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

1   On the dynamics of *Sardina pilchardus*:

2   orbits of stability and environmental forcing.

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18   <u>Abstract.</u>

19   The dynamics of *Sardina pilchardus* in the Iberian upwelling area are

20   examined. Spawning stock biomass (*SSB*), recruitment (*R*) and production

21   (*R/SSB*) data for years 1978-2006 are analyzed in relation to both

22   Upwelling Index (*UPW*) and Sea Surface Temperature (*SST*). It is observed

23   that the population system oscillates in two relatively stable orbits (shown

24   by multiresolution decomposition of the recruitment series) as the external

25   forcing (*UPW* and *SST*) are the inverse of one another, and, as the

26   synchrony is lost between both of the external variables, *R* and *R/SSB* shift

27   towards highly steep, negative (depensatory) trends. It is proposed that

28   such mechanics may have induced both recruitment failures and significant

29   decreases in abundance in the Iberian sardine stock. The observed

30   relationships are assumed to validate a complex dynamical continuum

31   (multiple orbits of stability) and variable carrying capacity, alternative

32   population model. Also, radial systems with two orbits of stability are

33   proposed for the *R-SSB* and *S/SSB* relationships. Results are discussed both

34   in relation to classical and alternative SR models in order to approach stock

35   rehabilitation and fishing mortality issues as the population shift toward

36   low recruitment and abundances. Finally, certain factors to consider in

37   exploitation strategies for systems with multiple orbits of stability are

38   discussed.

39

40   Key words.

41   *Sardina pilchardus*, stock, recruitment, production, orbits of stability,

42   dynamical continuum, variable carrying capacity, Iberian upwelling, sea

43   surface temperature, environmental forcing.

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45   Introduction.

46   Several authors have suggested possible links between stocks/populations

47   of small pelagic species (sardine and anchovies, for instance) and the

48   environmental forcing (i.e. upwelling intensity, climatic variability) and,

49   also, the difficulty to apply traditional population approaches which are

50   based on both a single equilibrium and an invariant carrying capacity.

51   Barange et al. (2009) argued both that (a) Small pelagic fish species are

52   characterized by marked fluctuations in numbers because of their high

53   dependence on highly variable, environmentally driven, annual recruitment

54   pulses and (b) These species, also, display low frequency, multi-decadal

55   productivity cycles. Also, it was suggested by Chavez et al. (2003) that (a)

56   There was an alternation of abundance between sardines and anchovies

57   which (b) cannot be explained by means of fishing pressure; (c) A

58   variability (seen as biological regime shifts) which could be linked to large-

59   scale atmospheric or oceanic forcing at the basin level and (d)

60   Environmental forcings which act on multiple time scales. Furthermore,

61   Schwartzlose et al. (1999) suggested that (a) Sardine (*S. sagax*) and

62   anchovy (*Engraulis spp.*) fluctuate out of phase with each other as a

63   consequence of one or a few strong year classes are triggered rather than as

64   a response to a vacant niche; (b) Excessive fishing pressure on strong year

65   classes early in the recovery stage may prevent a species from assuming

66   dominance so that the natural succession is influenced and (c) Near

67   simultaneous fluctuations of fish stocks in widely separated regions support

68   the view that they are sometimes influenced by climate operating at a

69   global scale. Moreover, Hsieh et al. (2009) suggested that the catches on

70   two anchovy species (*E. heteroloba* and *E. punctifer*) were mainly

71   determined by the abundance (strength) of *E. japonicus* whereas

72   relationships with environmental variables (water temperature and river

73   runoff) were transient. Also, Machu et al. (2009) suggested, as a result of a

74   coupled physical-biogeochemical modelling experiment, that recruitment

75   of sardines (*S. pilchardus*) could be related to the delay between high

76   abundance of plankton and favorable spawning conditions and Relvas et al.

77   (2009) observed (a) A generalized warming trend in the Canary upwelling

78   system (an important ground for sardine recruitment) and suggested both

79   that (b) significant decadal changes in the mesoscale patterns and (c) Such

80   a large-scale variability can reorganize communities and trophic

81   relationships.

82

83   Two of the most widely accepted frameworks used to describe the

84   theoretical relationship between parental stock and recruitment (also,

85   referred as the "SR" relationship/system) are the Beverton and Holt (1957)

86   and Ricker (1954) models (also, referred herein as "classical models").

87   These approaches were developed for the identification of the best

88   parameterization of the SR relationship. Their principal task was the

89   determination of the best mathematical function (shape and number of

90   parameters) which would permit better determination of coefficients

91   involving the fewest parameters. These classical models, which established

92   a general theoretical framework for modelling population dynamics in the

93   1950's, consist of extinction curves where recruitment reaches either an

94   asymptotic maximum (Beverton-Holt) or becomes low at high spawning

95   stock sizes (Ricker). Both of these models were unified by Shepherd

96   (1982) whose functional form is given by

97

98
$$R = \frac{\alpha \cdot S}{1 + \left(\dfrac{S}{K}\right)^{\delta}}$$
(1)

99   where R is recruitment, S is the spawning stock abundance and K the

100   threshold abundance above which density-dependent effects dominate (i.e.

101   the carrying capacity). The parameters α and δ are referred as the slope at

102   the origin and degree of compensation involved, respectively. The classical

103   dome-shaped (for $\delta > 1$) and asymptotic (for $\delta = 1$) functional forms

104   proposed by Ricker (1954) and Beverton-Holt (1957), respectively can be

105 described within the same framework. An example for each of the models

106 with arbitrary parameter values is shown in Figure 1.

107

108 While the classical models provided important insights into population

109 dynamics and thus implied significant advances to fishery science, they are

110 tools with limited degrees of resolution (capacity to incorporate and

111 describe complex dynamics). Several authors (Clark (1976), Sharp et al.

