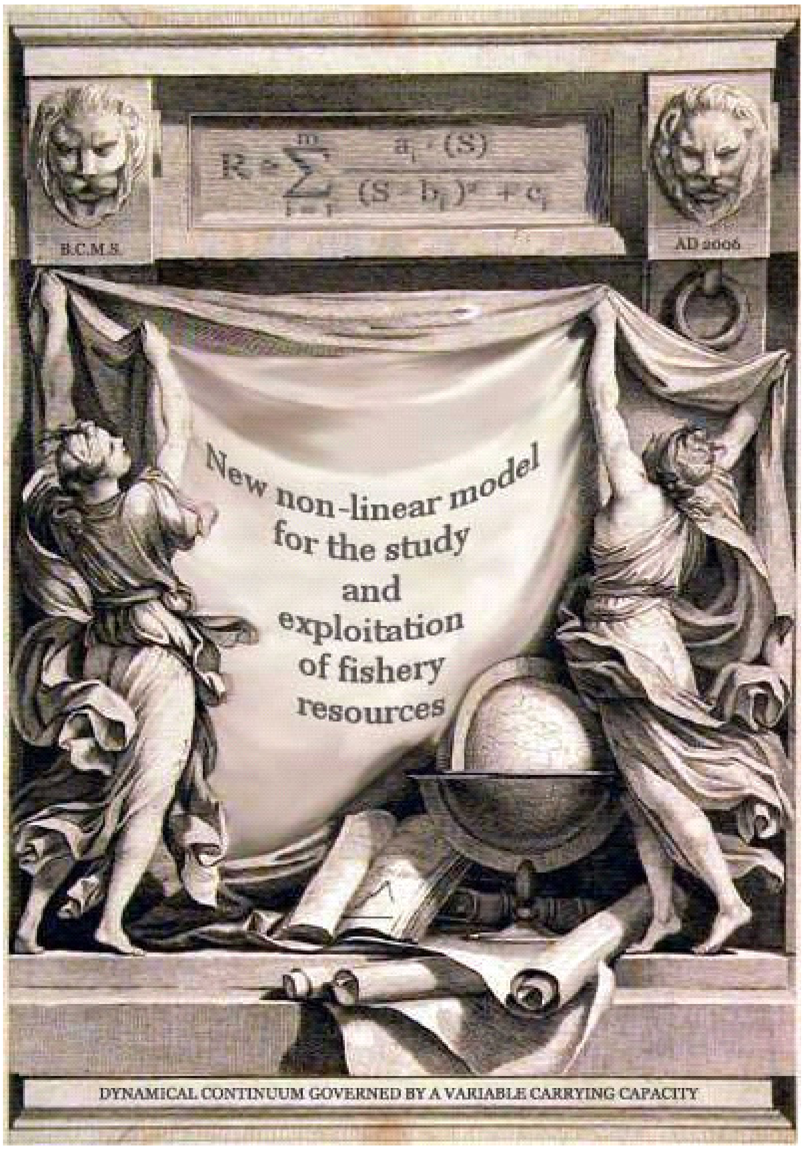

NEW NON–LINEAR MODEL
FOR THE STUDY AND EXPLOITATION
OF FISHERY RESOURCES

DOCTORAL THESIS PRESENTED BY

ALDO P. SOLARI

UNIVERSITY OF LAS PALMAS DE GRAN CANARIA

AD 2008

University of Las Palmas de Gran Canaria
Faculty of Marine Sciences
Biodiversity and Conservation Group

“NEW NON–LINEAR MODEL FOR THE STUDY AND EXPLOITATION OF FISHERY RESOURCES”

Doctoral thesis presented by

Aldo P. Solari

Directed by
Research Professor Dr. Carlos Bas Peired

and co–directed by
Dr. José Juan Castro
and
Dr. Juan Manuel Martín–González

Submitted in fulfillment of the requirements
of the degree of Doctor of Philosophy

The Director

The Co–director The Co–director

The Doctoral candidate

Las Palmas de Gran Canaria, 2008

[nota]

Lectura de la Memoria de la presente Tésis Doctoral celebrada el Sábado 5 de Julio de 2008, en la Facultad de Ciencias del Mar de la Universidad de Las Palmas de Gran Canaria (ULPGC).

El tribunal se constituyó por los doctores:

Serge Garcia
ex Director de FAO/FIRM, Presidente del Tribunal

Eduardo Balguerías
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Decano de la Facultad de Ciencias del Mar

Ricardo Haroun
Conservación y Biodiversidad, Depto. de Biología, ULPGC.

José Luis Trenzado
Depto. de Física, ULPGC.

Calificación de la Tésis:

"Sobresaliente Cum Laude por unanimidad de todo el tribunal".

[fin de nota]

OCEANO PATRIA NOSTRA

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Sumario en Castellano (Summary in Spanish).

DEDICATION

This thesis is dedicated to my grandmother, mother and wife,

Brenda,

María Teresa,

and

Silvia,

respectively.

Strong women,

comrades who never quit.

FOREWORD

The seeking of knowledge is fundamental both to our character and identity and I put forward this thesis with great pride. I feel highly privileged for having had the opportunity to work together, hand-to-hand, with my supervisors and colleagues. At these "cross roads", we became bonded together by the challenges and adversities associated to the proposal of new, forward ideas. Also, the long discussions shaped the progress of the work and nurtured further ideas. And the ethical framework of mutual recognition, respect and espirit-de-corps became a footprint in our group.

From my childhood hero, *Capt. Jacques-Yves Cousteau*, and the first diving kit my grandmother bought me, at age six, to the discussions with *Research Professor Dr. Carlos Bas* on the new ideas we have put forward, the path was rather long. But the dream and vocation are still there. These were happy days and we worked with great freedom, and easy among ourselves. This work group became a "forge" which allowed us to shape a new tool. This thesis may be both science and art, and a disciplined execution of a plan, as well.

From the begining, the ground idea was to approach the field of population dynamics from a "social contract" perspective in which the proposed research work could contribute to the progress of our society.

I, for one, as a disciple of *Research Professor Dr. Carlos Bas*, shall bear and communicate both his scientific and ethical heritage, now and in the future. That is my compromise.▪

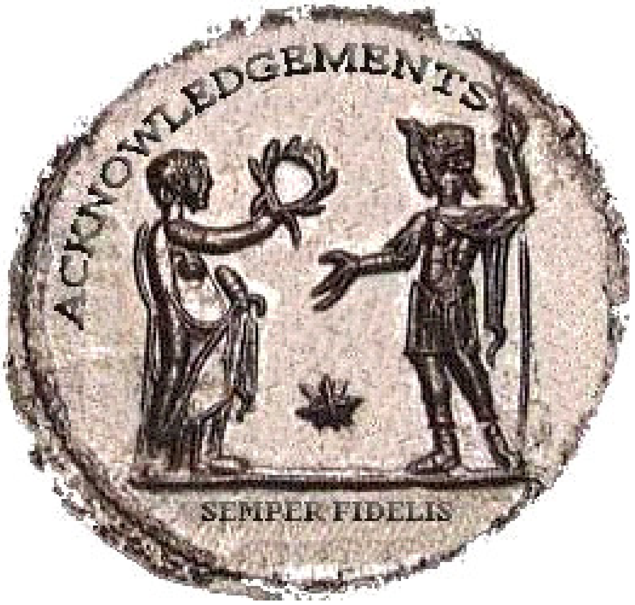
HISTORICAL NOTE

AND DEVELOPMENT OF THE PRESENT FRAMEWORK

Back in Sweden, due to the complexity of the proposed thesis work (the production of a new, non-linear framework for the study and exploitation of fishery resources), *Bernt Dybern* (former Director of the Swedish Institute or Marine Research, IMR), *Dr. Armin Lindqvist* (Swedish fisheries representative at FAO for many years, IMR) and *Dr. Per Olov Larsson* (Chief of Demersal Fish Research, IMR) proposed *Research Prof. Dr. Carlos Bas Peired* (former Director of the Institute of Marine Sciences in Barcelona and an international authority in fishery resources) as the potential supervisor for the tasks ahead. The Swedish institutional "clockwork" contributed to find him, arrange the student aid (contacts and scolarship) and, provided I was accepted as his disciple, come to the University of Las Palmas de Gran Canaria (ULPGC) where he was creating/consolidating the Fishery Resources Group. There was some urgency to produce a new, dynamical framework as recruitment in Baltic cod had been poor for several years and a new theoretical "tool" was needed. Earlier theoretical approaches dated from the begining of the 50's (Beverton-Holt, Ricker) and 1972 (Paulik). After a letter to Prof. Carlos Bas and a call back from him, he agreed without hesitation to undertake the supervision of the research tasks, and that was the begining of this well worth "journey". All of the original aims were accomplished and the new theoretical framework came to be further developed and applied to other species of relevance in the world of fisheries. Currently, there are several further developments of this work in national and international projects and several new ideas and "spin-offs" standing by to be shaped and formalized as time permits.

Originally, we developed the new framework using a case study on stock and recruitment in cod, mainly for the Baltic (ICES) areas 25-32. However, as the model was published (an editorial process which took twenty three months), it was suggested by our senior colleagues that we should seek to validate the framework on further case studies. We subsequently approached Icelandic cod and, later on, shifted our work towards fish and cepahlopod dynamics in FAO fishing area 34 (Eastern Central Atlantic): we chose both tropical tunas, particularly, skipjack tuna and the common *Octopus*, stocks which are critical in the area due to their importance as fishery resources. Both of these cases became the grounds for further developments of the framework and gave rise to several colaborations and projects, as well. Moreover, the skipjack and *Octopus* cases showed dynamical similarity at several spatial scales (which we first detected analyzing Sea Surface Temperature in FAO Area 34) and it was conceptually incorporated into the framework. Some of the key concepts of the model advanced from “steady-state” to “seudo-equilibrium” to “dynamical continuum” (not a semantic matter, indeed) and we were first to formalize the concept of “variable carrying capacity”. Furthermore, we incorporated a perturbation term into the model in which we may introduce environmental forcings and continued working on the general concept of the population seen as a multi-oscillatory system with global and local dynamics which we may described as a summation of non-linear functions. Moreover, we did exploratory analysis on the whole of the FAO fisheries data base and came to the conclusion that the present framework could be applied to over 120 fish stocks worldwide. The framework opened up a new research line in which we may review old “problems” in a new light and attempt to understand the dynamics behind the data. This may prove critical to estimate future ranges of recruitment in the short and medium terms (8-12 years in advance), determine sustainable ranges of captures, and for conservation purposes, as well. ▪

ACKNOWLEDGEMENTS



SEMPER FIDELIS

The framework presented herein is the result of a team work in which all of the authors have been instrumental, as well as other parties (individuals and institutions) which contributed with funding, data and other kinds of support (scientifical, moral and ethical).

There are three key individuals in the production of this thesis to whom I feel the deepest of the gratitudes:

Research Professor Dr. Carlos Bas Peired who has had the "compass and chart" in this endeavour: as a pioneer, he has "shown the way" by-the-example with the greatest of the wisdoms and scientific intuition, and a "rock-solid" ethical code-of-conduct. Without his contribution this new framework could either have taken several more years to be formalized or never come into light. And without his teachings, as a scientist, I would probably still remain as a piece of "raw stone".

Professor Dr. Juan Manuel Martín-González who (as a true *bohemian* of science) contributed with a great open mind to the development of the framework with dynamical systems knowledge and numerical recipes.

Professor Dr. José Juan Castro who ever searched for projects and funding to keep the work-in-progress (and me) going and with his bioecological knowledge contributed with key ideas to several of the newer concepts in the framework.

They believed in the aims and scope of the proposed work and contributed decisively in all of the development steps, they worked hand-to-hand with me and showed a strong and remarkable vocation, creativity and patience.

Also, I would like to mention the many individuals and institutions which contributed to the progress of this thesis work:

There are several *pioneers* in Fishery science who contributed with criticism, encouragement, used their precious time to review our manuscripts and, above all, helped us to shape many of the key concepts of the new framework:

Dr. Gary Sharp (Center for Climate/Ocean Resources Study, Monterey, California) and *Dr. Serge Garcia* (then, Director, Fisheries division, FAO) who both analyzed and discussed in detail our framework, suggested further validations and, through several discussions, provided insights that led us to shape the later concept of “dynamical continuum”, among several other aspects.

Dr. Eduardo Balguerías-Guerra (Chief of cephalopod research, Instituto Español de Oceanografía, IEO, Canarian Oceanographic Centre, Tenerife, Spain) who contributed with his extensive experimental knowledge on fish and cephalopod dynamics and opened up a wealth of invaluable colaboration “windows”.

Dr. John Caddy and *Dr. Jorge Csirke* (former and current directors of the Marine resources division at the FAO, respectively) were key reviewers of the concepts we proposed, as well.

I am truly proud to have had the opportunity to colaborate with these senior scientists whom I look up to as they have “led the way” in the study of the dynamics on fishery resources and the oceans.

Dr. Laurent Seuront and, particularly, *Dr. Sami Soussi* (Wimeraux Marine station, University of Lille 1, France) who shared ideas, reviewed our work and, from the very beginning, contributed with highly valuable comments to the skipjack and *Octopus* case studies, as well as to the development of many of the ideas proposed herein.

Dr. Gunnar Stefanson (Marine Research Institute, Reykjavik, Iceland) whose contribution was instrumental to obtain fisheries and oceanographic data from the the International Council for the Exploration of the Seas (ICES) and to the progress of our framework, as well.

Dimitris Evangelinos (Dept. of Physics, Aristotle University of Tessaloniki, Greece) who contributed with pedagogical advice concerning data analysis.

Dr. Unai Ganzedo López (University of the Basque Country, Spain) with whom we discussed the use of satellite derived approaches and climatic proxies in the framework.

Bernt Dybern, *Dr. Armin Lindqvist* and *Dr. Per Olov Larsson* from the Institute of Marine Research (IMR), and *Research Professors Dr. Lillemor Lewan*, *Dr. Boerje Karlsson*, *Dr. Boris Holm* and *Dr. Thorbjoern Fagerstroem* from Lund University (Sweden). Their unselfish contribution was the seed which allowed the start of this journey to meet and work with Prof. Carlos Bas.

Dolores Ojeda from the Ministry of Agriculture and Fisheries, Canarian Government, who assisted us in project matters.

Silvia Rodríguez (Systems engineer) who assisted me both to understand the internal “black boxes” in the package MathCAD, some of the programming routines and art work for this thesis.

From the University of Las Palmas de Gran Canaria *(“Domus Noster”)*, I wish to thank, particularly, the following principals and colleagues:

Rectors *Dr. Francisco Rubio-Royo* (retired) and *Dr. Manuel Lobo* (retired) for having appointed *Research Professor Dr. Carlos Bas* to create the Fishery

Resources Group and promoted him as Doctor Honoris Causa, respectively.

Deans (Faculty of Marine Sciences) *Dr. Joaquín Hernandez-Brito* (Dept. of Chemistry), *Dr. José Luis Pelegrí* (Physical Oceanography) and *Dr. Santiago Hernández-León* (Biological Oceanography).

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Dr. Antonio González-Guerra (Physics), *Dr. Julio Esclarín Monreal* (School of Computer Science), *Avelina Férnandez* (Librarian, Faculty of Marine Sciences) for their unselfish availability to help and resolve various matters.

From the Reception at the Faculty of Marine Sciences: *Víctor Suárez Santana*, *José María Heredia*, *Rito Mendoza Santiago*, *Santiago Delgado Alamo* for having taken care of my mail, facisimiles and other material with so much professionalism and service spirit.

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Data Sources.

A particular recognition goes to the American, European and international institutions which facilitated our research with their data. Without their assistance, part of our research would have been either more expensive or practially impossible to carry out. It should be remarked that American institutions served us as if we were their own tax payers – for which I am deeply thankful. The data sources were as follows:

National Climatic Data Center (NCDC); Jet Propulsion Laboratory (JPL), SIR-C project; Physical Oceanography Distributed Active Archive Center (PO.DAAC); National Meteorological Center (NMC); National Oceanic and Atmospheric Administration (NOAA); International Council for the Exploration of the Sea (ICES); International Commission for the Conservation of Atlantic Tunas (ICCAT); Food and

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Anonymous personnel both from the SIR-C project (Jet Propulsion Laboratory, NASA; Synthetic Aperture Radar data) and the AVHRR/SST sources from the National Climatic Data Center (NCDC, USA) who assisted in technical matters and satellite data retrieval.

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I wish to thank all of the concerned parties for having shown their trust in our work through the funding of the different projects arising from this thesis.

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Thank you all. *Thank you*.▪

PUBLICATIONS, WORKSHOP AND PROJECTS ARISING FROM THIS THESIS

The present thesis gave rise to the following publications and reports, international workshop and projects:

Publications and reports.

