On the dynamics of Sardina pilchardus: orbits of stability and environmental forcing.

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On the dynamics of *Sardina pilchardus*: orbits of stability and environmental forcing.

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Abstract.

The dynamics of *Sardina pilchardus* in the Iberian upwelling area are examined. Spawning stock biomass (SSB), recruitment (R) and production (R/SSB) data for years 1978-2006 are analyzed in relation to both Upwelling Index (UPW) and Sea Surface Temperature (SST). It is observed that the population system oscillates in two relatively stable orbits (shown
by multiresolution decomposition of the recruitment series) as the external forcing (UPW and SST) are the inverse of one another, and, as the synchrony is lost between both of the external variables, \( R \) and \( R/SSB \) shift towards highly steep, negative (depressantory) trends. It is proposed that such mechanics may have induced both recruitment failures and significant decreases in abundance in the Iberian sardine stock. The observed relationships are assumed to validate a complex dynamical continuum (multiple orbits of stability) and variable carrying capacity, alternative population model. Also, radial systems with two orbits of stability are proposed for the \( R-SSB \) and \( S/SSB \) relationships. Results are discussed both in relation to classical and alternative SR models in order to approach stock rehabilitation and fishing mortality issues as the population shift toward low recruitment and abundances. Finally, certain factors to consider in exploitation strategies for systems with multiple orbits of stability are discussed.

**Key words.**

*Sardina pilchardus*, stock, recruitment, production, orbits of stability, dynamical continuum, variable carrying capacity, Iberian upwelling, sea surface temperature, environmental forcing.
Introduction.

Several authors have suggested possible links between stocks/populations of small pelagic species (sardine and anchovies, for instance) and the environmental forcing (i.e. upwelling intensity, climatic variability) and, also, the difficulty to apply traditional population approaches which are based on both a single equilibrium and an invariant carrying capacity. Barange et al. (2009) argued both that (a) Small pelagic fish species are characterized by marked fluctuations in numbers because of their high dependence on highly variable, environmentally driven, annual recruitment pulses and (b) These species, also, display low frequency, multi-decadal productivity cycles. Also, it was suggested by Chavez et al. (2003) that (a) There was an alternation of abundance between sardines and anchovies which (b) cannot be explained by means of fishing pressure; (c) A variability (seen as biological regime shifts) which could be linked to large-scale atmospheric or oceanic forcing at the basin level and (d) Environmental forcings which act on multiple time scales. Furthermore, Schwartzlose et al. (1999) suggested that (a) Sardine (S. sagax) and anchovy (Engraulis spp.) fluctuate out of phase with each other as a consequence of one or a few strong year classes are triggered rather than as a response to a vacant niche; (b) Excessive fishing pressure on strong year classes early in the recovery stage may prevent a species from assuming
dominance so that the natural succession is influenced and (c) Near simultaneous fluctuations of fish stocks in widely separated regions support the view that they are sometimes influenced by climate operating at a global scale. Moreover, Hsieh et al. (2009) suggested that the catches on two anchovy species (*E. heteroloba* and *E. punctifer*) were mainly determined by the abundance (strength) of *E. japonicus* whereas relationships with environmental variables (water temperature and river runoff) were transient. Also, Machu et al. (2009) suggested, as a result of a coupled physical-biogeochemical modelling experiment, that recruitment of sardines (*S. pilchardus*) could be related to the delay between high abundance of plankton and favorable spawning conditions and Relvas et al. (2009) observed (a) A generalized warming trend in the Canary upwelling system (an important ground for sardine recruitment) and suggested both that (b) significant decadal changes in the mesoscale patterns and (c) Such a large-scale variability can reorganize communities and trophic relationships.