112 (1983), De Angelis (1988), Fogarty (1993), Solari et al. (1997), Bas et al.

113 (1999)) have suggested that these models do not include key factors of

114 specific situations and have a limited capacity to link internal (population)

115 and external (environmental) dynamics. While such argumentation may

116 hold true, it may be fair to recall that the classical models were put forward

117 before any relevant ecological systems theory was proposed.

118

119 <u>An alternative model.</u>

120 From the classical models which proposed single equilibrium relationships

121 with an invariant carrying capacity, we developed an alternative general

122 framework for multi-oscillatory, dynamic systems in our earlier studies

123 (Solari et al., 1997, originally published in this journal; Bas et al., 1999;

124 Solari et al., 2003 and Solari, 2008). A new model was put forward in

125 which recruitment (to the population, area and fishery) is considered as a

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126 system (henceforth regarded as "system") with dynamic features ranging

127 from chaos (the ceiling, when external conditions are extremely benign),

128 going through a range of relatively stable, converging cycles (as external

129 stress increases), to a quasi-standstill state with no clear oscillations (when

130 the minimum viable population is being approached). The proposed system

131 comprises of a dynamical continuum governed by a variable carrying

132 capacity with local dynamics in different orbits of stability (graphically

133 represented in Figure 2) and it is expressed as

134

$$R(S)_{pop,area,fishery} \cong \sum_{i=1}^{m} \frac{a_i \cdot (S)}{(S - b_i)^2 + c_i} \qquad (2)$$

136

137 where recruitment, R, to the population (pop), area or fishery is defined as

138 a summation of non-linear functions of the adult stock (or stock-in-area), S,

139 and the entries $i = 1 \dots m$ represent the number of dynamical states (orbits

140 of stability and pseudo-equilibria) in the system, being m the highest

141 equilibrium where the relationship reaches the "ceiling" or maximum

142 allowable carrying capacity (K_{max}). Pseudo-equilibria (E_i) are controlled by

143 the coefficients a_i (slope of the curve at the origin), being b_i and c_i the

144   density-dependent mortality entries. For instance, a_i fulfils a similar

145   function to the natural rate of increase in the logistic equation. These

146   coefficients will define each equilibrium state and their values may be

147   fixed. Also, values of b_i will define the ranges of stock for which pseudo-

148   equilibria may arise. We use the concept of "pseudo-equilibria" as we

149   assume that the population system will show responses to an ever-

150   changing environment, as well as the intrinsic density-dependent

151   processes, and thus "equilibrium values" will change rapidly.

152

153   Our proposed model was first in the literature to formalize the concepts of

154   (a) Variable carrying capacity and dynamical continuum as an expression

155   of the evolution of the population system which (b) could link all of the

156   known population mechanics (that is, density-dependent, density-

157   independent and inverse-density-dependent processes) in a relatively

158   simple equation. Also, the framework allowed us to show dynamical

159   similarity at several spatio-temporal scales for case studies on skipjack

160   tuna, *K. pelamis* (Solari et al., 2003) and the common *Octopus*, *O. vulgaris*

161   (Solari, 2008). The system, which is limited by a maximum carrying

162   capacity and an overall minimum viable population (K_0), is highly flexible

163   as it has the capacity to, persistently, evolve and return within a relatively

164 wide range of dynamical states allowing for the description of multi-

165 oscillatory population systems with features which may be caused by

166 stable; periodic; multi-periodic; and chaotic process dynamics.

167

168 In light of the proposed framework, we will now analyze the sardine

169 (*Sardina pilchardus*) *R*, *SSB* and *R/SSB* data in relation to *SST* and *UPW*

170 and attempt to put forward further theoretical propositions which may

171 contribute to (a) Explain and set into a framework the causal mechanisms

172 behind the observed data and (b) Discuss further aspects on management

173 and rehabilitation, particularly, for relatively low levels in both recruitment

174 and abundance.

175

176 <u>Methods.</u>

177 We used statistical tests which can and do provide indications of

178 periodicities, lags, dependencies and persistency or "memory effect"

179 (dependency on preceding values) in the series (auto- and cross

180 correlations): (a) Time series data were log transformed to meet conditions

181 for statistical normality; (b) Also, we worked on standardized data (with

182 mean = zero) as we were interested in trends, not in absolute numbers and

183 to facilitate visual comparison; (c) Data was smoothed with a five year

184   moving average window both to remove noise from the series and to

185   determine whether trends remained; (d) Further, we used simple

186   regressions to determine both the "replacement line" (i.e. recruitment

187   needed to replace the stock) and as an indicator of general equilibrium

188   values (in which the fitted system does neither grow nor decrease) and (e)

189   Polynomial regressions (incorporating three constants for each orbit of

190   stability) to approximate the dynamical continuum we propose. Also, we

191   chose to use the multi-resolution decomposition (MRD) of the wavelet

192   analysis (S+Wavelets, 2003) in order to determine sharp changes or peaks

193   (eight years processes, S8) in the recruitment series.

194

195   Data and results.

196   The *R* and *SSB* data series from 1978 to 2006 were estimated by ICES

197   (2007) from Virtual Population Analysis (VPA). The analytical assessment

198   used fishery dependent data (commercial catch-at-age) and fishery

199   independent data (acoustic surveys abundance-at-age, egg surveys

200   spawning biomass).

201

202   The *SST* data was extracted from the International Comprehensive Ocean-

203   Atmosphere Data Set (ICOADS) provided by the NOAA's Climate

204   Diagnostics Centre (CDC). The product used was the global "enhanced"

205 data set with a 1°x1° grid box (Woodruff et al., 1998) with centre at 39.5ºN

206 and 9.5ºW".