Solari, A. P., J. M. Martin-Gonzalez and C. Bas (1997). **Stock and recruitment in Baltic cod (*Gadus morhua*): a new, non-linear approach.** ICES Journal of Mar. Sc. 54:427-443.

European Union (1998). Report from the workshop ***"New non-linear model for stock-recruitment and management of fish stocks"***. Programme FAIR. J. M. Martín, C. Bas and A. P. Solari (editors).

Bas, C., A. P. Solari and J. M. Martin-Gonzalez (1999). **Considerations over a new recruitment model for exploited fish populations.** Royal Academy of Sciences and Arts, Vol. LVIII Nr. 5:157-183.

Castro, J. J., A. P. Solari, J. M. Martin-Gonzalez and C. Bas (1999). **Recruitment to the fishery of the skipjack tuna *Katsuwonus pelamis* in the Canary Islands area: application of a new conceptual framework.** Report to the Ministry of Fisheries and Agriculture, Canarian Government, Grant Order Nr. 540 to the Las Palmas University Foundation.

Solari, A. P., J. J. Castro and C. Bas (2001). **Fisheries control through indicator species and sea**

surface temperature: a case study off Mogan, island of Gran Canaria (Canary Islands). Report to the Project INNOVA, Las Palmas University Foundation (Grant order BP-28).

Solari, A. P., J. J. Castro and C. Bas (2002). **On skipjack tuna dynamics: similarity at several scales.** In "Scales in Aquatic Ecology. Measurement, analyses and simulation". Edited by Laurent Seuront (CNRS, France) and Peter G. Strutton (Monterey Bay Aquarium Research Institute, USA). CRC Press.

Solari, A. P., C. Bas and J. J. Castro (2003). **Especies indicadoras: un nuevo concepto para el control y gestión de la pesca con nasas, en Canarias.** VectorPlus 21:6 (In Spanish).

Solari, A. P., J. J. Castro, S. Souissi, E. Balguerías, V. Hernández-García and C. Bas (2004). **On the dynamics of the common *Octopus*** (Cuvier, 1797). Presented at the European CEPHSTOCK Workshop, Imperial College, London (31st August-2nd Sept. 2004).

Solari, A. P., J. J. Castro, S. Souissi, E. Balguerías, V. Hernández-García and C. Bas (2004). **On the dynamics of the common *Octopus* (Cuvier, 1797): towards a new system- framework.** In review process.

Castro, J. J., E. Balguerías, C. Bas y A. P. Solari (2006). **Sobre la dinámica del pulpo común, *Octopus vulgaris* (Cuvier, 1797): hacia un nuevo marco teórico.** Proyecto Nº PI042004/139 financiado por el Gobierno de Canarias. Consejería de Educación, Cultura y Deportes. Dirección General de Universidades e investigación. Investigador Responsable: José J. Castro. Resolución: 17 de agosto de 2004 (BOC Nº 166 de 27 de agosto de 2004). Duración: 2005-2006. In Spanish.

Castro, J. J., A. P. Solari, A. Delgado de Molina, J. Ariz, Mª S. Rodríguez y C. Bas (2007). **Dinámica poblacional y posibles estrategias de conservación del atún bonito-listado (*Katsuwonus pelamis*) en el Atlántico Centro Oriental.** Informe del Proyecto (PI042005/126) de la Consejería de Educación, Cultura y Deportes del Gobierno de Canarias. Grupo de Biodiversidad y Conservación de la Universidad de Las Palmas de Gran Canaria. Julio de 2007. (In Spanish).

Balguerías, E., C. Bas, J. J. Castro, A. Faraj, D. Jouffre and A. P. Solari (2007). **ISTAM Project Report (1/2), WP/3, Environmental Models, "Multi-oscillatory System Approach".** July, 2007. (authors oredered alphabetically).

European workshop.

The new, theoretical framework as put forward in **Solari A., J. M. Martín and C. Bas (1997), *"Stock and recruitment in Baltic cod (Gadus morhua): a new, non-linear approach"***, published in the **ICES Journal of Marine Science 54:427-443** gave rise to an offer from the Fisheries Directorate XIV of the European Union to celebrate an international workshop.

The workshop ***"New non-linear model for stock-recruitment and management of fish stocks"*** was sponsored by the European Union through the Framework IV programme in research and technical development for Agriculture and Agro-Industries (FAIR) with Award of Grant Reference MAC/12/97, the Ministry of Agriculture and Fisheries of the Canarian Autonomous Government (Viceconsejería de Agricultura y Pesca del Gobierno Autónomo de Canarias) and the University of Las Palmas de Gran Canaria, and held in Las Palmas between March the 31st and April the 2nd, 1998. Proposals for further developments, testing and viability of application of the model upon the study and management of demersal and pelagic fish stocks were discussed by fishery scientists from Sweden, Iceland, Denmark, France and Spain. A report from the workshop is reproduced in Appendix II of this thesis.

National projects.

Dynamical framework for the conservation and sustainable exploitation of the common *Octopus* (*Octopus vulgaris*, Cuvier, 1797) in the Northwestern African upwelling zones. Principal investigator: Dr. José J. Castro. Project Nº AGL2006-10444/ACU financed by the Ministry of Education and Science. Current project, 2007-2009. In cooperation with the Instituto Español de Oceanografía (IEO, Tenerife, Spain).

Population dynamics and possible conservation strategies of the skipjack tuna (*Katsuwonus pelamis*) in the Eastern Central Atlantic. Project Nº PI042005/126 financed by the Canarian Government, Ministry of Education, Culture and Sports and the General Direction of universities and research (BOC Nº 120, 22th, June, 2006). Principal investigator: Dr. José J. Castro. Current project, 2006-2007. In cooperation with the Instituto Español de Oceanografía (IEO, Tenerife, Spain).

Castro, J. J., E. Balguerías, C. Bas and A. P. Solari. **Sobre la dinámica del pulpo común, *Octopus vulgaris* (Cuvier, 1797): hacia un nuevo marco teórico.** Project Nº PI042004/139 financed by the Ministry of Science and Education. Principal investigator: Dr. José J. Castro. Resolution: 17th, August, 2004 (BOC Nº 166 , 27th, August, 2004). Length of project: 2005-2006.

Solari, A. P., J. J. Castro and C. Bas (2001). **Fisheries control through indicator species and sea surface temperature: a case study off Mogan, island of Gran Canaria (Canary Islands).** Project INNOVA, Las Palmas University Foundation (Grant order BP-28). Duration: 2000-2001.

Castro, J. J., A. P. Solari, J. M. Martin-Gonzalez and C. Bas (1999). **Recruitment to the fishery of the skipjack tuna *Katsuwonus pelamis* in the Canary Islands area: application of a new conceptual framework.** Project financed by the Ministry of Agriculture and Fisheries, Canarian Government, Grant Order Nr. 540 to the Las Palmas University Foundation. Principal investigator: Dr. José J. Castro.

Participation in international projects.

Improve Scientific and Technical Advices for fisheries Management (ISTAM, 2006-2008). Project Nº SSP-200n-022774 financed by the Comission of European Communities, RTD Programe "Specific Support Policies" for the integration of European coordination and research in fishery matters in Northwest Africa. Principal investigator: Nicolas Bez, Institut de Recherche pour le Développement, IRD, France. http://www.projet-istam.org/

Presentation of the framework at the Imperial College in London.

Invitation to the CEPHSTOCK workshop celebrated at the Imperial College (London) to put forward the new framework (after *Solari et al., 1997*), applied to cephalopod dynamics, in the study "**On the dynamics of the common *Octopus (Cuvier, 1797)*: a new framework**". August 30th-31st, 2004.

Thesis abstract.

A novel modeling approach is put forward in which recruitment (to the population, area and fishery) is regarded as a system or summation of non-linear functions 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).

A system which consists of a dynamical continuum governed by a variable carrying capacity with local dynamics in different orbits of stability is proposed. The author is first to formalize in the scientific literature the concepts of variable carrying capacity, multiple, linked orbits of stability and seudo-equilibria, and dynamical similarity at several spatio-temporal scales, as well. The model has been the first which could link all of the known population mechanics (that is, density-dependent, density-independent and inverse-density-dependence processes) in a relatively simple equation. This system model which is limited by a maximum carrying capacity and an overall minimum viable population is highly flexible as it has the capacity to, persistently, evolve and return within a 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 dynamics.

The proposed framework offers several conceptual and practical advantages over the classical models and it may allow to ask better questions and do a more realistic assessment in stock dynamics. Some of the key concepts spinning off the model are as follows: (i) the persistency and plasticity of the population system, that is the ability of the stock to withstand both environmental perturbations and high fishing mortality and rehabilitate from low orbits of stability; (ii) the differential effects of fishing mortality during density-dependent and density-independent compensations and depensations; (iii) the understanding of (a) population collapses due to the effects from density-independent depensations combined to high fishing mortality and (b) density-dependent and density-independent mechanisms may induce the rehabilitation of the stock towards higher orbits of stability; (iv) the short and medium term estimation of recruitment due to trends (slopes and temporal evolution) in external “best descriptor” variables (such as Sea Surface Temperature, SST, SST Anomaly, SSTA, North Atlantic Oscillation, NAO, upwelling strength,

among others and climate proxies); (v) the explanation of the high variability in the data and determination of how combined, multivariate correspondences, memory effects, time lags, periodic oscillations, noise and sensivity to external conditions may affect the population system; (vi) the existence of dynamical similarity at several spatio-temporal scales and extrapolation of trends between different scales.

Furthermore, new concepts are proposed on (a) global and local dynamics; (b) residuals, signal, noise and dispersion in the data; (c) harvesting in systems with multiple orbits of stability; (d) conditions which may lead to the extinction of the commercial fishery; (e) forward and backwards bending nature of catches, fishing effort, and abundance; (f) incorporation of multivariate perturbations into the model and (g) approximations to the multi-oscillatory model by different curve fitting methods and the matter on autocorrelated residuals and population systems with strong dependencies on wave-like external variables.

The author validates the proposed framework in the case studies which are put forward in the thesis: it is shown that the dynamical patterns in the different cases consist systems with multiple orbits of stability and that population trends are due to the combined effects from internal population mechanics as well as the external environment and fishing mortality:

(i) Baltic cod showed (on data until 1993) two orbits of stability and, according to our theoretical criteria, we were able to estimate future trends in the population system: in our original study (Solari et al., 1993), it was estimated that Baltic cod was nearby the minimum viable population due to the combined effects from high fishing mortality and negative effects from external perturbations. However, a rehabilitation towards a low equilibrium state was expected due to likely positive trends in external perturbations. An update of the Baltic cod series until year 2006 showed our estimation was correct, that is, the stock-recruitment system established itself onto a low orbit of stability in which it still remains.

(ii) The Icelandic cod case was determined to turn around either two or, alternatively, three orbits of stability. In this study, we found validated that at high and levels of fishing mortality, the proposed model may describe persistency at low equilibria (whereas the Shepherd approach predicts unstability and extinction).

(iii) The skipjack tuna study contributed information to further validate several aspects of the proposed framework: (a) in order to analyse skipjack data, we sampled SST at several spatial scales and found similar trends; this led us to investigate whether skipjack showed dynamical similarity; (b) two orbits of stability were clearly defined; (c) it was found that catches from different fleets, applying different fishing efforts showed similarity at three spatial scales, as well. Such knowledge supported our assumptions on the differential effects of fishing mortality, the forward-backwards bending nature of fishing effort, the use of catches as a proxy for abundance and the potential ability to estimate trends in recruitment from smaller to wider areas. Also, a theoretical, self similar system we simulated and set in a dynamically referenced frame, in order to discuss the concept of similarity at several scales and migration of the tuna stocks.

(iv) The study on the common Octopus contributed with the following: (a) a first step towards the first population framework for cephalopods in FAO fishing Area 34; (b) catches were used as a proxy for abundance and three orbits of stability were identified; (c) population trends were related NAO pulses which was considered an external forcing determining the variable carrying capacity of the system; (d) a sub-model for the NAO effect upon the fishery system is proposed in which a similar pulse from an external variable may imply two different responses in the population. Also, we updated the data to catch and effort (and abundace) series from the Saharan and Mauritanian upwelling zones to find striking similarities in the multi-oscillatory nature of the systems, validate the use of catches as a proxy for abundance, again and determine that Octopus dynamics in both of the upwelling areas may be similar. It was shown, again, that different fleets applying different efforts mauy reflect similar trends in recruitment to the fishery. Finally, the study contributes further with a 3-orbit of stability variation of the original model and another on the relationship between SST and *Octopus* abundance off Mauritania.

(v) The almadraba fishery was an historical incursion aimed at investigating the past in order to understand both the present and future. This study contributed with knowledge on climate change and the dynamics of tunas (biased towards bluefin) in absence of industrial fisheries or recruitment overfishing (years 1525-1756): (a) the fishery system showed three main areas of stability with local dynamics and was suggested to be controlled by trends both in maxima (as temperature is above the mean) and minima (as temperaure is below the mean) during a "mini" ice age starting in the mid 1600's which implied an environmental induced collapse on the fishery; (b) a theoretical representation of a multi-oscillatory attractor is proposed for the fishery system and (c) we suggest that contemporary (20th century) data for the bluefin tuna fishery shows a similar response to Sea Surface Temperature Anomaly in the Northern hemisphere. Finally, several of the new dynamical concepts of the framework are discussed.

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Fig. 2.2. Spawning stock and recruitment (+) in Baltic cod as estimated in fishery areas 25-32 for years 1973-1993 (after Ices, 1993) interpolated by a cubic spline. A and B describe the low and high equilibrium states (cycles), respectively. Density-dependent compensation and depensation within cycles are indicated by the closed arrows; density-independent compensation (C) and depensation (D) between cycles and inverse dendity-dependence (E) are indicated by the open arrows. The replacement line is given by a simple regression through the origin. N = number of individuals.

Fig. 2.3. Estimated spectral density from spawning stock (+) and recruitment (o) series in Baltic cod as estimated in fishery areas 25-32 for years 1973-1993 (after Ices, 1993). Maxima were detected for periods of around 16 and 4 years, respectively.

Fig. 2.4. Graphical representation of the dynamic system with m equilibrium states (Eq. 2.1) proposed for the SR relationship in Baltic cod in ICES fishery areas 25-32 for years 1973-93 (after Ices, 1993). K_m, K_{m-1}, K_{m-2} represent both the minimum viable populations for the equilibrium states m, m-1 and m-2 and the carrying capacities for their immediate lower equilibria, respectively. E_m, E_{m-1}, E_{m-2}, E_0 represent equilibria around which the SR relationship may turn in density-dependent compensation and depensation phases. K_{max} is the maximum allowable carrying capacity and any values of stock surpasing this ceiling will induce a shift towards lower equilibria. K_0 is the floor or minimum viable population below which the SR relationship may tend to zero (extintion of commercial fishery). System persistence and local stability are shown in all three cases of stability analyses (dotted lines) while $K_0 < S < K_{max}$ and $R(K_0) < R < R_{max}$. An *m* number of oscillatory phenomena ranging from limit cycles to chaos and inverse density-dependence are allowed in this system.

Fig. 2.5. Graphical representation of an arbitrary single-equilibrium state (Eq. 2. 2.). Stability analyses is shown by dotted lines. K_0 = minimum viable population; E = equilibrium; K_{max} = maximum allowable carrying capacity; R_{max} = maximum recruitment.

Fig. 2.6. The SR relationship shaped by variations in the rate of increase a_m while the mortality parameters b_m and c_m are fixed. m and m -1 are the equilibrium states; R = recruitment; max = maximum; E = equilibrium; K = carrying capacity.

Fig. 2.7. An example of transition between equilibrium states in the SR relationship. Increments of a_m over critical values may result in $R_{m-1\ max} > R(K_{m-1})$ followed by a shift to a higher equilibrium state. A case of transition is shown by the stability analyses (dotted lines). m and m -1 are the equilibrium states; R = recruitment; max = maximum; E = equilibrium; K = carrying capacity.

Fig. 2.8. Example of transition in the SR relationship from the equilibrium state m-1 (unbroken line) towards a higher equilibrium (m) through increments in both a_{m-1} and b_{m-1} (b, b' ... b''). R = recruitment; max = maximum; equilibria are indicated by the dots.

Fig. 2.9. Spawning stock and recruitment (+) in Baltic cod as estimated in fishery areas 25-32 for years 1973-1993 (after Ices, 1993) interpolated by a cubic spline and fitted by least-squares according to the functional forms proposed by the present model (unbroken line), Shepherd (1982, dashed line) and Myers (1995, dotted line). Years of start of time series (1973) and record capture (1984, 4.5*10^5 Tn) are indicated by the asterisk and circle, respectively. The replacement line is given by a simple regression through the origin; N = number of individuals.