Two of the most widely accepted frameworks used to describe the theoretical relationship between parental stock and recruitment (also, referred as the “SR” relationship/system) are the Beverton and Holt (1957) and Ricker (1954) models (also, referred herein as “classical models”).
These approaches were developed for the identification of the best parameterization of the SR relationship. Their principal task was the determination of the best mathematical function (shape and number of parameters) which would permit better determination of coefficients involving the fewest parameters. These classical models, which established a general theoretical framework for modelling population dynamics in the 1950’s, consist of extinction curves where recruitment reaches either an asymptotic maximum (Beverton-Holt) or becomes low at high spawning stock sizes (Ricker). Both of these models were unified by Shepherd (1982) whose functional form is given by

\[
R = \frac{\alpha \cdot S}{1 + \left(\frac{S}{K}\right)^\delta}
\]  

(1)

where \( R \) is recruitment, \( S \) is the spawning stock abundance and \( K \) the threshold abundance above which density-dependent effects dominate (i.e. the carrying capacity). The parameters \( \alpha \) and \( \delta \) are referred as the slope at the origin and degree of compensation involved, respectively. The classical dome-shaped (for \( \delta > 1 \)) and asymptotic (for \( \delta = 1 \)) functional forms proposed by Ricker (1954) and Beverton-Holt (1957), respectively can be
described within the same framework. An example for each of the models
with arbitrary parameter values is shown in Figure 1.

While the classical models provided important insights into population
dynamics and thus implied significant advances to fishery science, they are
tools with limited degrees of resolution (capacity to incorporate and
describe complex dynamics). Several authors (Clark (1976), Sharp et al.
(1983), De Angelis (1988), Fogarty (1993), Solari et al. (1997), Bas et al.
(1999)) have suggested that these models do not include key factors of
specific situations and have a limited capacity to link internal (population)
and external (environmental) dynamics. While such argumentation may
hold true, it may be fair to recall that the classical models were put forward
before any relevant ecological systems theory was proposed.

An alternative model.

From the classical models which proposed single equilibrium relationships
with an invariant carrying capacity, we developed an alternative general
framework for multi-oscillatory, dynamic systems in our earlier studies
(Solari et al., 1997, originally published in this journal; Bas et al., 1999;
Solari et al., 2003 and Solari, 2008). A new model was put forward in
which recruitment (to the population, area and fishery) is considered as a
system (henceforth regarded as “system”) with dynamic features ranging from chaos (the ceiling, when external conditions are extremely benign), going through a range of relatively stable, converging cycles (as external stress increases), to a quasi-standstill state with no clear oscillations (when the minimum viable population is being approached). The proposed system comprises of a dynamical continuum governed by a variable carrying capacity with local dynamics in different orbits of stability (graphically represented in Figure 2) and it is expressed as

\[
R(S)_{\text{pop,area,fishery}} \approx \sum_{i=1}^{m} \frac{a_i \cdot (S)}{(S - b_i)^2 + c_i}
\]  

(2)

where recruitment, \( R \), to the population (pop), area or fishery is defined as a summation of non-linear functions of the adult stock (or stock-in-area), \( S \), and the entries \( i = 1 \ldots m \) represent the number of dynamical states (orbits of stability and pseudo-equilibria) in the system, being \( m \) the highest equilibrium where the relationship reaches the “ceiling” or maximum allowable carrying capacity (\( K_{\text{max}} \)). Pseudo-equilibria (\( E_i \)) are controlled by the coefficients \( a_i \) (slope of the curve at the origin), being \( b_i \) and \( c_i \) the
density-dependent mortality entries. For instance, $a_i$ fulfils a similar
function to the natural rate of increase in the logistic equation. These
coefficients will define each equilibrium state and their values may be
fixed. Also, values of $b_i$ will define the ranges of stock for which pseudo-
equilibria may arise. We use the concept of “pseudo-equilibria” as we
assume that the population system will show responses to an ever-
changing environment, as well as the intrinsic density-dependent
processes, and thus “equilibrium values” will change rapidly.

Our proposed model was first in the literature to formalize the concepts of
(a) Variable carrying capacity and dynamical continuum as an expression
of the evolution of the population system which (b) could link all of the
known population mechanics (that is, density-dependent, density-
independent and inverse-density-dependent processes) in a relatively
simple equation. Also, the framework allowed us to show dynamical
similarity at several spatio-temporal scales for case studies on skipjack
tuna, *K. pelamis* (Solari et al., 2003) and the common *Octopus, O. vulgaris*
(Solari, 2008). The system, which is limited by a maximum carrying
capacity and an overall minimum viable population ($K_0$), is highly flexible
as it has the capacity to, persistently, evolve and return within a relatively
wide range of dynamical states allowing for the description of multi-
oscillatory population systems with features which may be caused by
stable; periodic; multi-periodic; and chaotic process dynamics.