207

208 The Ocean Coastal Upwelling Indices (*UPW*) as developed by Bakun

209 (1996) were calculated from ICOADS wind data on a global enhanced data

210 set with 2º degree grid box, extending between latitude 43ºN - 37ºN and

211 longitude 9ºW, yearly and for the four quarters.

212

213 The bivariate (two-tailed) Pearson correlation matrix showed the following

214 results on the log transformed series: (a) *R* and *R/SSB* (production) are

215 highly correlated to *SST* ($p<.01$ for both of the cases); (b) While *UPW*

216 showed no significant correlations to neither *R* nor R/SSB, there were

217 certain *UPW* ranges for which it appears production may be promoted

218 whereas beyond those ranges production may be depressed; (c) The yearly

219 *UPW* series was significantly correlated to the series from the 1st quarter

220 ($p<.05$) and highly significantly for the remaining 2nd-4th quarters ($p<.01$);

221 The 3rd and 4th quarters showed the highest correlations (.64 and .61,

222 respectively); (d) We chose the pooled catch data (N=92, years 1915-2006)

223 as it was highly significantly correlated ($p<.01$ for all cases) to the series

224 from the Northwest, Southwest and South of Portugal. A multiple

225 regression (p<.001) on *NAO*, *EA* (East Atlantic pattern), *SST* and *UPW*

226 showed that the contribution of *SST* upon *R* was strongest (p<.05).

227

228 In Figure 2, we show an ad hoc model for the abundance and recruitment in

229 the European sardine (*S. pilchardus*) in the Iberian upwelling zone years

230 1978 to 2006: three orbits of stability with corresponding "steady states"

231 (E_i), maximum carrying capacity (K_{max}) and minimum viable population

232 (K_0). Every orbit will be limited by a local ceiling (K_i) and floor (K_{0i}). The

233 dynamical continuum is represented by the non-linear fit and global

234 equilibrium values (or replacement line) are given by the simple regression

235 through the origin (dashed line). Arrows to the right and left indicate the

236 population positive and negative growths. An *m* number of oscillatory

237 phenomena ranging from limit cycles to chaos and inverse density-

238 dependence are allowed in this system. Values and noise are arbitrary.

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

240

241 The European sardine (*S. pilchardus*) recruitment (*R*) and spawning stock

242 biomass (*SSB*), log transformed (Log), smoothed (S, bold line) and

243 standardized (Z) series in the Iberian upwelling zone for years 1978-2006,

244 as estimated by ICES (2007) are shown in Figure 3.

245

246   Production (recruitment per spawning stock biomass, *R/SSB*) of the

247   European sardine (*S. pilchardus*) in the Iberian upwelling zone for years

248   1978-2006 (raw data after ICES, 2007) is shown in Figure 4. Series were

249   log transformed (Log), smoothed (S, bold line) and standardized (Z).

250

251   The phase plane of production (recruitment per spawning stock biomass,

252   *R/SSB*) with lag 1 of the European sardine (*S. pilchardus*) in the Iberian

253   upwelling zone for years 1978-2006 (Figure 5). The original series were

254   log transformed, smoothed and standardized. The relationship turns in two

255   similar orbits of stability within certain ranges beyond which growth

256   becomes steeply negative. The dashed line is a linear regression through

257   the origin.

258

259   In Figure 6, we show the stock and recruitment relationship for the

260   European sardine (*S. pilchardus*) in the Iberian upwelling zone during years

261   1978-2006. Series were standardized (Z), smoothed (S, bold line) and log

262   transformed (Log). The lag to recruitment is one year. The rectangle

263   indicates the oscillations or orbits of stability (A, B) which may be caused

264   both by density-dependent pseudo-cycles and environmental pulses. The

265   dashed linear line is a simple regression through the origin.

266

267   In Figure 7, we show the S8 wavelet analysis (multiresolution

268   decomposition, MRD) on the the raw (non-transformed) European sardine

269   (*S. pilchardus*) recruitment series from the Iberian upwelling zone for years

270   1978-2006. The dashed lines indicate the peaks for the sum of the signals

271   and eight year (D1-D2) and smoothed, low frequency (S2) processes. We

272   used the raw data in order to show the peaks more clearly. Considering the

273   length of the series, we assume the peaks between 6-7 to 15 years (both in

274   the sum of the signals and the 8-16 years processes represented by D1-D2,

275   respectively) detect both of the orbits of stability (A-B in Fig. 5 a) we

276   propose for the SR system.

277

278   The Sea Surface Temperature (with centre at 39.5º N and 9.5º W) and

279   Ocean Coastal Upwelling Indices (latitude 43-37º N and longitude 9º W)

280   for years 1978-2006 (after ICOADS/NOAA, 2007) series is shown in

281   Figure 8. Data values were standardized (Z), smoothed (S) and log

282   transformed (Log). It is proposed that as the external forcing (*UPW* and

283   *SST*) are the inverse of one another (between years 1985-1996), recruitment

284   (*R*) and production (*R/SSB*) in *S. pilchardus* may oscillate in two relatively

285   stable orbits (Fig. 6). Once the synchrony is broken between both of the

286   external variables, *R* and *R/SSB* shift towards relatively steep negative

287   trends. This forcing is an example of the so called "optimal environmental

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288 window", as proposed by Cury and Roy (1989). Linear trends are simple

289 regressions through the origin.