Fig. 2.10. The sinusoidal perturbation P_t which affected stock and recruitment in the simulation. Circled values were chosen to plot simulation results (Fig. 2.11-12).

Fig. 2.11. The stock-recruitment relationship (above) and spawning stock trajectory (below) in a simulation of a fish population which has survivorship $\delta = .6$, age-at-maturity $\tau = 3$, variable rate of increase at two levels of stability and is affected by a sinusoidal perturbation. Simulation results are plotted for three values of the perturbation: around the mean (unbroken line) and upper (dotted-dashed line) and lower (dashed line) limits. The spawning stock trajectory corresponds to the SR relationship shown by the unbroken line.

Fig. 12. The stock-recruitment relationship (above) and spawning stock trajectory (below) in a simulation of a fish population which has survivorship $\delta = .3$, age-at-maturity $\tau = 3$, variable rate of increase at two levels of stability and is affected by a sinusoidal perturbation. Simulation results are plotted for three values of the perturbation: around the mean (unbroken line) and upper (dotted-dashed line) and lower (dashed line) limits. The spawning stock trajectory corresponds to the SR relationship shown by the unbroken line.

Fig. 2.13. The stock-recruitment relationship (above) and spawning stock trajectory (below) in a simulation of a fish population which has survivorship $\delta = .05$, age-at-maturity $\tau = 3$, variable rate of increase at two levels of stability and is affected by a sinusoidal perturbation. Simulation results are plotted for three values of the perturbation: around the mean (unbroken line) and upper (dotted-dashed line) and lower (dashed line) limits. The spawning stock trajectory corresponds to the SR relationship shown by the unbroken line.

Fig. 2.8.1. The updated standardized (Z) Baltic cod Spawning Stock Biomass (SSB; upper caption) and Recruitment series (after ICES, 2007; lower caption). Dashed line represents the raw data. Bold lines are the smooted series and a linear regression.

Fig. 2.8.2. The spectrum on the standardized (Z) Baltic cod Spawning Stock Biomass (SSB, left caption) and Recruitment series (after ICES, 2007). There are common peaks for approximately 5 to 8 years periodicities.

Fig. 2.8.3. The upper caption shows the relationship between the standardized (Z) Baltic cod Spawning Stock Biomass (SSB) and Recruitment series (after ICES, 2007). A-C indicate the equilibria around which the orbits of stability turn. According to Solari et al. (1997), based on data until 1993, the stock-recruitment system was suggested to rehabilitate (from years 1993 and on) to a low orbit of stability (C,

indicated by the rectangle). Both theoretical criteria proposed by the new model and estimations of short to medium term trends were validated by the updated series. The lower caption shows the local dynamics in the low (C) orbits of stability. The straight (replacement) lines are linear regressions through the origin and the non-linear fittings are polynomial (even distance weighted least squares shows similar results) and cubic in the upper and lower plots, respectively. Numerals between parenthesis indicate the year of start of the series.

Fig. 2.8.4. Graphical representation (model) of the stock-recruitment system in Baltic cod as proposed by Solari et al. (1997) based on the updated series after ICES (2007) for years 1966-2006. The system is considered as a dynamical continuum (with global and local dynamics) governed by a variable carrying capacity. E_{i+1}, E_{i} and E_{i-1} are the equilibrium states around which the orbits of stability (dashed elliptic trajectories) turn. Orbits of stability are due to approximately 8 years long density dependent processes (4 years long phases of compensation and depensation, respectively). Shifts between orbits are due to the combined effects from the environment and fishing mortality. The effects of fishing are differential and the system may shift towards the minimum viable population (K_0) as high and intense fishing occurs during simultaneous density-independent and density-dependent depensatory trends. The lower orbit around E_{i-1} (years 1992-2006, last year of available series) was estimated by Solari et al. (1997) in 1995 based upon ICES data up to 1993: the theoretical criteria and inference/estimations proposed in the framework were validated. SSB is the Spawning Stock Biomass and Recruitment may refer either to numbers in year class 2 or 3. The straight (replacement) line is a linear regression through the origin and the non-linear fitting incorporate three constants for each orbit of stability.

Fig. 2.8.5. Log transformed (log) and standardized (Z) Swedish Catch (Tn) and Effort (Hours) series (above left) and their relationship (above right) on cod in Baltic sea areas 25-27, years 1983-2006 (after ICES, 2007). As the stock-recruitment system follows orbits of stability, the nature of the Catch and Effort relationship is a forwards (compensatory) and backwards (depensatory) bending which is clearly shown by the data above. Start of the series (in the phase plane caption) is indicated by the numeral between parenthesis.

Chapter 3.2

Fig. 3.2.1. Spawning stock (dashed line) and recruitment (continuous line) series in Icelandic cod (numbers-at-age), years 1956-97 (after ICES, 1997).

Fig 3.2.2. The spectral density of the smoothed stock-recruitment series In Icelandic cod, years 1956-1997. The highest peaks correspond to periods of approximately 10 years. Stock = spawning stock; rec = recruitment.

Fig. 3.2.4. The stock-recruitment relationship in Icelandic cod both interpolated by a cubic spline and smoothed (dotted line). A, B and C represent a high equilibrium, an intermediate and a low equilibrium state. Density-dependent compensation (🡅) and depensation (🡇) are represented by the arrows on the spline. Also, D (➔) and E (🡄)

represent density-independent compensatory and depensatory transitions; the 1956 and 1997 labels are the start and end year of the series, respectively.

Figure 3.2.5. The stock-recruitment relationship in Icelandic cod both interpolated by a cubic spline and smoothed (dotted line). A, B and C represent a high equilibrium, an intermediate and a low equilibrium state.

Chapter 3.3.

Figure 3.3.1. Three spatial scales of skipjack tuna sampling. The CECAF (Committee for Eastern Central Atlantic Fisheries) Division 34 (larger area indicated by the dashed line; from Gibraltar to the Congo river, Lat. 36°00'N-6°04'36"S, Long. 12°19'48"E-5°36'W); the Canary Islands archipelago (minor area indicated by the dashed line, Lat. 29°40'N-27°10'N, Long. 13°W-18°20'W) and the Port of Mogan (local waters off the southern shore, island of Gran Canaria, Lat. 27°55'N-Long. 15°47'W, indicated by the arrow). Map modified after FAO (2001).

Figure 3.3.2. Skipjack tuna series ($Tn*10^3$) from a local bait fishery at the Port of Mogan (island of Gran Canaria, Canary Islands, years 1980-96), after Hernández-García et al. (1998); overall pooled landings due local bait fisheries for the whole of the Canary Islands area (years 1975-93), after Ariz et al. (1995) and pooled landings due multigear (bait, long-line and purse-seine) both oceanic and coastal fisheries within the CECAF Division 34 (years 1972-96), after Fishstat/FAO (1999). The catches represent sampling series from three significantly different spatial scales. The straigh lines indicate the mean of the series.

Figure 3.3.3. The spectral densities of three skipjack tuna series from the Port of Mogan (island of Gran Canaria, Canary Islands, years 1980-96, Mogan series, after Hernández-García et al., 1998), the whole Canary Islands area (years 1975-93, Canarian series, after Ariz et al., 1995) and the CECAF Division 34 (years 1972-96, CECAF series, after Fishstat/FAO, 1999).

Figure 3.3.4. Phase space for the skipjack fishery landing series at the Port of Mogan (island of Gran Canaria, Canary Islands). The linear regression through the origin represents both the recruitment needed to replace the stock-at-spatial-location and overall equilibrium values. The 6th degree polynomial regression describe the evolution of the high and low steady-states indicated by “A” and “B”, respectively. Z indicates standarized values and N_t and N_{t+1} the generation of the values; 80 and 95 indicate the start and end year of the plotted values.

Figure 3.3.5. Phase space for the skipjack fishery landing series from the Canary Islands area (Eastern Central Atlantic). The linear regression through the origin represents both the recruitment needed to replace the stock-at-spatial-location and overall equilibrium values. The 6th degree polynomial regression describe the evolution of the high and low steady-states indicated by “A” and “B”, respectively. Z indicates standarized values and N_t and N_{t+1} the generation of the values; 75 and 92 indicate the start and end year of the plotted values.

Figure 3.3.6. Phase space for the skipjack fishery landing series from the CECAF Division 34 (Eastern Central Atlantic). The linear regression through the origin represents both the recruitment needed to replace the stock-at-spatial-location and overall equilibrium values. The 6th degree polynomial regression describe the evolution of the high and low steady-states indicated by "A" and "B", respectively. Z indicates standarized values and N_t and N_{t+1} the generation of the values; 72 and 95 indicate the start and end year of the plotted values.

Figure 3.3.9. Theoretical in-area stock and recruitment system proposed for three spatial scales in the Eastern Central Atlantic (Port of Mogan, Canary Islands area and CECAF Division 34). The linear regression represents the replacement line and the polynomial fit describes the dynamical evolution of the system. A and B are the high and low equilibrium states, respectively. The dot represents the transition point between the steady states, being the floor of A and carrying capacity of B, respectively. Density-independent compensation and depensation are represented by the arrows $\rightarrow$ and $\leftarrow$, respectively. Orbits of stability are indicated by the dashed ellipses on which arrows represent density-dependent compensation and depensation. Data values are arbitrary and were generated by sinusoidal waves plus noise.

Figure 10. A theoretical selfsimilar system resembling a stock-in-area [Z(R)] recruitment-to-the-area [Z(I)] relationship. Data values (N=19851) are dynamically referenced through linear regression, a sixth degree polynomial, a cubic spline (to show more detailed local dynamics) and 50 (inner) and 95% (outer) bivariate ellipses (also, confidence intervals). The random and sequential sampling of 10, 5, 1 and 0.1% of the total number of points (resembling captures from different spatial scales) showed similar tendencies: as in the skipjack fishery, the simulated system shows similar dynamical patters at different sampling windows. Different levels of numbers are obtained depending on the quadrant the sampling is carriedout. Iteration and data, parameter values and function are arbitrary.

Chapter 3.4

Figure 3.4.1. The FAO Fishing Area 34 (from Gibraltar to the Congo river, Lat. 36°00'N-6°04'36"S, Long. 12°19'48"E-5°36'W). Map modified after FAO (2001). Equidistant cylindrical projection.

Figure 3.4.5. The North Atlantic Oscillation (NAO; at Ponta Delgada, years 1961-97) and common Octopus (FAO Fishing Area 34, years 1962-2001) standardized (yearly means) raw (+) and smoothed (shown by the cubic spline) series.

Figure 3.4.6. Spectral analyses on both the North Atlantic Oscillation (NAO; at Ponta Delgada, years 1961-97) and common *Octopus* (FAO Fishing Area 34, years 1962-2001) standardized and smoothed series. Numerals over the peaks refer to number of years.

Figure 3.4.7. Above, left: the Stock-Recruitment (SR) system (plane N_t, N_{t+1}) for the *Octopus vulgaris* in FAO Fishing Area 34 (years 1962-2001). Raw (+) and smoothed (shown by the cubic spline) standardized series describe the dynamical trajectory. Global and local dynamics are indicated by the equilibrium states E_1-E_2 and

E_3-E_4, respectively. Filled arrows on the trajectory indicate compensation (➤) and depensation (◀). The memory effect is highly significant (Hurst exponent >1). Oscillations in the SR system may arise due pulses in both the North Atlantic Oscillation (NAO) which may control the variable carrying capacity. According to our theoretical criteria, a new compensatory trend for the SR system is expected, during the coming 4-8 years, as the NAO turns into a positive trend. Above, right: data was log transformed to determine both the "build-up" of the fishery, during the 1960's, and the approximate year (1967) as the fishery system started to oscillate (indicated by the dashed lines). The first peak of the series should reflect the first carrying capacity (K_i) of the system reached (in part, due to high and intense fishing) after which the population system kept oscillating due the combined effects from the environment and fishing mortality.

Figure 3.4.8 a (above, left) and b. An arbitrary example (values are standardized) of the effect of a North Atlantic Oscillation (NAO) pulse (continuous line) on the recruitment (either to the population or the fishery) in *Octopus vulgaris* (FAO Fishing Area 34): a similar external perturbation may lead either to a relatively higher (outter dashed line) or lower (inner dashed line) equilibrium depending on the level of numbers and carrying capacity during prior years and length and slope of the perturbation, as well. The phase plane is shown above (a) and time series below (b).

Fig. 3.4.9 a-b. Above left (a), Catch (Tn; thicker, continuous line) and Effort (days; dashed line) of the Spanish *Octopus* fishery within the Saharan upwelling zone for years 1976-1999 (after IEO, 2007); above right (b), Catch-Effort relationship fitted by a simple regression (straight line), a classical 2nd order approach (dashed line) and a polynomial approximation to our dynamical model. O1' and O2' orbits of stability.

Fig. 3.4.10 a-b. Above left (a), the phase plane of catches (considered to approximate the Stock-Recruitment system). O1 and O2 are orbits of stability. O3 (dotted area) is the future expected range of oscillation from year 2000. Arrow indicates an example of local dynamics. Above right (b), phase plane of the Mauritanean *Octopus* Abundance Index series (1971-2005, after FAO, 2006). O_1-O_3 indicate the orbits of stability as explained in our multi-oscillatory framework. This data clearly validates the dynamical model we have proposed and is similar to the Catch-Effort relationship we have shown for the Spanish *Octopus* fishery in the Saharan upwelling zone (after IEO, 2007).

Fig. 3.4.11. A (preliminary) model (based on our framwork) on the *Octopus* off the Saharian upwellingzone. Three orbits of stability with corresponding "steady states" (E_i), maximum carrying capacity (K_{max}) and minimum viable population (K_0). Also, every orbits 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 show the population positive and negative growth. This reconstruction may be useful for the Mauritanian case, as well (to be addressed in the second halft of the project by the Multi-oscillatory System Approach). Ground theoretical model after Solari et al. (1997).

Fig. 3.4.12 a-b. Above left (a), the Optimum Interpolated Sea Surface Temperature (SST, after Reynolds and Smith, 1994) series (yearly maxima) for the area (data was used as a proxy) Long. 17.5-19.5º W – Lat 19.5-21.5º N and Abundance Index series (afer FAO, 2006) on *Octopus* off Mauritania. Cross correlations between the series are highly significant and periodicities (peaks from Spectral analysis) fall into similar frequencies. The variables appear to be the inverse of each other (Pearson correlation, p<.01) from which we may infere that trends in SST maxima are a co-factor determining abundance (year class strength) in *Octopus* stock nucleii. Above right (b), trends (raw and smoothed data) in Sea Surface Temperature Anomaly (SSTA, after IGOSS, 2007) appears as one of the best descriptors for trends in the *Octopus* populations in FAO Area 34. Z values are standardized (mean = 0) to facilitate visual comparision.

Fig. 3.4.13. a-d. Proposed theoretical sub-models for the relationship between Optimum Interpolated Sea Surface Temperature (SST, after Reynolds and Smith, 1994) series (yearly maxima) for the arbitrary area (used as a proxy) ranging between Long. 17.5-19.5º W – Lat 19.5-21.5º N and the Abundance Index series (afer FAO, 2006) on *Octopus* off Mauritania: (a) above left, SST and AI [SST1(x), $AI1_{x+1}$] (no medium term linear trend) series as inverses with different amplitudes and (b) above right, the corresponding limit cycle [AI1(x), $AI1_{x+1}$]; (c) below left, SST2(x) and AI2(x), a medium term linear trend is considered and amplitudes and slopes of the trends variate; (d) below right, phase plane of the abundance [AI2(x), $AI2_{x+1}$] taking into account amplitudes and linear trends particular to each variable. Time is *x* (10 years).

Chapter 3.5

Figure 3.5.1 a. Geographic localization and names of eight out of the fourteen almadrabas along the Atlantic coast of Spain, during years 1525-1756. The Conil and Zahara almadrabas were the most productive with over 95% of the total captures, during the 231 years of the series (after López-Capont, 1997).

Fig. 3.5.1 b. Above, the "Hercules" almadraba with a purse-seine net, 400 mt in length, 42 mt in depth, an operation which required over 300 men (after Medina Sidonia Foundation, 2005).

Fig. 3.5.2. The log transformed and standardized (Z) Spanish "Almadraba" trap fishery (1525-1756, above) and annual global air temperature patterns (Northern hemisphere; after Mann et al., 1998; NOAA, 2007).

Fig. 3.5.3. Spectral analyses on the series of the Spanish "Almadraba" trap fishery (1525-1756, left caption) and annual global air temperature patterns (after Mann et al., 1998) over the Northern hemisphere (right caption).