In light of the proposed framework, we will now analyze the sardine
\textit{(Sardina pilchardus)} \( R \), \( SSB \) and \( R/SSB \) data in relation to \( SST \) and \( UPW \)
and attempt to put forward further theoretical propositions which may
contribute to (a) Explain and set into a framework the causal mechanisms
behind the observed data and (b) Discuss further aspects on management
and rehabilitation, particularly, for relatively low levels in both recruitment
and abundance.

Methods.

We used statistical tests which can and do provide indications of
periodicities, lags, dependencies and persistency or “memory effect”
(dependency on preceding values) in the series (auto- and cross
correlations): (a) Time series data were log transformed to meet conditions
for statistical normality; (b) Also, we worked on standardized data (with
mean = zero) as we were interested in trends, not in absolute numbers and
to facilitate visual comparison; (c) Data was smoothed with a five year
moving average window both to remove noise from the series and to determine whether trends remained; (d) Further, we used simple regressions to determine both the “replacement line” (i.e. recruitment needed to replace the stock) and as an indicator of general equilibrium values (in which the fitted system does neither grow nor decrease) and (e) Polynomial regressions (incorporating three constants for each orbit of stability) to approximate the dynamical continuum we propose. Also, we chose to use the multi-resolution decomposition (MRD) of the wavelet analysis (S+Wavelets, 2003) in order to determine sharp changes or peaks (eight years processes, S8) in the recruitment series.

Data and results.

The R and SSB data series from 1978 to 2006 were estimated by ICES (2007) from Virtual Population Analysis (VPA). The analytical assessment used fishery dependent data (commercial catch-at-age) and fishery independent data (acoustic surveys abundance-at-age, egg surveys spawning biomass).

The SST data was extracted from the International Comprehensive Ocean-Atmosphere Data Set (ICOADS) provided by the NOAA's Climate Diagnostics Centre (CDC). The product used was the global "enhanced"
data set with a 1°x1° grid box (Woodruff et al., 1998) with centre at 39.5ºN and 9.5ºW.

The Ocean Coastal Upwelling Indices (UPW) as developed by Bakun (1996) were calculated from ICOADS wind data on a global enhanced data set with 2º degree grid box, extending between latitude 43ºN - 37ºN and longitude 9ºW, yearly and for the four quarters.

The bivariate (two-tailed) Pearson correlation matrix showed the following results on the log transformed series: (a) $R$ and $R/SSB$ (production) are highly correlated to $SST$ (p<.01 for both of the cases); (b) While UPW showed no significant correlations to neither $R$ nor $R/SSB$, there were certain UPW ranges for which it appears production may be promoted whereas beyond those ranges production may be depressed; (c) The yearly UPW series was significantly correlated to the series from the 1st quarter (p<.05) and highly significantly for the remaining 2nd-4th quarters (p<.01); The 3rd and 4th quarters showed the highest correlations (.64 and .61, respectively); (d) We chose the pooled catch data (N=92, years 1915-2006) as it was highly significantly correlated (p<.01 for all cases) to the series from the Northwest, Southwest and South of Portugal. A multiple
regression (p<.001) on NAO, EA (East Atlantic pattern), SST and UPW showed that the contribution of SST upon R was strongest (p<.05).

In Figure 2, we show an ad hoc model for the abundance and recruitment in the European sardine (S. pilchardus) in the Iberian upwelling zone years 1978 to 2006: three orbits of stability with corresponding “steady states” (E_i), maximum carrying capacity (K_max) and minimum viable population (K_0). Every orbit will be limited by a local ceiling (K_i) and floor (K_0i). The dynamical continuum is represented by the non-linear fit and global equilibrium values (or replacement line) are given by the simple regression through the origin (dashed line). Arrows to the right and left indicate the population positive and negative growths. An m number of oscillatory phenomena ranging from limit cycles to chaos and inverse density-dependence are allowed in this system. Values and noise are arbitrary.

Ground theoretical model after Solari et al. (1997).

The European sardine (S. pilchardus) recruitment (R) and spawning stock biomass (SSB), log transformed (Log), smoothed (S, bold line) and standardized (Z) series in the Iberian upwelling zone for years 1978-2006, as estimated by ICES (2007) are shown in Figure 3.
Production (recruitment per spawning stock biomass, \(R/SSB\)) of the European sardine (\(S.\ pilchardus\)) in the Iberian upwelling zone for years 1978-2006 (raw data after ICES, 2007) is shown in Figure 4. Series were log transformed (Log), smoothed (S, bold line) and standardized (Z).