290

291 The phase planes of the external forcing (*SST* and *UPW*) and recruitment

292 (*R*, above left) and production (recruitment per spawning stock biomass,

293 *R/SSB*, right caption) for *S. pilchardus* in the Iberian upwelling zone, years

294 1978-2006 are shown in Figure 9 a-b. Both recruitment and production

295 show similar patterns: they oscillate in relatively stable orbits of stability

296 within certain ranges of *SST* and *UPW* beyond which the system shifts

297 toward steep negative trends. Series were standardized (Z), smoothed (S)

298 and log transformed (Log). Arrows show the direction of the trajectories.

299 Linear trends are simple regressions through the origin.

300

301 Also, we propose two further model options for the sardine dynamics in

302 the Iberian upwelling area. The phase planes showing two radial attractors

303 proposed for both recruitment and production per spawning stock biomass

304 for *S. pilchardus* in the Iberian upwelling zone, years 1978-2006 are shown

305 in Figure 10 a-b. Oscillations in relatively stable orbits may be governed

306 both by density-dependent processes and an environmental window which

307 may be represented by *SST* and *UPW*. *S* is spawning stock, *Rec* is

308 recruitment and simulation parameters and initial conditions were arbitrary.

309

Discussion.

311 Research on species such as sardine and anchovies is extensive. There are

312 factors affecting the dynamics of small pelagic species which suggest the

313 nonlinear, multivariate nature and complex interactions between density

314 dependent and density independent processes: decadal changes (Barange et

315 al. (2009), Relvas et al. (2009)), productivity cycles (Barange et al. (2009),

316 perturbations operating at several spatial scales, even at the basin-wide

317 scale (Chavez et al. (2003), Molinero et al. (2005)), transient relationships

318 (in abundances and catches; Hsieh et al. (2009), out-of-phase abundance

319 successions (Chavez et al. (2003), Hsieh et al. (2009)), delay between high

320 plankton production and recruitment (Machu et al. (2009), cascade

321 mechanisms (Molinero et al. (2005), among other features. Such evidence

322 may confirm that the multiple equilibriums paradigm is more appropriate in

323 aquatic ecosystems than the classical approach based on the existence of a

324 single stable equilibrium.

325 Hsieh et al. (2009) suggested that (a) Fluctuations of anchovy populations

326 might not simply be determined by any single but a nonlinear combination

327 environmental factors and (b) Fishing pressures and environmental changes

328 might have synergistically precipitated abundance declines. Also, Barangue

329 et al. (2009) argued that if out-of-phase sinusoidal trends in production

330   exist, consequences may be important and management procedures

331   designed under such an assumption could be more effective than traditional

332   approaches. It was suggested that (a) The biological mechanisms behind

333   alternating cycles and space utilization may be more complex than a simple

334   replacement and (b) the evolution of sardine and anchovy populations may

335   be described by models based on climate driven habitat changes.

336   Furthermore, Molinero et al. (2005) pointed out that a cascade of links

337   between different (large and local) spatial scale climatic patterns (driven by

338   long-term temperature anomalies) affected the dynamics and top-down

339   effects exerted by jellyfish on copepods. Also, it was argued that such a

340   cascade of links should be integrated into the assessment and modelling

341   studies of pelagic ecosystems.

342

343   There are three main aspects in our paper which we would like to stress: (a)

344   Both recruitment and production (*S. pilchardus* in the Iberian upwelling)

345   appear to be related to an environmental window caused by oscillations in

346   both *SST* and *UPW*: the phase planes of stock, recruitment and production

347   oscillate in relatively stable orbits of stability for certain ranges of *SST* and

348   *UPW* within which both of the external variables are the inverse of one

349   another; once the synchrony in the sine-cosine, wave-like patterns between

350   the external variables is broken, the trajectories of both recruitment and

351   production shift towards density-independent depensation and negative

352   growth occurs; if we are theoretically correct, we would, therefore, expect

353   both of the biological variables to adjust their temporal evolution onto

354   further pseudo-cycles once *SST* and *UPW* recover their "inverse

355   dynamics"; (b) Second, we put forward a new framework which may be

356   useful for the study and exploitation of *S. pilchardus* and other small

357   pelagics: invoking a multi-oscillatory system governed by a multivariate set

358   of external perturbations in which the orbits of stability in the population

359   are caused by inversely related overlapping relationships requires a highly

360   flexible framework; a multioscillatory system with two orbits (seen as

361   pseudo-cycles or radial attractors) can provide an alternative to describe the

362   observed dynamical system; (c) Third, although the classical models could

363   describe each of the orbits of stability as "discrete (unlinked) regimes",

364   these models propose the concepts of an invariant carrying capacity and a

365   single equilibrium which is likely insufficient to describe such complex

366   dynamics; as we see it, to describe the sardine R and R/SSB system in

367   relation to *SST* and *UPW*, requires both a variable carrying capacity and a

368   dynamical continuum which may help to link both (alternatively, several)

369   orbits of (quasi)-stability together.

370   Also, the results presented herein may be supportive of the "optimal

371   environmental window" concept proposed for recruitment success in

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372   upwelling areas by Cury and Roy (1989): (a) the authors relate Ekman-type

373   upwelling, vertical advection, new inputs of nutrients and turbulence to

374   wind speed and, with food availability, they are considered factors that

375   affect larval survival and pelagic fish recruitment and (b) their results

376   showed that for Ekman-type upwelling the annual recruitment increases

377   with upwelling intensity until wind speed reaches certain critical values

378   beyond which recruitment decreases (for which they infer the existence of

379   the so called "optimal environmental window"). We reach a similar

380   inference using our own theoretical model.

381

382   Moreover, we go further in the non-linear analysis to show a variable

383   carrying capacity determined by certain ranges of the external forcing (*SST*

384   and *UPW*) outside of which recruitment and production shift from

385   relatively stable orbits of stability or pseudo-cycles toward density-

386   independent depensation and, hence, negative population growth.