Fig. 3.5.4. The wavelet analyses on the capture series from the Spanish "Almadraba" fishery (years 1525-1756). A5 shows the denoised series in which we observe the medium and longer term periodicities in the catches. While there are shorter term oscillations, the longer overall trend is negative. D2 to D4 show the 2, 4, 8 and 16 years processes and there are three discrete zones (indicated by the dashed lines) starting approximately at years 1570, 1640 and 1687. The fishery may have been

governed by a relatively minor climatic change (a "mini" ice age) starting approximately around the year 1640 and reaching the maximum stress point between 1687-1705. The temporal evolution of noisy processes (D1) show clear differences between the marked zones and noise increases with time as the sampled populations reached the highest environmental stress. Also, density-dependent processes (assumed as recruitment to the population and fishery; D2 and D3) show a clear divergence (maxima and minima diverge) starting at year 1640. Also, oscillations of about 16 years (assumed as a consequence of solar activity cycles plus a lag of 4 which is a common recruitment delay in tunids) appear to be more stable.

Fig. 3.5.5. The phase plane (Z Log Captures N_t, N_{t+4}) on the series from the Spanish "Almadraba" fishery (years 1525-1756). Data was fitted by a simple regression through the origin (straight line) and a cubic spline. Two outliers were excluded from the series.

Fig. 3.5.6. The temperature (after Mann et al. 1998; NOAA, 2007) vs. captures relationship (values were standardized, Z, log transformed and lagged 4 years) on the series from the Spanish "Almadraba" fishery (years 1525-1756). A'-C' indicate three multi-oscillatory areas of stability and K_i the carrying capacity of the fishery. The outlier from year 1703 may show the relative effect of a war on the fishery as the value is compared to the range of other minima (M_i) in the catch series. Data was fitted by a simple regression through the origin and a polynomial. The dots are the singular points (seudo-equilibria) for each area of stability. The fishery system appears to be controlled by maxima in temperature (for the higher temperature range above the mean) and by minima and "mini" ice age (for the lower temperature range below the mean).

Fig. 3.5.7. A theoretical representation of an attractor (Stock-in-area vs Recruitment-to-area or fishery) proposed for the Spanish "Almadraba" 231 year series (1525-1756). The superimposed trajectories represent the longer term cycle within the attractor (ellipse or limit cycle), the intermediate showing the local, shorter term oscillations and the outter which is the interpolation of data points (dots) with a certain white noise. Noise in this context is considered the differences between datavalues and their closest points from the intermediate trajectory. The dashed line is the dynamical continuum which may evolve (from seudo-equilibrium A_i) either towards the carrying capacity of the system (K_i) and an upper orbit of stability (A_{i+1}) or the minimum viable population (K_0) and a lower orbit (A_{i-1}). The system is auto-similar and operates at different scales of numbers. R is recruitment to area, fishery and population.

Fig. 3.5.8. Captures North East Atlantic + Mediterranean (1950 2002, after FishStat/FAO, 2003) y SST Anomaly (after Kaplan, 1998; IRI/LDEO, 2007). Cross correlation between the 4 year lagged series is highly significant ($p<.01$).

Fig. 3.5.9. The multi-oscillatory system proposed for bluefin tuna catches in the North East Atlantic plus the Mediterranean (1950 2002, after FishStat/FAO, 2003) and SST Anomaly (after Kaplan, 1998; IRI/LDEO, 2007).

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CHAPTER 1

Classical
Recruitment Models

1. Classical recruitment models.

Two of the key assumptions underlying fishery theory are those that (a) recruitment, considered as the influx of juveniles into the adult population, is a process of crucial importance for the continuity of the fish stock and (b) populations under exploitation are naturally limited in a way that will permit them to respond in a compensatory way to fishing (Beverton and Holt (1957), Ricker (1975), Cushing (1977, 1983), Clark (1976), Beyer (1988, 1989), Rothschild (1986)).

The Beverton and Holt (1957) and Ricker (1954) functions (henceforth referred as "classical approaches/models") are two widely accepted approaches for describing the theoretical relationship between parental stock and recruitment (also, referred herein as the "SR" relationship). These classical models, which established a general theoretical framework for modelling recruitment dynamics, consist of extinction curves where recruitment reaches either an asymptotic maximum (Beverton-Holt) or becomes low at high spawning stock sizes (Ricker). Also, they were developed for the same goal: the identification of the best parameterization of the SR relationship and their principal task was the determination of the best mathematical function (shape and number of parameters) which would permit to increase the determination of coefficients involving the fewest parameters.

Clark (1976), Sharp et al. (1983), De Angelis (1988), Fogarty (1993), Solari et al. (1997), Bas et al. (1999) and other authors suggested that the classical models provided important insights into SR dynamics but may not include key factors of specific situations and had a limited capacity to link internal (population) and external (environmental) dynamics to each other. This lack of specificity would become an important shortcoming. Also, Gulland (1989) observed that these models continue, to a very large extent, to be used in providing quantitative advice to fishery managers - which may even hold true in the beginning of the 21st century.

However, two more advanced frameworks were proposed during the 70's and 80's. On the one hand, Paulik (1973) described an overall spawner-recruit model which was formed from the concatenation of survivorship functions. This approach could exhibit multiple (stable) equilibria and complex dynamics and was the result of a multiplicative process where the initial egg production could be modified by non-linear functions specific to each life-stage and cohort- population size: the main shortcoming was the interdependency between the functions due the multiplicative nature of the model. On the other hand, Shepherd (1982) unified the dome-shaped and asymptotic approaches proposed by Ricker (1954) and Beverton-Holt (1957), respectively, but could neither incorporate multiple stable equilibria nor depensatory dynamics.

We shall continue this section by a general figure showing the classical approaches, based on the concepts of a unique equilibrium and a single, invariant carrying capacity. This introductory step may be helpful for understanding both the argumentation and premises to the new non-linear framework which we will put forward in the next chapter. The Shepherd (1982) functional form is given by

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

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 α and δ 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 is shown in Fig. 1.1.

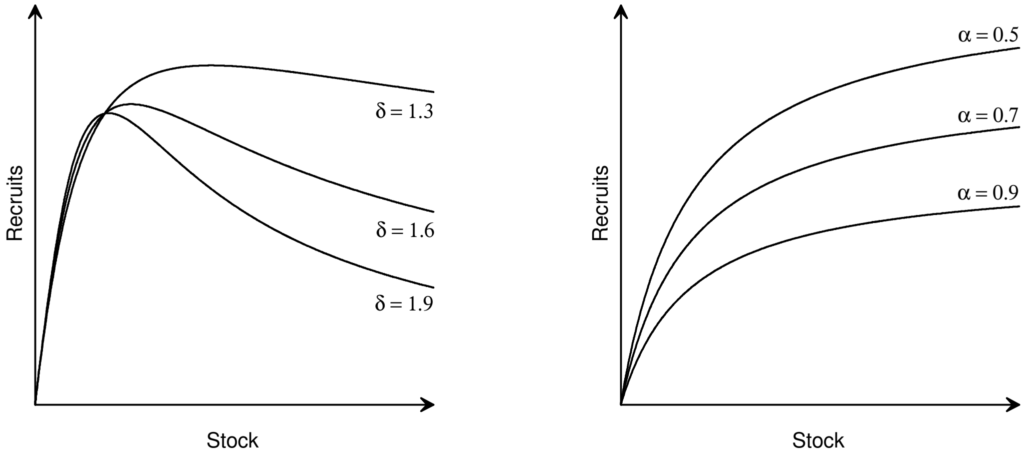

Figure 1.1 Two arbitrary examples of the Shepherd (1982) functional form with parameter values describing the Stock-Recruitment relationship as proposed by Ricker (1954, for $\delta > 1$, left caption) and Beverton-Holt (1957, for $\delta = 1$, right caption).

1.1 Critique.

Recruitment involves multiple interacting population groups and extrinsic variables which are continuously perturbed from some approximately known state via human induced and/or natural phenomena (Atkinson 1987). A particular SR relationship might imply multiple equilibria, variable carrying capacity, compensation and depensation phases at several levels of numbers and other dynamic features which should be addressed.

The classical approaches excluded dynamical features critical to understand the mechanics behind the data (linking and transition mechanisms between steady states, system behaviour, extinction of the commercial fishery, environmental interactions, among other factors) and were are highly restrictive as they assumed that (a) populations under exploitation would respond in a compensatory way to fishing under all conditions of numbers, fishing mortality and environmental perturbations; (b) during the temporal evolution of the SR system (over forty years for many of the available population series), a single equilibrium was assumed; (c) an invariant carrying capacity although the environment generally follows an ever changing transition scheme; (d) the weight of all of the data points would be the same (temporal evolution and dependencies within and between variables were ignored) and (d) residuals were assumed to be the result of a random process. It is clear that, a best statistical fit under those assumptions will both perform poorly and be unable to explain a major part of the variability in the data and mechanics from a complex, multivariate, dynamical system.

In our view, there was an urgent need to develop a flexible framework which would allow us both to ask better questions and understand causal mechanisms to dynamical patterns behind the data.

In Chapter 2, we shall put forward and discuss in detail the new, non-linear framework we developed with an example on Baltic cod dynamics.

To understand this thesis, the detailed lecture of Chapter 2 is mandatory. In subsequent case studies (given in the sections 2-6 of Chapter 3), several aspects of the new framework are assumed to be known by the reader and they are omitted (to avoid repetition).▪

CHAPTER 2

The New Framework

with an example on Baltic cod dynamics

“ ... **For the first time I saw an operational version of a SSR** [Stock-Recruitment-Relationship] **with some chances of reflecting reality ...”**

Letter from Dr. Serge Garcia (IN 16/2, 1997) on Solari et al. (1997).
Director, Fishery Resources Division, FAO.

2.1 Abstract.

The stock and recruitment (SR) relationship in Baltic cod is studied. In light of the field data, the authors suggest that the SR relationship oscillates at two levels of stability (cycles) due to the interaction between density-dependent compensation and depensation. Furthermore, density-independent transitions between equilibrium states are assumed due to fisheries mortality and medium and long term periodicities in the abiotic environment which may induce compensatory and depensatory effects upon stock and recruitment. These mechanics are related to concepts such as variable carrying capacity, multiple equilibria, minimum viable population and inverse density dependence. Carrying capacity is regarded as a critical threshold between different equilibrium states and the minimum viable population as an unstable equilibrium below which the SR relationship may not rehabilitate. A modelling approach is put forward where the SR-relationship is regarded as a system or summation of non-linear functions 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) which may lead to inverse density-dependence (depensatory dynamics). This SR-system is considered as highly flexible as it has the capacity to, persistently, evolve and return within a range of equilibrium states. Also, it is proposed that the SR relationship is, at the present time, nearby the minimum viable population due to the combined effects from high fishing mortality and negative effects from external perturbations. However, a SR rehabilitation towards a low equilibrium state is expected, during the coming years, due to likely positive trends in external perturbations. A simple numerical simulation is put forward where the SR system is perturbed by a sinusoidal external variable at three constant levels of mortality. This work was based on data up to year 1993. An update of the series until year 2006 is put forward at the end of the chapter where several of the concepts and estimations based on the new framework are validated.

2.2 Introduction.

Recruitment failures in Baltic cod (*G. morhua*) during recent years (Anon 1992, ICES 1993, Larsson 1994) may show the need for a greater insight into it's specific dynamics. There is an increasing body of evidence indicating that recruitment success in Baltic cod may be affected by fluctuations in salinity, temperature and oxygen contents at depths where the cod eggs are deposited (Bagge 1993, Bagge et al. 1993, Plikshs et al.1993, Waller et al. 1993). Also, Carlberg et al. (1992) observed that the water volume in the Baltic basins in which the cod eggs can develop until hatching, defined as "reproduction volume" (RV), is very limited.

Moreover, Kosior et al. (1989) pointed out that the abundance of Baltic cod depends mainly on environmental conditions during the spawning period and Baranova and Uzars (1986) observed that variations in growth and maturation were due to density-dependent mechanisms: mean length, weight and annual growth zones of otoliths in 2-7-year-old cod were lower due to the appearance of strong year classes.

Furthermore, the abiotic environment seems to follow, beyond seasonal variations, medium- and long-term periodicities. Kalejs et al. (1989 a., b.) suggested that 8-, 15- and 23-year periods in winter severity and fresh water inflow into the Baltic Sea could cause appreciable changes in salinity, oxygen and heat content, vertical exchange and hence in the reproduction conditions to fish.

Hence, the premises to approach the SR relationship in Baltic cod, as we see them, may be as follows: (a) Density dependent, short term and (b) density-independent medium- and long term oscillations; (c) variable carrying capacity; (d) multiple equilibria and (e) external conditions during spawning. These terms should be coupled into a relationship which configures a relatively complex, non-linear, dynamic system.

The purposes of this study were (i) to investigate the stock and recruitment dynamics in Baltic cod, in light of our criteria, attempting to model the SR relationship out of the field data; (ii) to compare the goodness-of-fit from our approach to those from the models proposed by Shepherd (1982) and Myers et al. (1995) which unified the dome-shaped and asymptotic SR approaches by Ricker (1954) and Beverton-Holt (1957) and modified the Beverton-Holt functional form to allow for depensatory dynamics, respectively; (iii) to raise further discussion on issues concerning features in this particular SR relationship, where dynamic systems and chaos criteria will be addressed (Cook (1976), May (1976), Kot et al. (1988), Rietman (1989), Schaffer and Kot (1986), Conan (1994)). Furthermore, we aim to put forward a simple model which may be useful in fisheries management and, beyond the classical models, is sufficiently flexible to enable us to qualitatively explain stock and recruitment in Baltic cod.

2.3 Background to the model.

Spawning stock and recruitment series in Baltic cod from ICES fishery areas 25-32, years 1972-1993 (Anon, 1993) are shown in Fig. 2.1 and the SR relationship for the same field data, interpolated by a cubic spline, is shown in Fig. 2.2.: this SR relationship is assumed to turn around a low and a high equilibrium state described as *A* and *B*, respectively. Also, it is further assumed that there are density-independent transitions between these equilibria: *C* and *D*, which may imply compensatory and depensatory phases, respectively. During these transition phases, when parental stock either increases *(C)* or decreases *(D)*, recruitment remains relatively stable. However, as the equilibria *(A, B)* are reached, parental stock remains relatively stable whereas oscillations in recruitment become high. Furthermore, we used the Welch method (after Oppenheim and Schafer, 1975) to estimate the spectral density of both series (Fig. 2.3): it appears the method detected two maxima around the periods of 16 and 4 years, respectively. Hence, we intend to base our approach in that the SR relationship in Baltic cod may be determined by the following factors: (i) In absence of extreme external perturbations, oscillations around equilibria

(*A* and *B* in Fig. 2.1, 2) may be induced by density-dependent mechanisms and are limited by a particular carrying capacity operating in each equilibrium state; (ii) Transitions between equilibrium states (*C* and *D* in Fig. 2.1, 2) which may be determined by medium- and long term cycles in the abiotic environment and by high fishing mortality during depensation phases.

2.4 The model.

The SR relationship in our model is proposed to consist of two coupled, cyclic phenomena which operate similarly but in two different temporal scales and are due to different causal mechanisms. The suggested criteria are as follows:

(i) highly non-linear, short-term (≅ 4-8 years) oscillations which may exhibit behaviour ranging from limit cycles to chaos (A, B in Fig. 2.1-2): these are assumed to turn around stable, variable equilibria which are related to both variations in carrying capacity ($K_{i,\ i\ =\ 1\ ...\ m}$) and mean numbers in spawning stock and recruits. These oscillations *within cycles* may be induced by the interaction between population growth (compensatory phases) and density-dependent mortality (depensatory phases), the particular SR delay for Baltic cod (i.e. three years) and external short-term inputs. Also, a minimum viable population ($0 < K_0$) is assumed under which stock and recruitment may not rehabilitate due to depensatory dynamics at low spawning stock sizes (E in Fig. 2.1-2): i.e. the SR relationship, being less sensitive to benign external conditions, may tend to zero (extinction of commercial fishery);

(ii) a non-linear, medium-term (≅ 16 years), density-independent oscillation governed by the environment and by fishing mortality (C, D in Fig. 2.1-2): due to cyclic environmental variations, carrying capacity is assumed to be variable allowing density-independent compensatory or depensatory effects *between cycles* towards higher and lower equilibria, respectively. As the SR relationship shifts to higher equilibria, the amplitude between maxima and minima may diverge. This divergence may, however, be limited by the maximum allowable carrying capacity (K_{max}), a threshold which may shift the SR relationship towards lower equilibria;

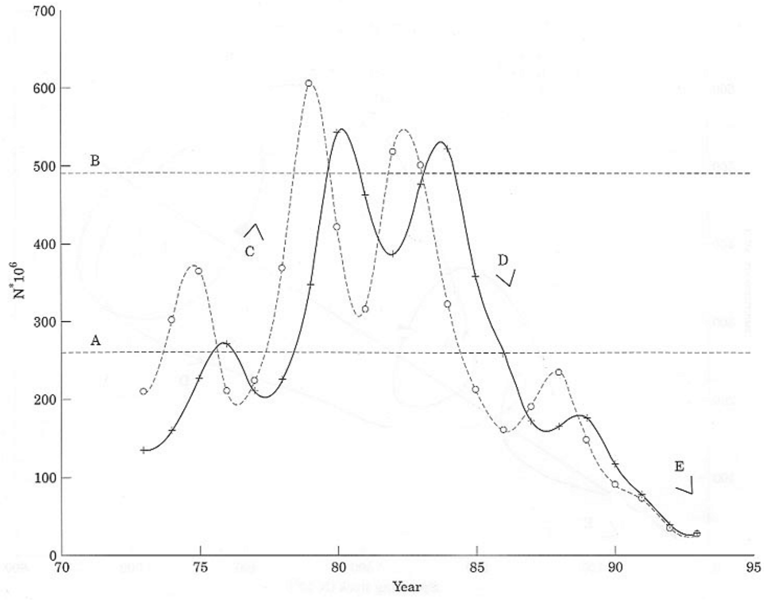

Figure 2.1. Spawning stock (dashed line) and recruitment (unbroken line) series in Baltic cod as estimated in fishery areas 25-32 for years 1973-1993 (after ICES, 1993). A and B describe the low and high equilibrium states, respectively. Density-independent compensation (C) and depensation (D) and inverse density-dependence (E) are indicated by the arrows. N = number of individuals.

