1 - R_{M,i}(T_{M,i}(t))),$$

where  $M_{\min,i}$  is the minimum natural mortality rate and  $M_{\max,i}$  is the maximum natural mortality rate for species  $i$ .  $R_{M,i}(T_{M,i}(t))$  specifies the temperature dependence of mortality in species  $i$ ,

$$R_{M,i}(T_{M,i}(t)) = \exp\left[-\frac{1}{2}(T_{M,i}(t) - T_{\text{opt},M,i})^2 / \sigma_{M,i}^2\right],$$

where  $T_{\text{opt},M,i}$  is the optimal temperature for the survival of species  $i$  and  $T_{M,i}(t)$  is given by

$$T_{M,i}(t) = \int w_{M,i}(\tau) T_t(\tau) d\tau,$$

where  $w_{M,i}$  is the seasonal probability density of mortality in species  $i$ .

We assume length-dependent fishing mortality rates  $F_{i,1,a}(t) = F(L_{i,1,a}(t))$  and  $F_{i,M,a,a_M}(t) = F(L_{i,M,a,a_M}(t))$  typical for trawl-type fishing,

$$F(L) = \frac{F_{\max,i}}{1 + \exp(-(L - L_{F,i}) / \sigma_{F,i})},$$

where  $F_{\max,i}$  is the maximum fishing mortality rate in species  $i$ ,  $L_{F,i}$  is the length at which fish of species  $i$  experience half of this maximum fishing mortality rate, and  $\sigma_{F,i}$  determines the steepness of the sigmoid selectivity curve for species  $i$ .

### **Evolutionary dynamics**

To account for life-history evolution, we will try to consider selection pressures and selection responses using the techniques presented by Arlinghaus et al. (2009) and Matsumura et al. (submitted). Potentially evolving life-history traits of interest include the length increment  $h_{\max,i}$ , the gonadosomatic index  $g_i$ , and the intercept  $-c_{i,0} / c_{i,1}$  of the probabilistic maturation reaction norm.

## Relevance and link to EEP's research plan

This project aims to reproduce the observed global phenomenon of sardine-anchovy cycles and to understand the causal mechanisms underlying these long-term stock fluctuations. It will thus contribute to a better understanding of factors influencing the sustainable exploitation of living marine resource, and is linked to EEP's research project on *Evolutionary Fisheries Management*.

## Expected output and publications

I intend to publish this work as a co-authored article in an international scientific journal.

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