387

388   According to our criteria, there are certain critical factors to consider in

389   exploitation strategies for systems with multiple orbits of stability. There

390   are several key concepts spinning off from our alternative model that may

391   allow us to further investigate some of the aspects relating possible

392   sustainable exploitation strategies such as: (a) differential effects of fishing

393   mortality: during density-dependent (intrinsic to the population) and

394   density-independent (environmentally induced) compensations (positive

395   growth) and depensations (negative growth), the impact of fisheries may be

396   different; and also, the negative impacts of fishing may be less during

397   compensatory phases; this implies that fishing pressure could be relatively

398   higher during compensations, depending on the current orbits of stability or

399   level of numbers; on the other hand, the consequences of high and intense

400   exploitation may be of a negative nature once the trajectory of the

401   population becomes depensatory (negative population growth); the

402   differential effects of fishing (positive and negative growths during both

403   density-dependent and density-independent processes) together with length

404   and degree of the slopes in the trends should be further investigated; (b)

405   Understanding of fishery collapses (or shifts to low orbits of stability with

406   low oscillations in numbers) due to depensatory processes induced by the

407   combined effects from the environment and high fishing mortality: the

408   highest negative impacts in the population may be expected during density-

409   independent and density-dependent depensations operating simultaneously;

410   such processes may lead both recruitment and production towards low

411   levels from which a rehabilitation will not occur until a new environmental

412   pulse ("inverse dynamics" between SST and UPW) make it possible and

413   (c) Short and medium term estimation of recruitment due to trends (slopes

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414   and temporal evolution) in external "best descriptor" variables (such as

415   *SST*, *SST* Anomaly, *SSTA*, North Atlantic Oscillation, *NAO*, upwelling

416   strength, among others).

417

418   Also, our alternative model allows analysis of factors such as the high

419   variability in the data and determination of how combined, multivariate

420   correspondences, memory effects, time lags, periodic oscillations, noise

421   and sensitivity to external conditions may affect the population system. We

422   should further investigate whether there may be dynamical similarity at

423   several spatio-temporal scales and the potential extrapolation of trends

424   between different scales of changes in *S. pilchardus*. Clearly, the forward

425   and backwards bending nature of catches, fishing effort, and abundance,

426   and the incorporation of multivariate perturbations into the model and

427   aspects related to auto correlated residuals in population systems with

428   strong dependencies on pulses from wave-like external variables should be

429   taken into account. The flexibility of the theoretical framework we propose

430   and multiplicity of factors which may be incorporated into a relatively

431   simple model may be some of the advantages of our approach.

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557   [END OF TEXT PART]

"On the dynamics of *Sardina pilchardus*: orbits of stability and environmental forcing"
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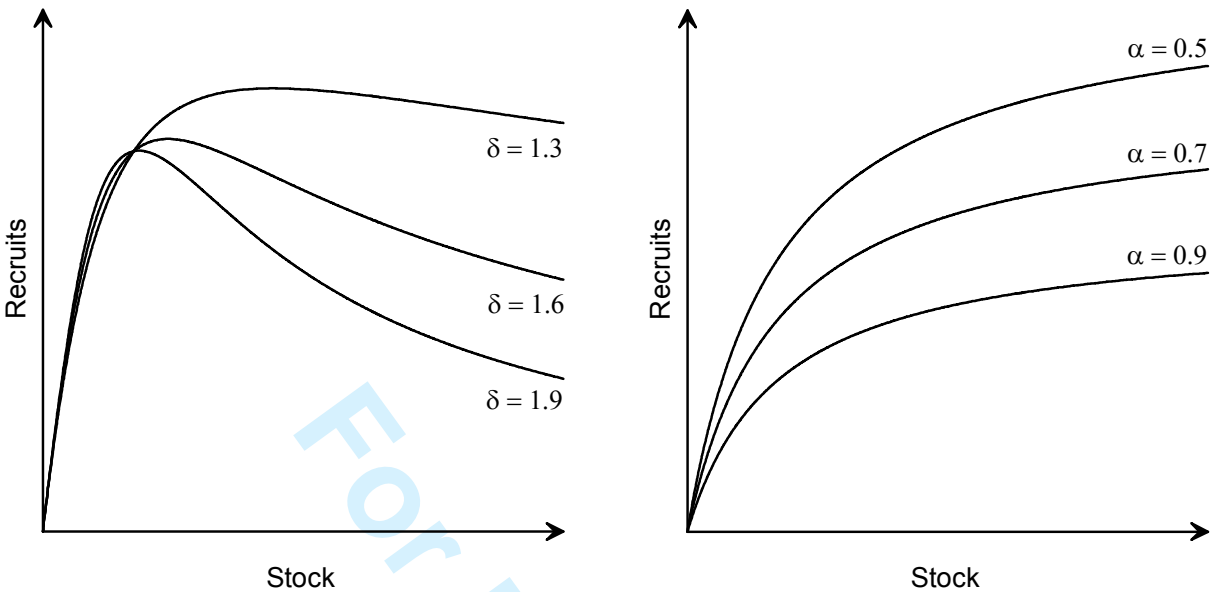
Fig. 1. Two arbitrary examples of the Shepherd (1982) functional form with parameter values describing the Stock-Recruitment relationship as proposed by Ricker (1954, for $\delta > 1$, left caption) and Beverton-Holt (1957, for $\delta = 1$, right caption).