(iii) During depensation phases, high fishing mortality and poor environmental conditions (henceforth referred as negative perturbations) may affect the SR relationship by shifting the oscillations towards either lower equilibria or the minimum viable population (D, E in Fig. 2.1-2).

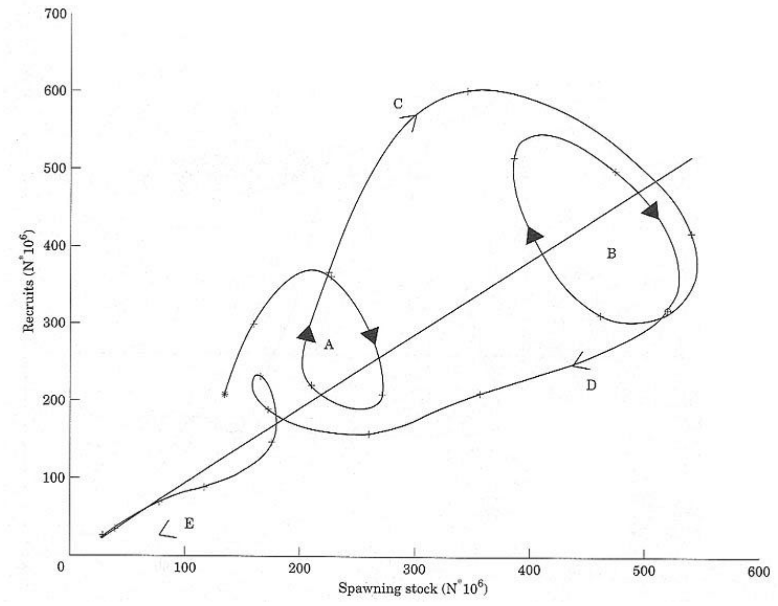

Figure 2.2. Spawning stock and recruitment (+) in Baltic cod as estimated in fishery areas 25-32 for years 1973-1993 (after Ices, 1993) interpolated by a cubic spline. A and B describe the low and high equilibrium states (cycles), respectively. Density-dependent compensation and depensation within cycles are indicated by the closed arrows; density-independent compensation (C) and depensation (D) between cycles and inverse density-dependence (E) are indicated by the open arrows. The replacement line is given by a simple regression through the origin. N = number of individuals.

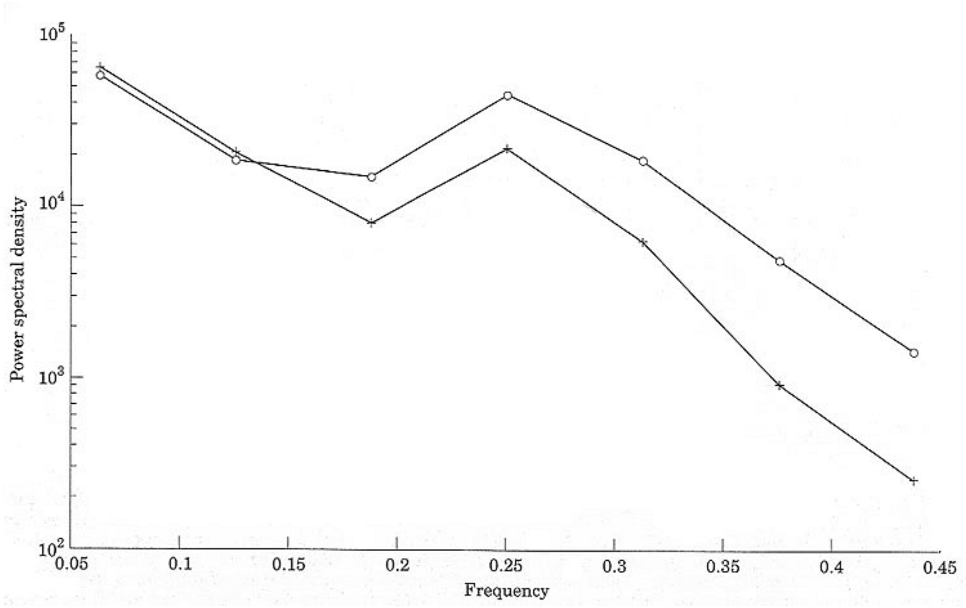

Figure 2.3. Estimated spectral density from spawning stock (+) and recruitment (o) series in Baltic cod as estimated in fishery areas 25-32 for years 1973-1993 (after Ices, 1993). Maxima were detected for periods of around 16 and 4 years, respectively.

Also, dependence between stock and recruitment (SR dependence) is assumed to be stronger and less sensitive to external inputs while the relationship is either below the minimum viable population or when density-dependent mechanisms are operating. During transitions between equilibrium states, while $K_0 < S < K_{max}$, the SR dependence may be weaker and more sensitive to environmental variations. Furthermore, we should stress that K_{max} is considered, in our study, as a theoretical-only issue: we assume that the SR relationship will not tend towards K_{max} in a dynamic process permanently affected both by sinusoidally distributed external variables and relatively high fishing mortality.

A series of discrete equilibrium states may be induced by the interaction between spawning stock, recruitment and external variables which may affect the process. As external perturbations destabilize a particular equilibrium state shifting it either to it's upper or lower limits, the SR relationship may evolve towards a new equilibrium. Thus, we consider that any particular equilibrium state in the SR relationship may be given by a maximum value of recruitment, an equilibrium point around which stock and recruitment oscillate and a critical stock density, K_i. Also, if the SR relationship either surpasses or shifts below any particular K_i, it may evolve towards a new equilibrium state with higher, respectively lower values of stock and recruitment. Furthermore, we assume that the SR relationship is limited by a ceiling or highest equilibrium state which bears both the maximum allowable- recruitment, R_{max}, and carrying capacity, K_{max}. In this way, parental stock may increase until an equilibrium is reached whereby density-dependent depensation starts operating. Furthermore, shifts to higher equilibria (density-independent compensation) with higher carrying capacities may only occur when stock and recruitment increase due to benign external conditions. On the contrary, if external conditions (environment, fisheries) induce a density-independent depensatory effect, the SR relationship may shift to lower equilibria with lower carrying capacities.

To synthesize our criteria, recruitment, R, is defined in Eq. 2.1 as the summation of non-linear functions of spawning stock, S, given by

$$R \cong \sum_{i=1}^{m} \frac{a_i \cdot (S)}{(S-b_i)^2 + c_i} \qquad (2.1)$$

where the entries i = 1 ... m represent the number of equilibrium states in the SR relationship, being m the highest equilibrium where the SR relationship reaches the ceiling or maximum allowable carrying capacity. Equilibrium states 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 spawning stock for which equilibrium states may arise.

A case of Eq. 2.1 with *m* equilibrium states is graphically represented in Fig. 2.4. This case describes the SR relationship as a relatively complex dynamic system bearing several equilibrium states and which is characterized by the following features:

(i) K_m, K_{m-1}, K_{m-2}, which represent: (a) the minimum viable populations for the equilibrium states m, m-1 and m-2, respectively; (b) the values of spawning stock below which the relationship may shift towards lower equilibria; (c) the carrying capacity for the immediate lower equilibrium state, respectively;

(ii) E_m, E_{m-1}, E_{m-2}, E_0 which represent the equilibria around which the SR relationship turns in density-dependent compensation and depensation phases;

(iii) K_{max} and K_0 are the ceiling and floor, respectively. K_{max} is the maximum allowable carrying capacity in the SR system and any values of stock surpassing this ceiling or upper limit will induce a shift towards lower equilibria. K_0 is the minimum viable population, a critical value and unstable equilibrium under which the SR relationship will tend to zero (extinction of commercial fishery);

(iv) $R_{max} = R(K_{max})$ is the maximum allowable recruitment and any values surpassing this ceiling will either lead to lower equilibria or to extinction. Furthermore, $R_{m\ max}$,$R_{m-1\ max}$, $R_{m-2\ max}$ and $R_{0\ max}$ represent the ceiling in recruitment for their respective equilibria and the threshold above which the SR relationship may shift towards higher equilibrium states, $R_{m\ max} < R_{max}$. Also, as maximum recruitment values approach the replacement line, the SR relationship comes into a critical stage where perturbations may induce shifts to either higher or lower equilibria. In this way, the SR system defined by our functional form may allow for the continuity of stock and recruitment within a wide range of density-independent and density-dependent limits of variation. This flexibility to shift between equilibria allows the SR relationship both to evolve and return between higher and lower equilibrium states whereby the SR system may be persistent. Also, while the SR relationship is below K_0, the extinction of the fishery -not of the stock- is invoked;

(v) Three cases of local stability analyses (dotted lines) are shown for the equilibrium states m, m-1, m-2 as well as the overall persistency while $K_0 < S < K_{max}$ and $R(K_0) < R < R_{max}$.

To further analyze our model and to clarify the role of the coefficients a_i, b_i and c_i, a single equilibrium state (m = 1) is described by Eq. 2.2 (graphically represented in Fig. 2.5)

$$R \cong \frac{a \cdot (S)}{(S-b)^2 + c} \qquad (2.2)$$

where the numerator, or density-independent term, describes population growth when a > 0, and the denominator describes the density-dependent mortality term for a particular carrying capacity. Furthermore, by making the right hand side of Eq. 2.2 equal to zero, the intersection points with the replacement line, K_0 and E, become

$$K_0 = b - \sqrt{a-c} \qquad (2.3\ \text{a.})$$

and

$$E = b + \sqrt{a-c} \qquad (2.3\ \text{b.})$$

where a > c is the condition to allow the intersections. Also, adding expressions (2.3. a.) and (2.3. b.), the coefficient b, which is the middle point between the intersections, is given by

$$b = \frac{K_0 + E}{2} \qquad (2.4)$$

As the coefficient b is constant in the case described by Eq. 2.2, the intersection points with the replacement line will be situated around b. Furthermore, the maximum value of spawning stock, S_{max}, for which there is maximum recruitment is obtained by making equal to zero the first derivative of function (2) . Hence, S_{max} becomes

$$S_{max} = \sqrt{b^2 + c} \qquad (2.5)$$

which corresponds to the maximum recruitment given by

$$R_{max} = \frac{a}{2 \cdot \left(\sqrt{b^2 + c} - b \right)} \qquad (2.6)$$

As the parameter c tends to zero, recruitment will tend to infinity and S_{max} will tend to b. Also, R_{max} will increase with increments of both a (while b and c remain either stable or constant) and with the difference between K_0 and E_m. Hence, while the slopes in an equilibrium state become steeper, the value of K_0 may either decrease or tend to zero whereas the maximum recruitment may increase. In this way, our functional form may include approximations to both the Rickerian and logistic approaches for high values of a, i.e. when recruitment success and carrying capacities are high due to extremely good external conditions and relatively low fishing mortality. The functional form described in Eq. 2.1-2 formalizes some of our ideas about the SR relationship in Baltic cod. The function has clear maxima in stock and recruitment as well as a minimum viable population and allows for shifts between equilibria and complex behaviour.

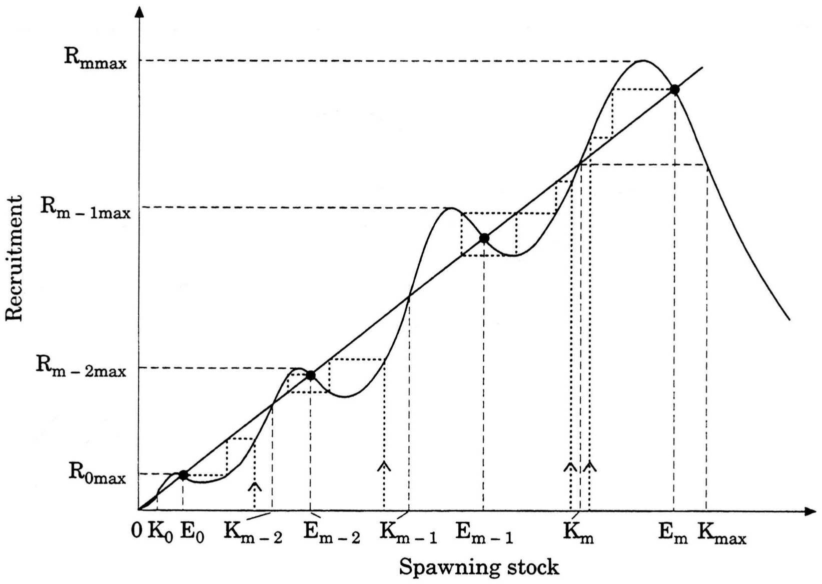

Figure 2.4. Graphical representation of the dynamic system with m equilibrium states (Eq. 2.1) proposed for the SR relationship in Baltic cod in ICES fishery areas 25-32 for years 1973-93 (after Ices, 1993). K_m, K_{m-1}, K_{m-2} represent both the minimum viable populations for the equilibrium states m, m-1 and m-2 and the carrying capacities for their immediate lower equilibria, respectively. E_m, E_{m-1}, E_{m-2}, E_0 represent equilibria around which the SR relationship may turn in density-dependent compensation and depensation phases. K_{max} is the maximum allowable carrying capacity and any values of stock surpassing this ceiling will induce a shift towards lower equilibria. K_0 is the floor or minimum viable population below which the SR relationship may tend to zero (extinction of commercial fishery). System persistence and local stability are shown in all three cases of stability analyses (dotted lines) while $K_0 < S < K_{max}$ and $R(K_0) < R < R_{max}$. An *m* number of oscillatory phenomena ranging from limit cycles to chaos and inverse density-dependence are allowed in this system.

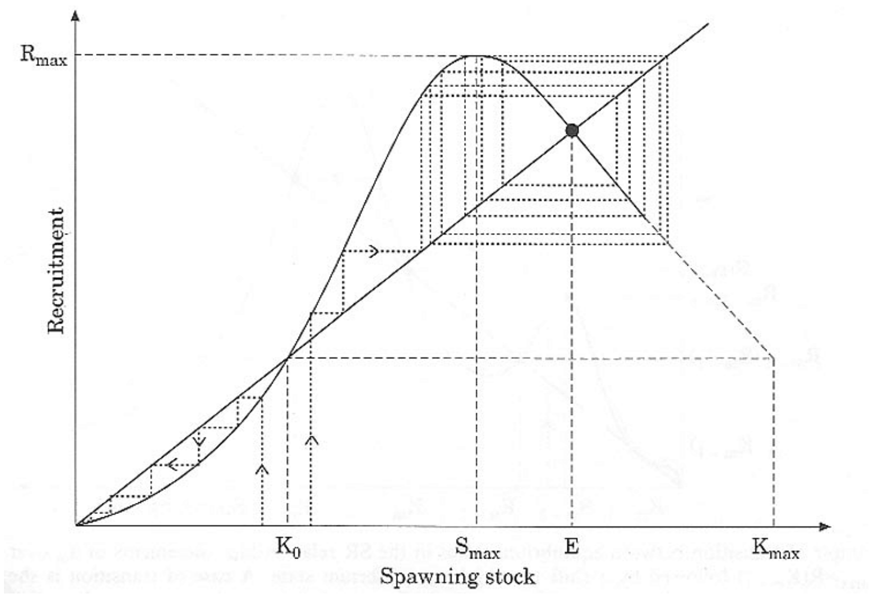

Figure 2.5. Graphical representation of an arbitrary single-equilibrium state (Eq. 2. 2.). Stability analyses is shown by dotted lines. K_0 = minimum viable population; E = equilibrium; K_{max} = maximum allowable carrying capacity; R_{max} = maximum recruitment.