The phase plane of production (recruitment per spawning stock biomass, \(R/SSB\)) with lag 1 of the European sardine (\(S.\ pilchardus\)) in the Iberian upwelling zone for years 1978-2006 (Figure 5). The original series were log transformed, smoothed and standardized. The relationship turns in two similar orbits of stability within certain ranges beyond which growth becomes steeply negative. The dashed line is a linear regression through the origin.

In Figure 6, we show the stock and recruitment relationship for the European sardine (\(S.\ pilchardus\)) in the Iberian upwelling zone during years 1978-2006. Series were standardized (Z), smoothed (S, bold line) and log transformed (Log). The lag to recruitment is one year. The rectangle indicates the oscillations or orbits of stability (A, B) which may be caused both by density-dependent pseudo-cycles and environmental pulses. The dashed linear line is a simple regression through the origin.
In Figure 7, we show the S8 wavelet analysis (multiresolution decomposition, MRD) on the raw (non-transformed) European sardine \textit{(S. pilchardus)} recruitment series from the Iberian upwelling zone for years 1978-2006. The dashed lines indicate the peaks for the sum of the signals and eight year (D1-D2) and smoothed, low frequency (S2) processes. We used the raw data in order to show the peaks more clearly. Considering the length of the series, we assume the peaks between 6-7 to 15 years (both in the sum of the signals and the 8-16 years processes represented by D1-D2, respectively) detect both of the orbits of stability (A-B in Fig. 5 a) we propose for the SR system.

The Sea Surface Temperature (with centre at 39.5º N and 9.5º W) and Ocean Coastal Upwelling Indices (latitude 43-37º N and longitude 9º W) for years 1978-2006 (after ICOADS/NOAA, 2007) series is shown in Figure 8. Data values were standardized (Z), smoothed (S) and log transformed (Log). It is proposed that as the external forcing (UPW and SST) are the inverse of one another (between years 1985-1996), recruitment (R) and production (R/SSB) in \textit{S. pilchardus} may oscillate in two relatively stable orbits (Fig. 6). Once the synchrony is broken between both of the external variables, R and R/SSB shift towards relatively steep negative trends. This forcing is an example of the so called “optimal environmental
window”, as proposed by Cury and Roy (1989). Linear trends are simple regressions through the origin.

The phase planes of the external forcing (SST and UPW) and recruitment (R, above left) and production (recruitment per spawning stock biomass, R/SSB, right caption) for S. pilchardus in the Iberian upwelling zone, years 1978-2006 are shown in Figure 9 a-b. Both recruitment and production show similar patterns: they oscillate in relatively stable orbits of stability within certain ranges of SST and UPW beyond which the system shifts toward steep negative trends. Series were standardized (Z), smoothed (S) and log transformed (Log). Arrows show the direction of the trajectories.

Linear trends are simple regressions through the origin.

Also, we propose two further model options for the sardine dynamics in the Iberian upwelling area. The phase planes showing two radial attractors proposed for both recruitment and production per spawning stock biomass for S. pilchardus in the Iberian upwelling zone, years 1978-2006 are shown in Figure 10 a-b. Oscillations in relatively stable orbits may be governed both by density-dependent processes and an environmental window which may be represented by SST and UPW. S is spawning stock, Rec is recruitment and simulation parameters and initial conditions were arbitrary.
Discussion

Research on species such as sardine and anchovies is extensive. There are factors affecting the dynamics of small pelagic species which suggest the nonlinear, multivariate nature and complex interactions between density dependent and density independent processes: decadal changes (Barange et al. (2009), Relvas et al. (2009)), productivity cycles (Barange et al. (2009), perturbations operating at several spatial scales, even at the basin-wide scale (Chavez et al. (2003), Molinero et al. (2005)), transient relationships (in abundances and catches; Hsieh et al. (2009)), out-of-phase abundance successions (Chavez et al. (2003), Hsieh et al. (2009)), delay between high plankton production and recruitment (Machu et al. (2009)), cascade mechanisms (Molinero et al. (2005), among other features. Such evidence may confirm that the multiple equilibriums paradigm is more appropriate in aquatic ecosystems than the classical approach based on the existence of a single stable equilibrium.