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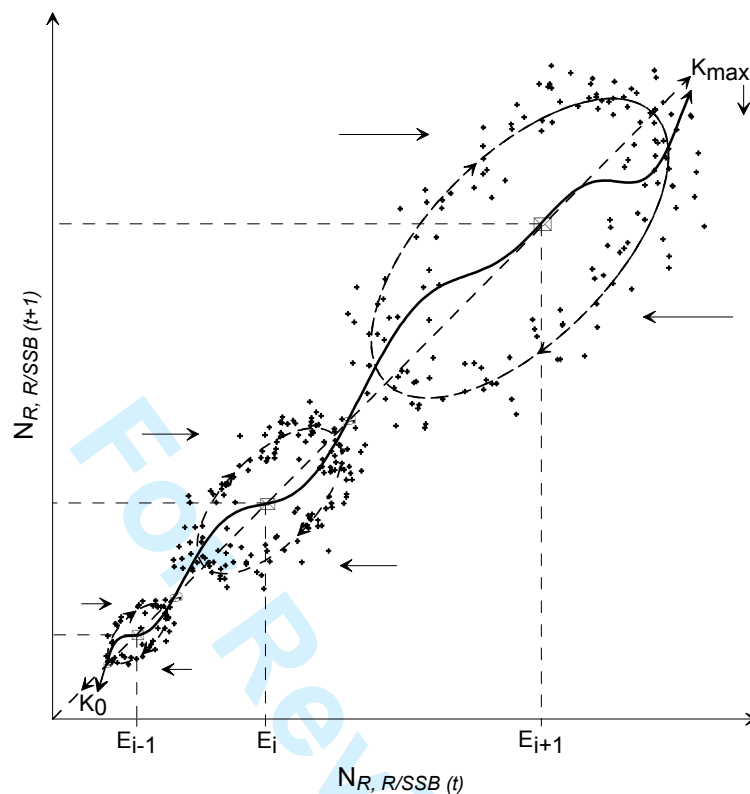
Fig. 2. An ad hoc model for the abundance and recruitment in the European sardine (*Sardina pilchardus*) in the Iberian upwelling zone years 1978 to 2006: three orbits of stability with corresponding "steady states" (E_i), maximum carrying capacity (K_{max}) and minimum viable population (K_0). Every 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).