In Fig. 2.6, 2.7 and 2.8, three cases of stock and recruitment are described for different values of the parameters a_i, b_i and c_i (Eq. 2.1):

Fig. 2.6 shows three examples of how the SR relationship is shaped while a_m variates and b_m and c_m are fixed. An arbitrary value of a_m returned the SR relationship described by the unbroken line while variations of a_m for the other two cases were $a'_m = a_m + .3 * a_m$ (dashed line) and $a''_m = a_m - .15 * a_m$ (dotted-dashed line). For a'_m, $R_{m\ max} > R_{max}$ which causes spawning stock values to surpass K_{max} and be followed by a shift of the SR relationship towards the lower equilibrium state. For a"$_m$, $R_{m\ max}$ is below the replacement line which causes the equilibrium state m to disappear.

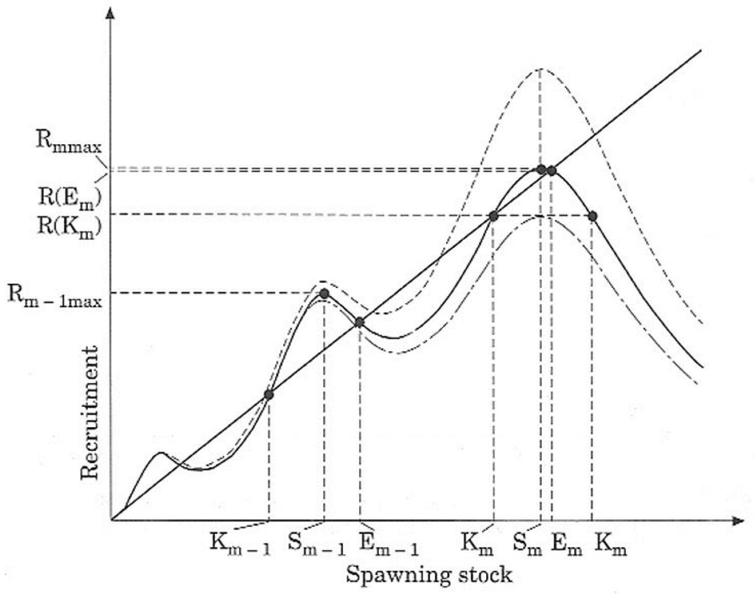

Figure 2.6. The SR relationship shaped by variations in the rate of increase a_m while the mortality parameters b_m and c_m are fixed. m and m -1 are the equilibrium states; R = recruitment; max = maximum; E = equilibrium; K = carrying capacity.

Fig. 2.7 shows an example of transition in the SR relationship from the equilibrium state m-1 (unbroken line) towards a higher equilibrium (m) through an increment in a_{m-1} (dashed line). The increment in a_{m-1} results in a $R_{m-1\ max} > R(K_m)$: this may imply that spawning stock values may surpass the carrying capacity (K_m) for the equilibrium state m-1 and, hence, a shift towards the higher equilibrium, m, is induced. Furthermore, the model allows for situations of persistence within anyone equilibrium state: the SR relationship may not shift towards higher equilibria if population increments are not sufficiently large. For instance, spawning stock values may range within the stability limits for a particular equilibrium state although there have been increments in recruitment (see the stability analyses in the figure).

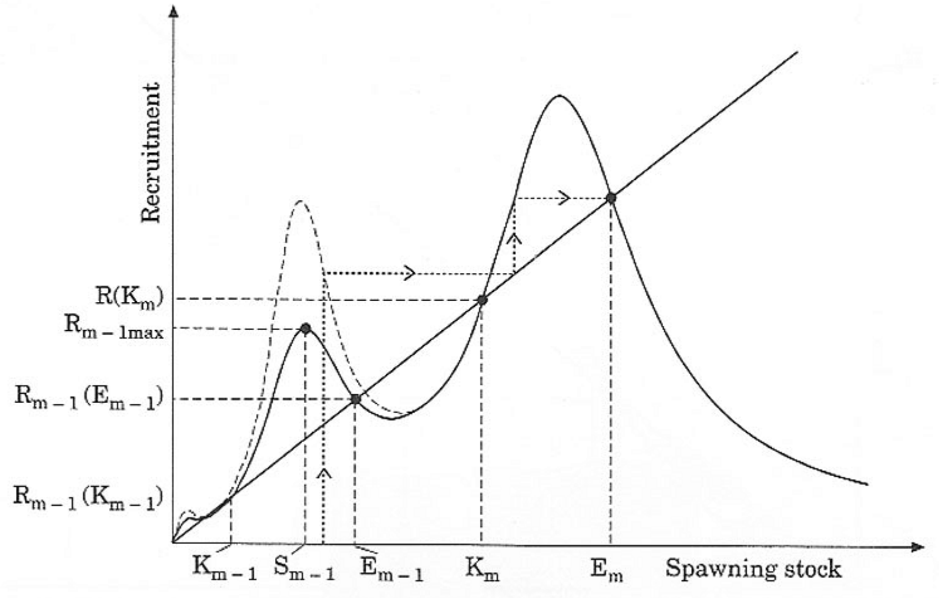

Figure 2.7. An example of transition between equilibrium states in the SR relationship. Increments of a_m over critical values may result in $R_{m\text{-}1\ max} > R(K_{m\text{-}1})$ followed by a shift to a higher equilibrium state. A case of transition is shown by the stability analyses (dotted lines). m and m -1 are the equilibrium states; R = recruitment; max = maximum; E = equilibrium; K = carrying capacity.

Fig. 2.8 shows another example of transition in the SR relationship from the equilibrium state m-1 (unbroken line) towards a higher equilibrium (m) through increments in both $a_{m\text{-}1}$ and $b_{m\text{-}1}$. As external conditions allow sufficiently large increments in recruitment and spawning stock, a_{m-1} and b_{m-1} increase implying a shift towards a higher equilibrium. Also, the shift towards the higher equilibrium state may come about whenever spawning stock values have surpassed the replacement line. Furthermore, K_0 increases with the difference between K_0 and E_{m-1} whereby the SR system may shift from locally stable cycles to chaos.

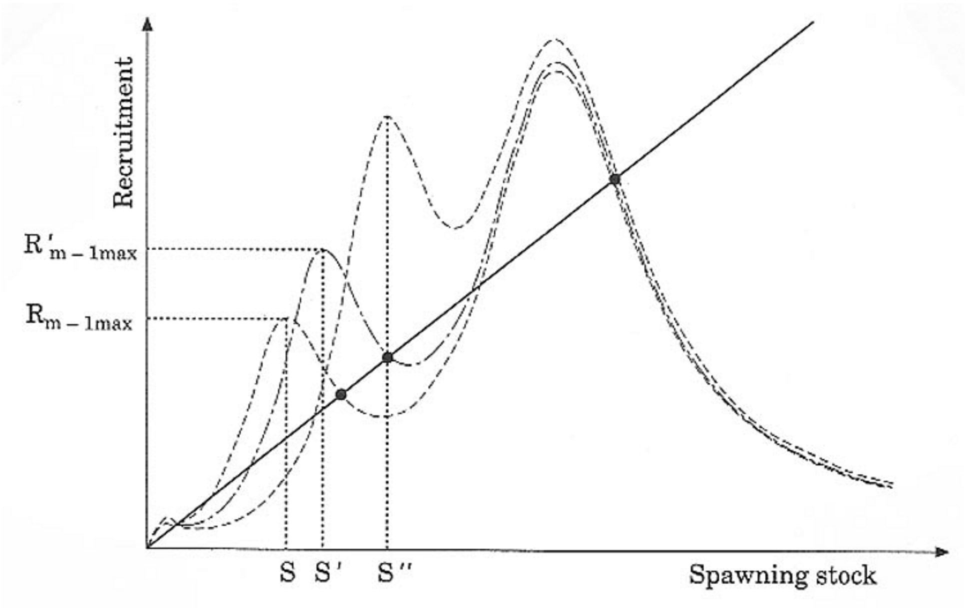

Figure 2.8. Example of transition in the SR relationship from the equilibrium state m-1 (unbroken line) towards a higher equilibrium (m) through increments in both a_{m-1} and b_{m-1} (b, b' ... b"). R = recruitment; max = maximum; equilibria are indicated by the dots.

We compared the goodness-of-fit from our approach (Eq. 2.7) to those from the models proposed by Shepherd (1982, Eq. 2.8) and Myers et al. (1995, Eq. 2.9). Our functional form to fit the field data is given by

$$R \cong \frac{a_1 \cdot S}{(S-b_1)^2+c_1}+\frac{a_2 \cdot S}{(S-b_2)^2+c_2} \qquad (2.7)$$

where the entries R, S, a_i, b_i and b_i are those defined for Eq. 2.1, assuming the SR series reflects two equilibria. Moreover, the Shepherd (1982) SR functional form is given by

$$R = \frac{\alpha \cdot S}{1 + \left(\frac{S}{K}\right)^{\delta}} \qquad (2.8)$$

where R is recruitment, S is the spawning stock abundance, K the threshold abundance above which density-dependent effects dominate (i.e. the carrying capacity). The parameters α and δ are referred as the slope at the origin and degree of compensation involved, respectively. This approach could unify, within a single framework, both the classical dome-shaped (for $\delta > 1$) and asymptotic (for $\delta = 1$) functional forms proposed by Ricker (1954) and Beverton-Holt (1957), respectively. Also, Myers et al. (1995) proposed an extension of the Beverton-Holt spawner and recruitment function modified to allow for depensatory dynamics. The functional form is given by

$$R = \frac{\alpha \cdot S^{\delta}}{1 + \left(\frac{S^{\delta}}{K}\right)} \qquad (2.9)$$

where *R* is recruitment of new fish to the population; *S* is a metric spawner abundance; and α, K and δ are all positive parameters. Depensatory dynamics are characterized by $\delta > 1$ and a sigmoidally shaped recruitment curve with an unstable equilibrium point at low spawning stock values.

The curve fittings on the spawning stock (age classes 4-9 + "gr" or age classes > 10) and recruitment (i.e. 3 year old cod) data (years 1973-1993) from fishery areas 25-32 in the Baltic (after ICES, 1993) are shown in Fig. 9. Data values were fitted by least-squares according to Eq. 2.7-9. The replacement line is given by a linear regression through the origin. The Root Mean Square Error (RMSE) was considered as a measure of the goodness-of-fit of the proposed models. Our approach fitted the SR data with a RMSE = 93.1218 while the functional forms proposed by Shepherd (1982) and Myers et al. (1995) showed RMSE = 95.6728 and RMSE = 97.2648, respectively. Furthermore, strong depensatory dynamics were detected on the SR series by the Myers et al. (1995) model which showed a $\delta = 1.886$. This value of the δ parameter is similar to that reported by Myers et al. (1995) for stocks of *Culpea harengus* (spring spawners in Icelandic waters) for which depensatory dynamics were reported. Results are further summarized on Table 1.

Table 2.1. Parameter estimates and goodness-of-fit as measured by RMSE (Root Mean Square Error) for the stock-recruitment functional forms (SR) proposed in our approach (equation 7), Shepherd (1982), Myers *et al.* (1995) and a simple linear regression through the origin. Stock and recruitment series for Baltic cod form 1973-1993 in fishery areas 25-32 (Anon., 1993). All models were fit to the data using least-squares.

SR Model	**Parameter estimates**	**RME**
Equation 7	$a_1 = 6975.04$, $b_1 = 151.32$, $c_1 = 7042.91$ $a_2 = 6974.04$, $b_2 = 384.83$, $c_2 = 33793.69$	93.12
Shepherd (1982)	$\alpha = 1.21$, $\delta = 5.43$, $K = 564.87$	95.67
Myers (1995)	$\alpha = 0.026$, $\delta = 1.89$, $K = 18389.60$	97.26
Regression	slope (α) = 0.96	111.94

Fig. 2.9 shows the replacement line is crossed by density dependent oscillations at two different levels of stock and recruitment (lower and higher equilibria). Also, the transition between the equilibrium states may be due to density-independent compensatory and depensatory effects induced by external inputs (environment and fishing mortality). In 1977, when the spawning stock was about to more than double, fishing mortality was higher ($F = 0.93$) than during 1984 ($F = 0.90$) when a shift to lower stock sizes followed. This may suggest both that higher fishing mortality is allowed during strong compensation (such as during 1977) and that a relatively minor reduction in the level of captures might not change the SR trend under density-independent depensation. Furthermore, fishing mortality had been relatively high during years 1980-83 (≅ 3.8*10^5 Tn/year), when the SR relationship oscillated within the higher equilibrium state. The record capture (≅ 4.5*10^5 Tn) which followed in 1984 occurred during a period when the SR relationship was affected by two depensatory stages: (a) A density-dependent depensatory phase within the higher equilibrium state and (b) A density-independent depensatory phase induced by negative trends in reproduction volume (RV), oxygen and salinity. Larsson (1993) reported a reduction of the reproduction volumes in the Bornholm, Gdansk and Gotland basins during years 1987-1993. According to our model, the combined effects from the negative perturbations may have induced a shift towards the lower equilibrium state which subsequently broke into a trend towards K_0.

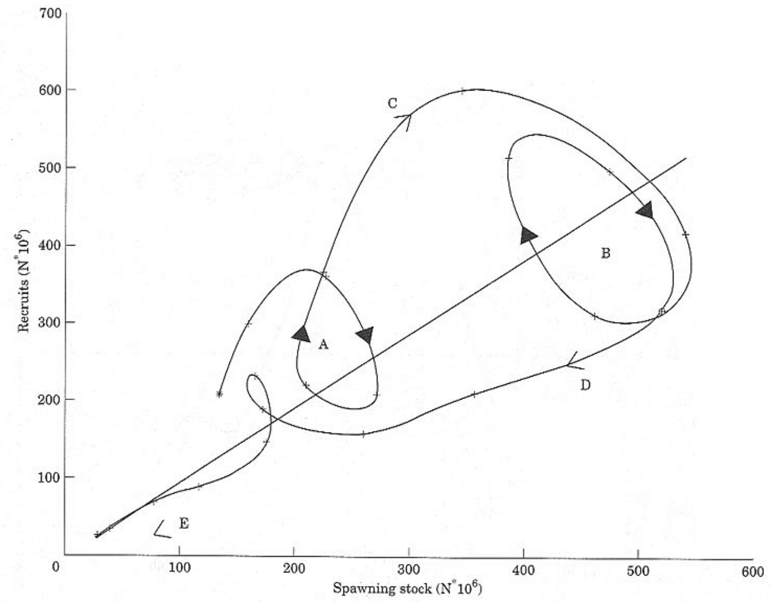

Figure 2.9. Spawning stock and recruitment (+) in Baltic cod as estimated in fishery areas 25-32 for years 1973-1993 (after Ices, 1993) interpolated by a cubic spline and fitted by least-squares according to the functional forms proposed by the present model (unbroken line), Shepherd (1982, dashed line) and Myers (1995, dotted line). Years of start of time series (1973) and record capture (1984, 4.5*10^5 Tn) are indicated by the asterisk and circle, respectively. The replacement line is given by a simple regression through the origin; N = number of individuals.

2.5 Simulation.

In order to analyse the performance of our model, a simple numerical simulation is put forward. For simplicity, let consider the SR relationship as a two equilibrium system for which the parameters a_i, b_i and c_i are fixed and determine it's stability limits. An external, sinusoidal perturbation will affect the SR relationship at three constant levels of mortality of spawning stock. To simulate these phenomena, we will use a delayed difference equation. In this way, the spawning stock at the beginning of any particular year, S_{t+1}, is given by

$$S_{t+1} = \sigma \cdot S_t + R\left(S_{t-\tau}\right) \qquad (2.10)$$

where σ is the survivorship coefficient affecting the spawning stock, S_t, and recruitment is a function of the existing parental stock τ years before. Hence, recruitment is given by

$$R\left(S_{t+1}\right) = \frac{a_1 \cdot S_{t-\tau}}{\left(S_{t-\tau} - b_1\right)^2 + c_1} + \frac{a_2 \cdot \left(1 + P_t\right) \cdot S_{t-\tau}}{\left(S_{t-\tau} - b_2\right)^2 + c_2} \qquad (2.11)$$

where the entries a_i, b_i and b_i are those defined for Eq. 2.1, τ is a fixed delay of three years (i.e. the age-at-maturity for Baltic cod) and P_t is a sinusoidal perturbation consisting of 20 values (graphically represented in Fig. 10). The iteration was carried out for 20 generations resulting in a time series of 400 values. The resulting SR relationships for $P_t = 1, 8, 13$ (representing values around the mean (unbroken lines) as well as the lower (dashed lines) and upper (dashed-dotted lines) limits of the perturbation, respectively; circled in Fig. 10) and spawning stock trajectories for $P_t = 1$ are shown in Fig. 2.11-12.