Hsieh et al. (2009) suggested that (a) Fluctuations of anchovy populations might not simply be determined by any single but a nonlinear combination environmental factors and (b) Fishing pressures and environmental changes might have synergistically precipitated abundance declines. Also, Barange et al. (2009) argued that if out-of-phase sinusoidal trends in production...
exist, consequences may be important and management procedures
designed under such an assumption could be more effective than traditional
approaches. It was suggested that (a) The biological mechanisms behind
alternating cycles and space utilization may be more complex than a simple
replacement and (b) the evolution of sardine and anchovy populations may
be described by models based on climate driven habitat changes.
Furthermore, Molinero et al. (2005) pointed out that a cascade of links
between different (large and local) spatial scale climatic patterns (driven by
long-term temperature anomalies) affected the dynamics and top-down
effects exerted by jellyfish on copepods. Also, it was argued that such a
cascade of links should be integrated into the assessment and modelling
studies of pelagic ecosystems.

There are three main aspects in our paper which we would like to stress: (a)
Both recruitment and production (S. pilchardus in the Iberian upwelling)
appear to be related to an environmental window caused by oscillations in
both SST and UPW: the phase planes of stock, recruitment and production
oscillate in relatively stable orbits of stability for certain ranges of SST and
UPW within which both of the external variables are the inverse of one
another; once the synchrony in the sine-cosine, wave-like patterns between
the external variables is broken, the trajectories of both recruitment and
production shift towards density-independent depensation and negative growth occurs; if we are theoretically correct, we would, therefore, expect both of the biological variables to adjust their temporal evolution onto further pseudo-cycles once SST and UPW recover their “inverse dynamics”; (b) Second, we put forward a new framework which may be useful for the study and exploitation of S. pilchardus and other small pelagics: invoking a multi-oscillatory system governed by a multivariate set of external perturbations in which the orbits of stability in the population are caused by inversely related overlapping relationships requires a highly flexible framework; a multioscillatory system with two orbits (seen as pseudo-cycles or radial attractors) can provide an alternative to describe the observed dynamical system; (c) Third, although the classical models could describe each of the orbits of stability as “discrete (unlinked) regimes”, these models propose the concepts of an invariant carrying capacity and a single equilibrium which is likely insufficient to describe such complex dynamics; as we see it, to describe the sardine R and R/SSB system in relation to SST and UPW, requires both a variable carrying capacity and a dynamical continuum which may help to link both (alternatively, several) orbits of (quasi)-stability together.

Also, the results presented herein may be supportive of the “optimal environmental window” concept proposed for recruitment success in
upwelling areas by Cury and Roy (1989): (a) the authors relate Ekman-type
upwelling, vertical advection, new inputs of nutrients and turbulence to
wind speed and, with food availability, they are considered factors that
affect larval survival and pelagic fish recruitment and (b) their results
showed that for Ekman-type upwelling the annual recruitment increases
with upwelling intensity until wind speed reaches certain critical values
beyond which recruitment decreases (for which they infer the existence of
the so called “optimal environmental window”). We reach a similar
inference using our own theoretical model.

Moreover, we go further in the non-linear analysis to show a variable
carrying capacity determined by certain ranges of the external forcing (SST
and UPW) outside of which recruitment and production shift from
relatively stable orbits of stability or pseudo-cycles toward density-
independent depensation and, hence, negative population growth.