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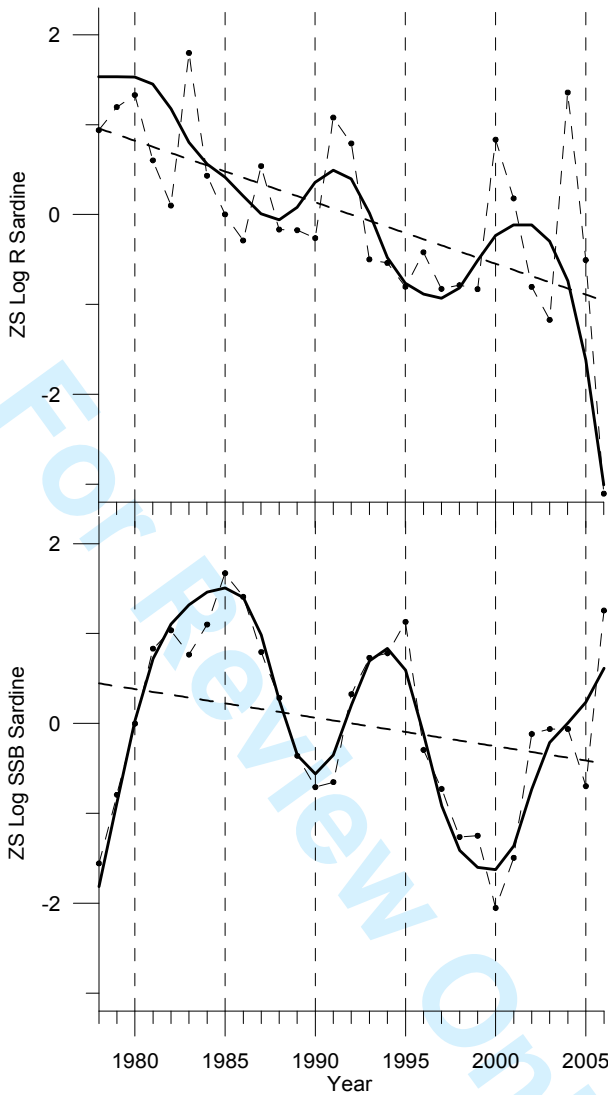
Fig. 3. The European sardine (*Sardina pilchardus*) recruitment (*R*) and spawning stock biomass (*SSB*), log transformed (Log), smoothed (S, bold line) and standardized (Z) series in the Iberian upwelling zone for years 1978-2006, as estimated by ICES (2007).
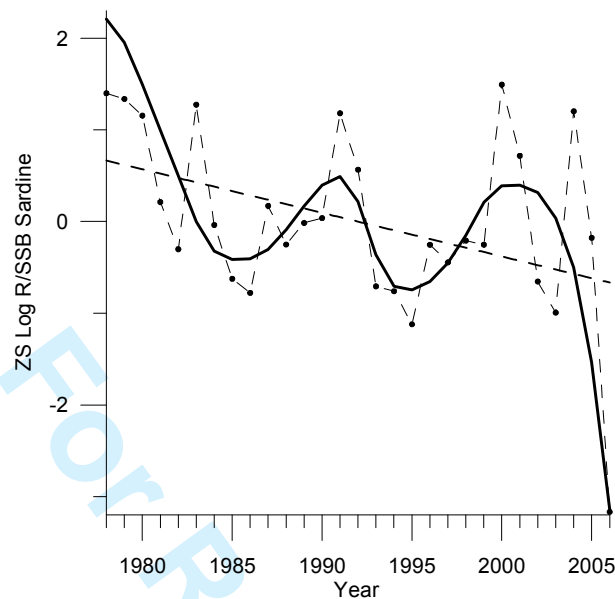
Fig. 4. Production (recruitment per spawning stock biomass, *R/SSB*) of the European sardine (*Sardina pilchardus*) in the Iberian upwelling zone for years 1978-2006 (raw data after ICES, 2007). Series were log transformed (Log), smoothed (S, bold line) and standardized (Z).
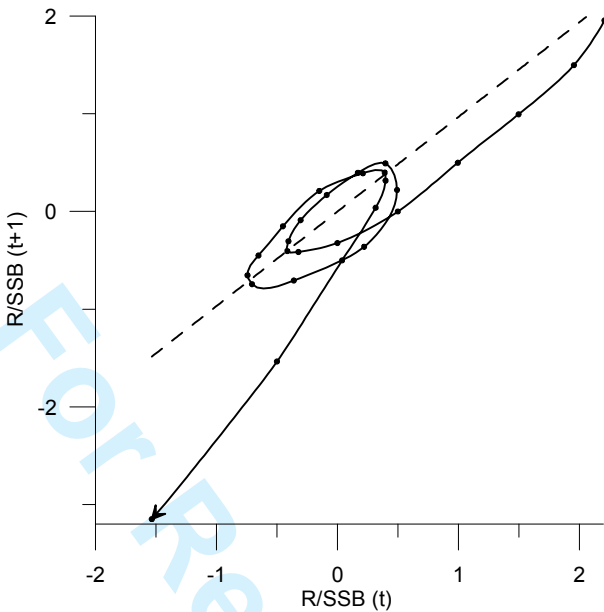
Fig. 5.   The phase plane of production (recruitment per spawning stock biomass, *R/SSB*) with lag 1 of the European sardine (*Sardina pilchardus*) in the Iberian upwelling zone for years 1978-2006. The original series were log transformed, smoothed and standardized. The dashed line is a linear regression through the origin.
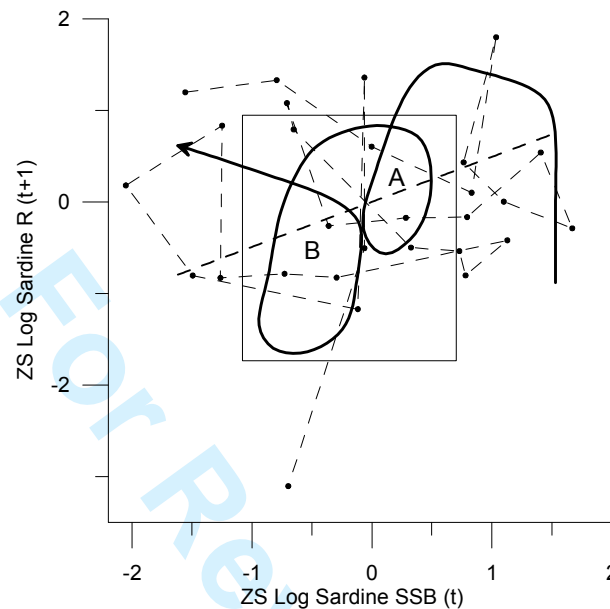
Fig. 6. The stock and recruitment relationship in the European sardine (*Sardina pilchardus*) in the Iberian upwelling zone for years 1978-2006. Series were standardized (Z), smoothed (S, bold line) and log transformed (Log). The lag to recruitment is one year. The rectangle indicates the orbits of stability (A, B). The dashed lines is a simple regression through the origin.
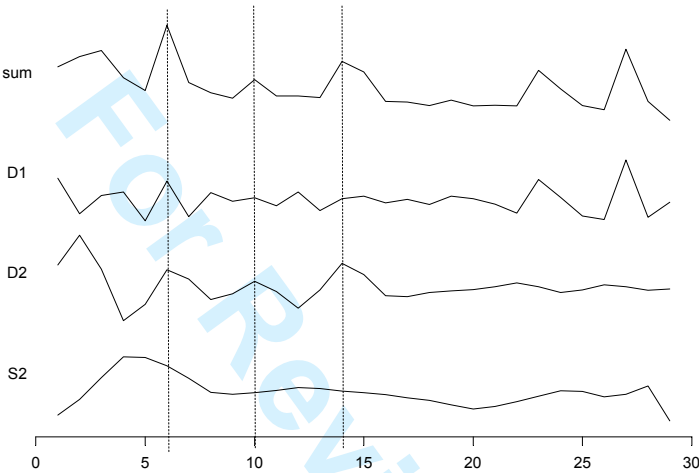