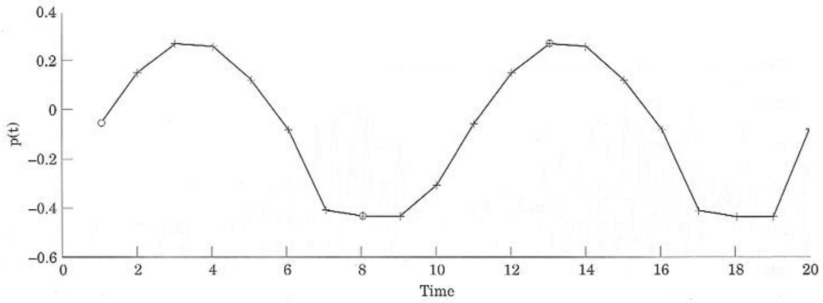

Figure 2.10. The sinusoidal perturbation P_t which affected stock and recruitment in the simulation. Circled values were chosen to plot simulation results (Fig. 2.11-12).

Fig. 2.11 shows the simulation output for a case where $\sigma = 0.6$ (i.e. 40% of the spawning stock is harvested). The relatively low level of mortality of the spawning stock allows for high density-dependent oscillations around a single, high equilibrium state. This simulation output could be approached by a classical dome-shaped SR model because the minimum viable population and possibility of depensatory dynamics become less clear and the high equilibrium state remains persistent while the SR relationship is affected by the lowest value of the perturbation (lower, dashed line).

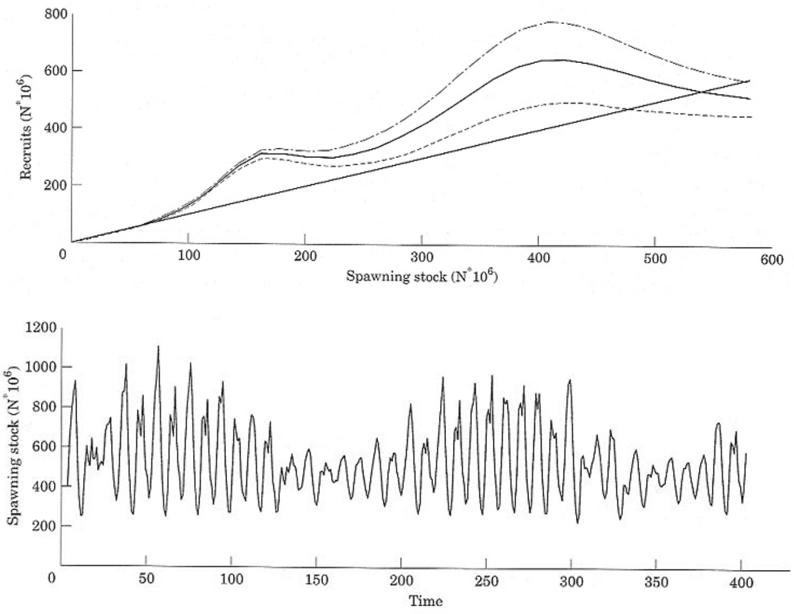

Figure 2.11. The stock-recruitment relationship (above) and spawning stock trajectory (below) in a simulation of a fish population which has survivorship $\delta = .6$, age-at-maturity $\tau = 3$, variable rate of increase at two levels of stability and is affected by a sinusoidal perturbation. Simulation results are plotted for three values of the perturbation: around the mean (unbroken line) and upper (dotted-dashed line) and lower (dashed line) limits. The spawning stock trajectory corresponds to the SR relationship shown by the unbroken line.

Fig. 2.12 shows the simulation output for a case where $\sigma = 0.3$ (i.e. 70% of the spawning stock is harvested). The relatively high level of mortality of spawning stock combined to the effect of the perturbation returns the following limits for the SR relationship: (a) while the perturbation is positive, stock and recruitment turns around a higher equilibrium state (upper, dotted-dashed line) whereas the relationship turns around two equilibria (unbroken line) while the perturbation becomes less positive (i.e. when P_t approaches a value around the mean). The spawning stock trajectory shows the levels of stock which correspond to both of the equilibria; (b) Furthermore, while the perturbation becomes negative, the

SR relationship turns around the lower equilibrium state (lower, dashed line) and the upper equilibrium state disappears. The situations described herein show a SR relationship which may shift to lower equilibrium states while harvests upon the spawning stock are relatively high and external perturbations become less benign. Moreover, the value of K_0 and likelihood of depensatory dynamics become more plausible under such conditions.

Fig. 2.13 shows the simulation output for a case where $\sigma = 0.05$ (i.e. 99.5% of the spawning stock is harvested). The high level of mortality of the spawning stock implies the SR relationship turns around two equilibria (dotted-dashed and unbroken lines) at lower stock and recruitment levels. However, the SR relationship shifts to a lower equilibrium state with lower amplitude of variation while values of P_t become more negative (lower, dashed line) being depensatory dynamics more likely to occur.

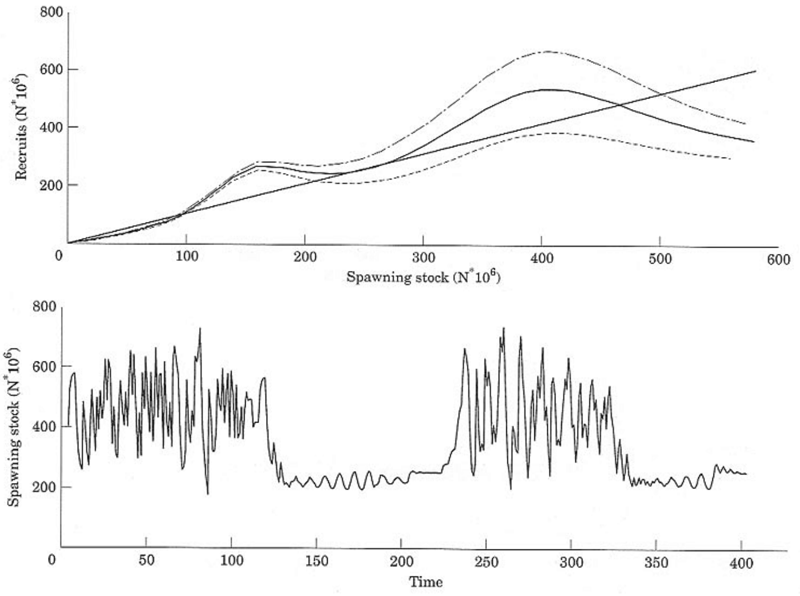

Figure 2.12. The stock-recruitment relationship (above) and spawning stock trajectory (below) in a simulation of a fish population which has survivorship δ = .3, age-at-maturity τ = 3, variable rate of increase at two levels of stability and is affected by a sinusoidal perturbation. Simulation results are plotted for three values of the perturbation: around the mean (unbroken line) and upper (dotted-dashed line) and lower (dashed line) limits. The spawning stock trajectory corresponds to the SR relationship shown by the unbroken line.

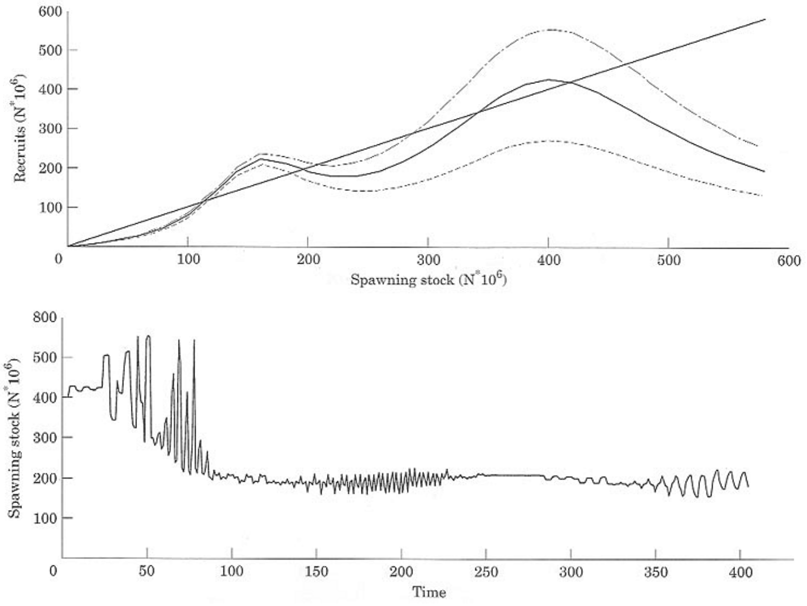

Figure 2.13. The stock-recruitment relationship (above) and spawning stock trajectory (below) in a simulation of a fish population which has survivorship $\delta = .05$, age-at-maturity $\tau = 3$, variable rate of increase at two levels of stability and is affected by a sinusoidal perturbation. Simulation results are plotted for three values of the perturbation: around the mean (unbroken line) and upper (dotted-dashed line) and lower (dashed line) limits. The spawning stock trajectory corresponds to the SR relationship shown by the unbroken line.

The cases described in Fig. 2.11-13 show a few of the possible outcomes of our model and how the combined effects from increasing fishing mortality as well as positive and negative environmental perturbations could affect stock and recruitment.

The present model may generate highly complex dynamics and, for simplicity, only the higher equilibrium state was perturbed as an example of a simple parameterization. However, it should be stressed that a parameterization to real world environmental perturbations may require that all parameters are affected by the external variables, subsequently increasing the degree of complexity of the output.

2.6 Discussion.

Recruitment in Baltic cod may be considered as the final result of a three year long process which, we assume, may be mainly governed by external conditions and density-dependent mechanisms affecting age class 0.

Paulik (1973) described an overall spawner-recruit model which was formed from the concatenation of survivorship functions. This approach could exhibit multiple (stable) equilibria and complex dynamics and was the result of a multiplicative process where the initial egg production could be modified by non-linear functions specific to each life-stage and cohort- population size. In contrast, the model we put forward does not consider the underlying processes of mortality during the early life stages. This is due to the unavailability of 0-year class data on Baltic cod. However, our model may be justifiable on an ad hoc basis because of the flexibility it affords and should be considered from this standpoint. Also, it may offer some conceptual advantages over the model described by Paulik (1973) to approach the SR system in Baltic cod: (i) equilibria may be independent from each other; (ii) at anyone moment, either a single equilibrium or several stable equilibria may operate for the overall stock-recruitment relationship; (iii) higher equilibria may disappear; (iv) transitions between equilibria may be more explicitly identified, described and mathematically controlled with regard to both density-dependent and density-independent inputs; (v) several maxima and minima may be described in the same relationship allowing for description of equilibrium states at different spatio-temporal scales, substocks and recruitment potential among different age classes; (vi) depensatory dynamics are allowed.

Moreover, the functional form proposed by Shepherd (1982) could incorporate several (but not all) of the dynamic features identified in our study when extended to the following formulation

$$R = \frac{\alpha \cdot S \cdot e^{\varepsilon_t}}{1 + \left(\frac{S}{K_t} \right)^{\gamma}} \tag{2.12}$$

where R and S are recruitment and spawning stock, respectively, α is the slope of the recruitment curve at the origin, K_t is a time-varying, density-dependent parameter which can be related to the carrying capacity of the environment, γ is a parameter controlling the degree of curvature of the function and ε_t is a random disturbance. Also, the time varying parameters could be expressed in a wave like frequency domain. Within this framework, recruitment may display several (uncoupled) maxima and be related to varying carrying capacities and periodic environmental perturbations. However, the approach proposed by Shepherd (1982) and the above extension (Eq. 2.12) could neither incorporate multiple stable equilibria nor depensatory dynamics.

Our model addresses dynamic features which, in part, may explain the phenomenology behind the SR relationship in Baltic cod:

Variable carrying capacity. This is, in our view, an important criterion in our approach: carrying capacity is regarded here as a critical transition stage between different equilibrium states as well as a varying spatio-temporal parameter. As the particular carrying capacity for a given equilibrium state is reached, the SR relationship jumps onto the next equilibrium. Even the maximum allowable carrying capacity is assumed to allow for the transition to lower equilibrium states rather than shifting the SR relationship towards extinction. In our view, this is compatible both with the evident persistence in the SR relationship, dynamic features of external conditions (environment) and the barrier to spawning stock numbers imposed by high fishing mortality. Also, there are strong indications both in field studies on Baltic cod and oceanographic conditions suggesting that stock and recruitment may be affected by a non-steady carrying capacity: resource limitation may vary at several spatio-temporal scales during the time span of the SR series. Moreover, in light of how the SR series develops, we find indications to assume that each equilibrium state may be affected by a particular carrying capacity: density-dependent mechanisms may covary with environmentally induced effects upon spawning stock numbers and equilibrium states are expected to be related to different spatio-temporal ranges in resource utilization. For instance, there are two levels of maxima in recruitment at two significantly different levels of spawning stock numbers for which two carrying capacities may be invoked, respectively (Fig. 2.1-2). Also, the variable carrying capacity concept may become increasingly complex as we address spatio-temporal variations in stock and recruitment (fishery subareas) as well as different delays related to environmental conditions.

Multiple equilibria and Chaos to cycles. In light of the classical models, the lack of causal relationships between stock and recruitment has lead to the discussion on whether the recruitment process is deterministic (Kot et al. 1988, Fogarty 1993). In our view, stock and recruitment in

Baltic cod may be a deterministic but highly complex phenomenon which is unpredictable in the long term: we propose the SR-system as a continuum 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 K_0 is being approached). In this highly flexible approach, the SR relationship is allowed to evolve and return within a range of equilibrium states whereby it may be self-regenerated and persistent.

Conrad (1986), Schaffer (1986) and Kot et al. (1988) suggested that chaotic mechanisms would serve to maintain the adaptability of the population. Chaotic behaviour has earlier been proposed by May (1976) for laboratory and field populations of insects, by Powers (1989) for a 2 species system of fish and by Schaffer and Kot (1986) and Kot et al. (1988) for outbreaks of insects pests and of human diseases. Also, Berg and Getz (1988) suggested that stock and recruitment, in a sardine-like population, moved along a path or attractor in some higher dimension coordinate system and Conan (1994) observed that lobster and snow crab landings in Atlantic Canada may follow two orbits of stability or cycles.

Also, May (1974) showed that the logistic equation may produce highly variable outcomes when a simple deterministic feed-back over a time lag is introduced. In our approach, as delays and dependencies between age-classes are included, the (simulated) SR-system may become more sensible to initial conditions to rapidly shift from relatively stable cycles into chaos. However, the SR data on Baltic cod may suggest that there may be relatively wide tolerances for each of the proposed equilibrium states. This may be due to effects of "memory" both from density dependent mechanisms and external inputs combined to delays. The concept of memory, in this context, refers to functions which describe inputs which may not jump but follow a relatively smooth, wave-like distribution pattern.

The proposed SR-system may, further, include all of the classical models. For instance, approximations to the Ricker and logistic approaches may be displayed by our model for high values of either or both a_i and/or b_i which may occur while environmental conditions are extremely benign. Also, while the SR relationship shifts to higher equilibria due to external, positive perturbations, oscillations may tend to become chaotic. We expect that a relatively high degree of variability in the SR relationship may reflect the dynamic process is healthy. Further, if the parameters of the model fall within the portion of phase-space leading to chaotic dynamics, the SR-system is allowed to rapidly shift between higher and lower equilibria: this implies an intrinsic feature in Eq. 2.1 to describe several coupled cycles of different period length.

Also, there is no clear example of a chaotic pattern in the data, probably, due to actual stress conditions in the Baltic Sea and limited degrees of freedom in the time series. However, the amplitude of oscillations is higher for the high equilibrium state relative to the lower equilibrium. This could be regarded as an indication of a trend (from cycles) to chaos as external perturbations become more positive.

Moreover, as external stress increases, stock and recruitment may develop towards lower equilibrium states with lower amplitudes of variation, approaching orbits of stability or limit cycles. In our view, the SR series analyzed in this study may consist of two cycles and a depensatory trend towards K_0. In this case, further negative perturbations during depensation phases may imply that the SR system remains at excessively low equilibria, preventing the rehabilitation both of the stock and commercial fishery.

Also, we assume that the SR-system is further affected by feed back mechanisms, multiple delays and non-linear relationships operating at several spatio-temporal scales, local and global stability and multiple memories related to the distribution of external perturbations. Bakun (1988) observed that recruitment does not reflect a single process but a large number of interacting processes. Our approach may be a flexible tool to allow the integration of such dynamic terms. Also, Conan (1994) pointed out that chaos theory applies to cases in which feed-back mechanisms would affect the abundance of a species and that, in such cases, the oscillations of the system when it is affected by disturbances should be modelled.