According to our criteria, there are certain critical factors to consider in
exploitation strategies for systems with multiple orbits of stability. There
are several key concepts spinning off from our alternative model that may
allow us to further investigate some of the aspects relating possible
sustainable exploitation strategies such as: (a) differential effects of fishing
mortality: during density-dependent (intrinsic to the population) and density-independent (environmentally induced) compensations (positive growth) and depensations (negative growth), the impact of fisheries may be different; and also, the negative impacts of fishing may be less during compensatory phases; this implies that fishing pressure could be relatively higher during compensations, depending on the current orbits of stability or level of numbers; on the other hand, the consequences of high and intense exploitation may be of a negative nature once the trajectory of the population becomes depensatory (negative population growth); the differential effects of fishing (positive and negative growths during both density-dependent and density-independent processes) together with length and degree of the slopes in the trends should be further investigated; (b) Understanding of fishery collapses (or shifts to low orbits of stability with low oscillations in numbers) due to depensatory processes induced by the combined effects from the environment and high fishing mortality: the highest negative impacts in the population may be expected during density-independent and density-dependent depensations operating simultaneously; such processes may lead both recruitment and production towards low levels from which a rehabilitation will not occur until a new environmental pulse (“inverse dynamics” between SST and UPW) make it possible and (c) Short and medium term estimation of recruitment due to trends (slopes
and temporal evolution) in external “best descriptor” variables (such as SST, SST Anomaly, SSTA, North Atlantic Oscillation, NAO, upwelling strength, among others).

Also, our alternative model allows analysis of factors such as the high variability in the data and determination of how combined, multivariate correspondences, memory effects, time lags, periodic oscillations, noise and sensitivity to external conditions may affect the population system. We should further investigate whether there may be dynamical similarity at several spatio-temporal scales and the potential extrapolation of trends between different scales of changes in S. pilchardus. Clearly, the forward and backwards bending nature of catches, fishing effort, and abundance, and the incorporation of multivariate perturbations into the model and aspects related to auto correlated residuals in population systems with strong dependencies on pulses from wave-like external variables should be taken into account. The flexibility of the theoretical framework we propose and multiplicity of factors which may be incorporated into a relatively simple model may be some of the advantages of our approach.
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Fig. 1. Two arbitrary examples of the Shepherd (1982) functional form with parameter values describing the Stock-Recruitment relationship as proposed by Ricker (1954, for $\delta > 1$, left caption) and Beverton-Holt (1957, for $\delta = 1$, right caption).
Fig. 2. An ad hoc model for the abundance and recruitment in the European sardine (*Sardina pilchardus*) in the Iberian upwelling zone years 1978 to 2006: three orbits of stability with corresponding “steady states” ($E_i$), maximum carrying capacity ($K_{\text{max}}$) and minimum viable population ($K_0$). Every orbit will be limited by a local ceiling ($K_i$) and floor ($K_{0i}$). The dynamical continuum is represented by the non-linear fit and global equilibrium values (or replacement line) are given by the simple regression through the origin (dashed line). Arrows to the right and left indicate the population positive and negative growths. An $m$ number of oscillatory phenomena ranging from limit cycles to chaos and inverse density-dependence are allowed in this system. Values and noise are arbitrary. Ground theoretical model after Solari et al. (1997).
Fig. 3. The European sardine (*Sardina pilchardus*) recruitment (*R*) and spawning stock biomass (*SSB*), log transformed (Log), smoothed (S, bold line) and standardized (*Z*) series in the Iberian upwelling zone for years 1978-2006, as estimated by ICES (2007).
Fig. 4. Production (recruitment per spawning stock biomass, $R/SSB$) of the European sardine ($Sardina pilchardus$) in the Iberian upwelling zone for years 1978-2006 (raw data after ICES, 2007). Series were log transformed (Log), smoothed (S, bold line) and standardized (Z).
Fig. 5. The phase plane of production (recruitment per spawning stock biomass, R/SSB) with lag 1 of the European sardine (Sardina pilchardus) in the Iberian upwelling zone for years 1978-2006. The original series were log transformed, smoothed and standardized. The dashed line is a linear regression through the origin.
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Fig. 9 a-b. Phase planes of the external forcing (Sea Surface Temperature, SST and Upwelling Index, UPW) and recruitment (R, above left) and production (recruitment per spawning stock biomass, R/SSB, right caption) for Sardina pilchardus in the Iberian upwelling zone, years 1978-2006. Series were standardized (Z), smoothed (S) and log transformed (Log). Arrows show the direction of the trajectories. Linear trends are simple regressions through the origin.
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Fig. 10 a-b. The phase planes showing two radial attractors proposed for recruitment and production per spawning stock biomass for *Sardina pilchardus* in the Iberian upwelling zone, years 1978-2006. Oscillations in relatively stable orbits may be governed both by density-dependent processes and an environmental window which may be represented by Sea Surface Temperature and Upwelling Index. S is spawning stock, Rec is recruitment. Parameter values are arbitrary.