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Fig. 7. The (S8) wavlet analysis (multiresolution decomposition, MRD) on the recruitment series on European sardine (*Sardina pilchardus*) from the Iberian upwelling zone for years 1978-2006. The dashed lines indicate the peaks for the sum of the signals and eight year (D1-D2) and smoothed, low frequency (S2) processes.
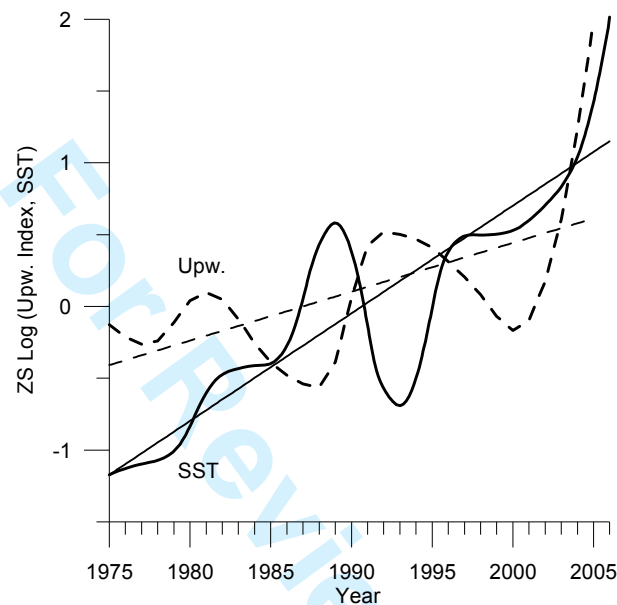
Fig. 8. The Sea Surface Temperature (SST; with centre at 39.5º N and 9.5º W) and Ocean Coastal Upwelling Indices (UPW; latitude 43-37º N and longitude 9º W) for years 1978-2006 (after ICOADS/NOAA, 2007) series. Data values were standardized (Z), smoothed (S) and log transformed (Log).
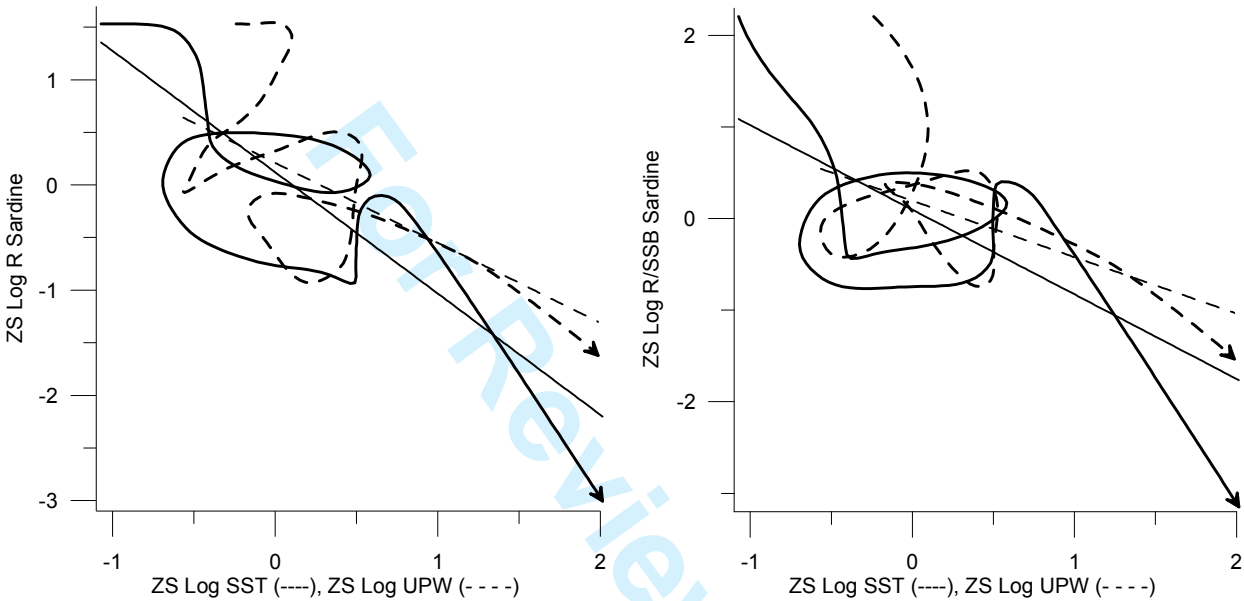
Fig. 9 a-b. Phase planes of the external forcing (Sea Surface Temperature, *SST* and Upwelling Index, *UPW*) and recruitment (*R*, above left) and production (recruitment per spawning stock biomass, *R/SSB*, right caption) for *Sardina pilchardus* in the Iberian upwlling zone, years 1978-2006. Series were standardized (Z), smoothed (S) and log transformed (Log). Arrows show the direction of the trajectories. Linear trends are simple regressions through the origin.
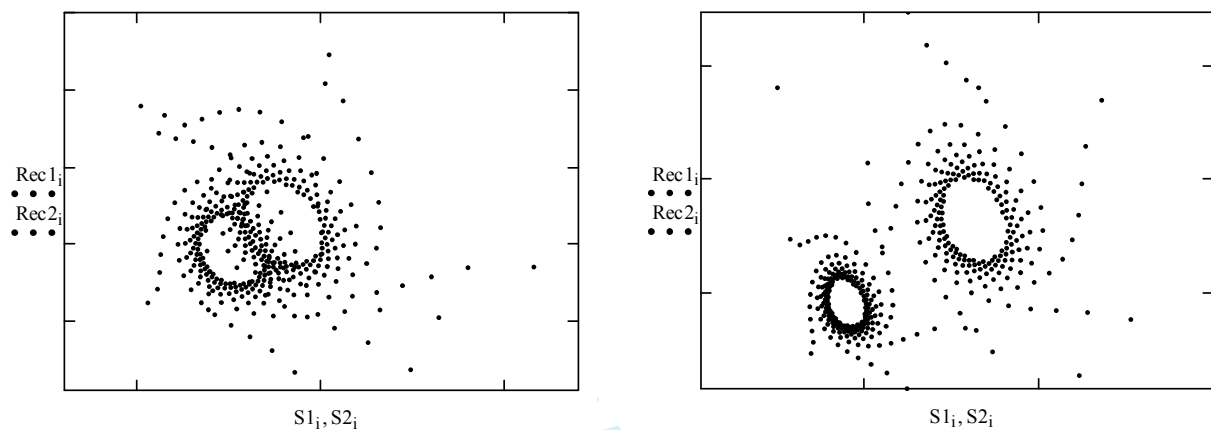
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Fig. 10 a-b. The phase planes showing two radial attractors proposed for recruitment and production per spawning stock biomass for *Sardina pilchardus* in the Iberian upwlling zone, years 1978-2006. Oscillations in relatively stable orbits may be governed 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.

[END OF CAPTIONS PART]