Recruitment (over fishing), K_0 and depensatory dynamics. Models of population dynamics in which per capita reproductive success declines at low population levels (variously known as depensation, Allee effect, and inverse density dependence) predict that populations can have multiple equilibria and may suddenly shift from one equilibrium to another. If such depensatory mortality exist, reduced mortality may be insufficient to allow recovery of a population after abundance has been severely reduced by harvesting (Myers et al. 1995).

Beyond the classical models, our approach proposes a SR-system in which spawning stock may not rehabilitate if highly stressed during depensation phases. Sjöstrand (1989) reported that fishing mortality in Baltic cod was 3.8*10^5 Tn/year during years 1980-83 followed by a record capture of 4.5*10^5 Tn in 1984. In our view, spawning stock was well rehabilitated during years 1980-83. Oscillations around the higher equilibrium state seemed fit and the system appeared to allow a fishing mortality of around 3.8*10^5 Tn/year. However, the record capture in 1984 was carried out under *two* depensatory phases: the higher cycle was under a density-dependent phase and spawning conditions were affected by negative trends in oxygen and salinity in the Baltic basins (for an overview on Reproduction Volume in the Baltic basins, refer to Larsson 1995). This may have implied a shift to the lower equilibrium state. Thus, we suggest that due to the combined effects from negative perturbations (decrease of reproduction volume and high fishing mortality) during the depensatory phases, the lower cycle was broken, causing the SR relationship to shift towards the minimum viable population K_0. This situation, in our view, implies that stock and recruitment may have come to oscillate nearby K_0. However, if our criteria are theoretically correct, we may next expect a stock and recruitment rehabilitation to a low equilibrium state (similar to A, Fig. 2.1. a., b.) due to compensatory effects induced by the positive trends in reproduction volume, salinity and oxygen during the coming years. It is, however, important to stress that a fishery yielding a constant maximum may not be practicable on Baltic cod: while stock and recruitment comes into depensatory phases, the combined effect from high fishing mortality and environmental stress may come to either settle the SR relationship around lower equilibria or induce a shift towards K_0. This may negatively affect the outcome of the commercial fisheries once the stock becomes rehabilitated. Furthermore, it should be stressed that depensatory dynamics should not be assumed a priori in a general context for other species. Myers et al. (1995) suggested that estimates of spawner abundance and number of surviving progeny for 128 fish stocks indicated only 3 stocks with significant depensation. Moreover, the depensatory structure of the model is dynamic as well: as the SR relationship tends to become chaotic at high equilibrium states, for instance when recruitment is high due to extremely benign external conditions, the value of K_0 will tend to zero. This implies a sufficiently wide tolerance to allow for perturbations (random or otherwise) which may be superimposed on the portion of phase-space describing the chaotic dynamics.

2.7 Acknowledgements for the present section.

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2.8 Series and model update (August, 2007).

In Solari et al. (1997), it was suggested that the Stock-Recruitment system in Baltic cod (Baltic sea areas 25-32) shifted towards the minimum viable population due to the combined effects from high fishing mortality during the early 80's and a negative trend in the so called "reproduction volume" (overlapping between oxygen and salinity conditions which may affect year class strength) during the mid 80's: there were peak catches during years 1982-1984 after which both density-dependent (due to population dynamics) and density-independent (due to the environment) depensations started to operate simultaneously.

In the proposed framework, both the theoretical argumentation and inference were based on data up to year 1993 and it was estimated that, according to the new model, stock and recruitment may rehabilitate. However, the rehabilitation was expected to be established onto a low equilibrium state/orbit of stability near the minimum viable population of the system (with low scale of numbers, small amplitude between maxima and minima and weak oscillations).

The series are now updated (after ICES, 2007) to show both that the theoretical criteria and estimations we put forward in the paper were correct. The stock-recruitment system (Fig. 2.8.1-3) established onto a low orbit of stability which still remained until the end of the available series (year 2006) and appears to have turned around twice in two cycles of approximately 8 years.

The framework we proposed allowed us to correctly explain some of the dynamics behind the data and estimate short and medium non-linear trends in the stock-recruitment system.

Although the ICES Working group on Baltic sea fisheries (ICES, 2007) corrected the series by means of accounting for both misreporting and discards. However, the multi-oscillatory nature of the stock-recruitment system is strong and remains similar. Corrections may be marginal for the dynamical patterns behind the data and smoothing and fitting methods will result in similar outputs both on the raw and log transformed series. Auto and cross correlations remain strong, as well. For instance, the memory effect (dependency on preceding values) is still 7 and 6 years for the spawning stock and recruitment, respectively. Also, the main periodicities detected by the spectral analysis (Fig. 2.8.2) fall within similar ranges (approximately 4-5 to 7-8 years). The 4-5 to 8-10 years cycling ranges are linked to density-dependent processes (compensatory and depensatory phases of around 4-5 years each). Also, the concept of recruit was changed by ICES (2007) to Age Class 2. However, we chose to use the older concept (or Age Class 3 as recruits) both to be coherent with our earlier work and due to the high cross correlation between the age classes.

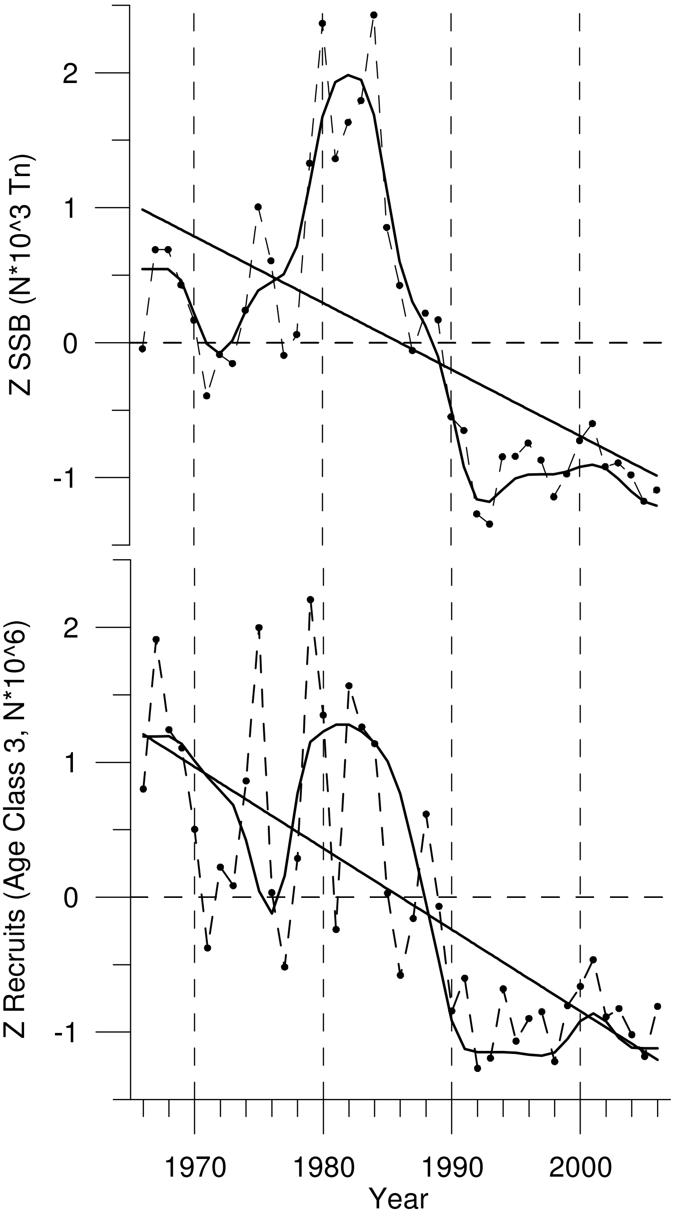

Figure 2.8.1. The updated standardized (Z) Baltic cod Spawning Stock Biomass (SSB; upper caption) and Recruitment series (after ICES, 2007; lower caption). Dashed line represents the raw data. Bold lines are the smoothed series and a linear regression.

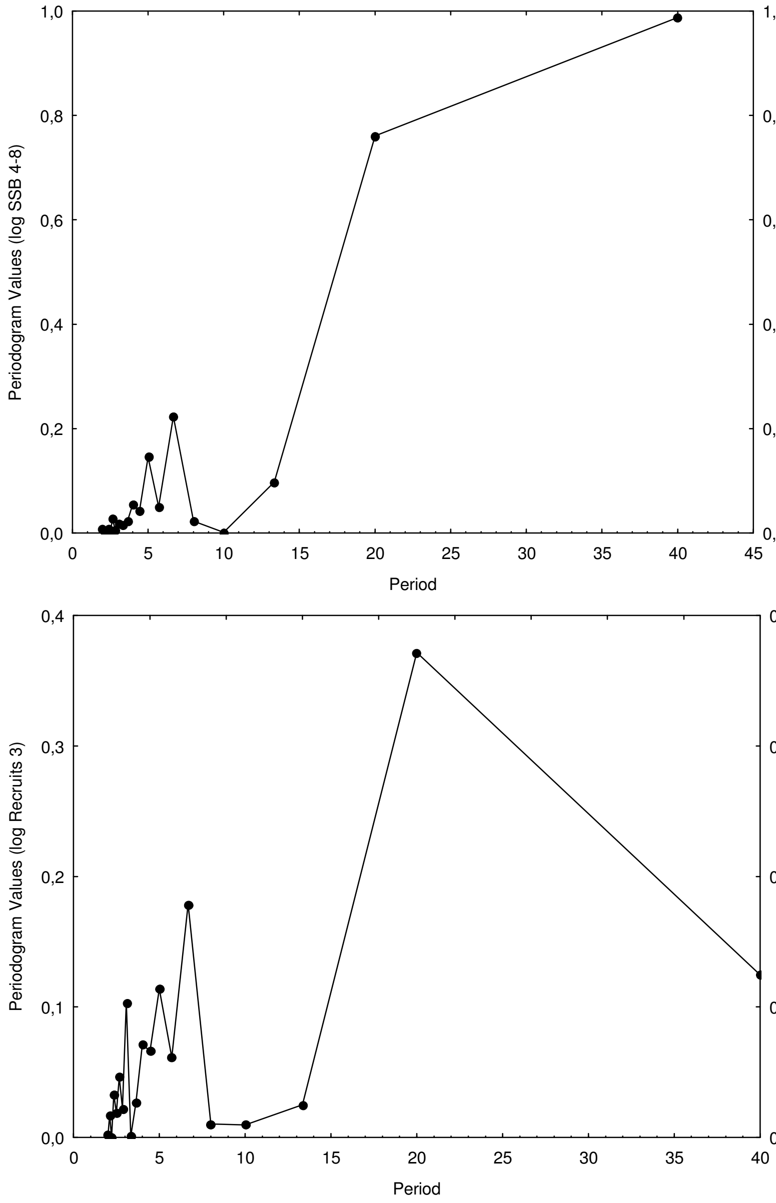

Figure 2.8.2. The spectrum on the standardized (Z) Baltic cod Spawning Stock Biomass (SSB, left caption) and Recruitment series (after ICES, 2007). There are common peaks for approximately 5 to 8 years periodicities.

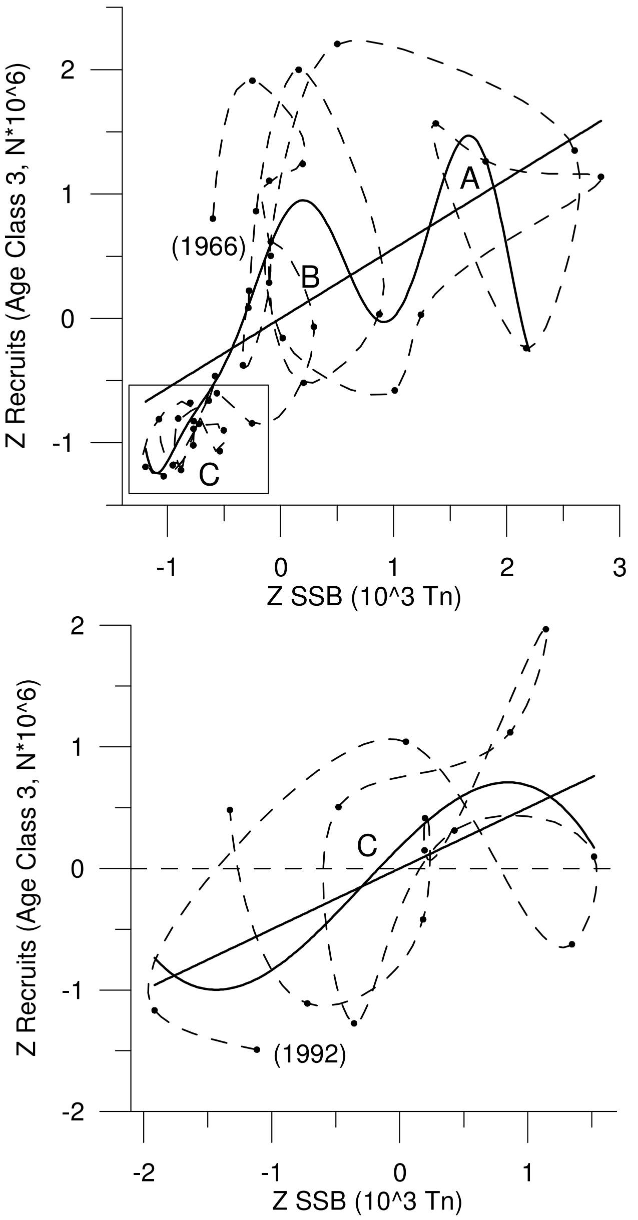

Figure 2.8.3. The upper caption shows the relationship between the standardized (Z) Baltic cod Spawning Stock Biomass (SSB) and Recruitment series (after ICES, 2007). A-C indicate the equilibria around which the orbits of stability turn. According to Solari et al. (1997), based on data until 1993, the stock-recruitment system was suggested to rehabilitate (from years 1993 and on) to a low orbit of stability (C, indicated by the rectangle). Both theoretical criteria proposed by the new model and estimations of short to medium term trends were validated by the updated series. The lower caption shows the local dynamics in the low (C) orbits of stability. The straight (replacement) lines are linear regressions through the origin and the non-linear fittings are polynomial (even distance weighted least squares shows similar results) and cubic in the upper and lower plots, respectively. Numerals between parenthesis indicate the year of start of the series.

Finally, we show an example of the forward-backwards bending nature of the Catch and Effort relationship (after Swedish data on cod for Baltic sea areas 25-27, years 1983-2006; ICES, 2007).

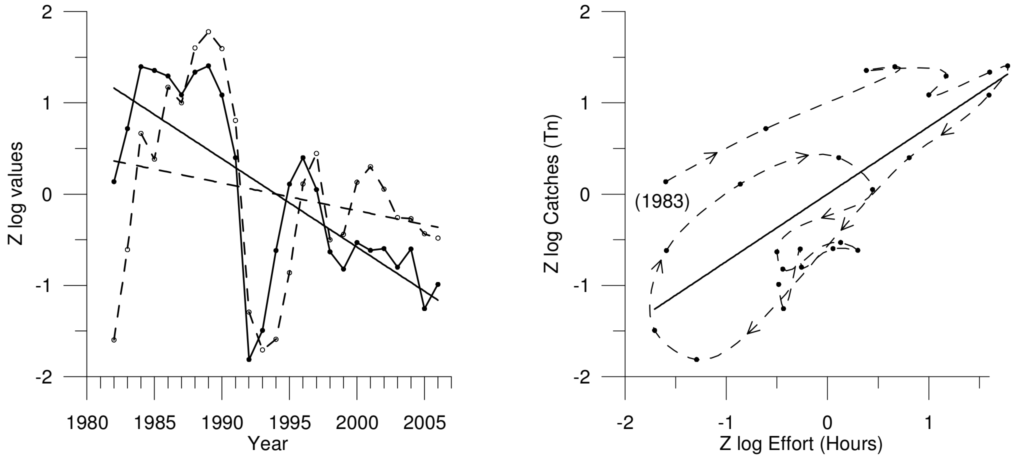

Figure 2.8.4. Log transformed (log) and standardized (Z) Swedish Catch (Tn) and Effort (Hours) series (above left) and their relationship (above right) on cod in Baltic sea areas 25-27, years 1983-2006 (after ICES, 2007). As the stock-recruitment system follows orbits of stability, the nature of the Catch and Effort relationship is a forwards (compensatory) and backwards (depensatory) bending which is clearly shown by the data above. Start of the series (in the phase plane caption) is indicated by the numeral between parenthesis.

The phase plane of the Catch and Effort relationship (Fig. 2.8.5, right caption) is interesting as it shows us further indications of both (i) the differential effects of Effort (and fishing mortality) upon the different density-dependent compensatory and depensatory phases of the population; (ii) the relatively long trends as there are density-independent (environmentally mediated) shifts between orbits of stability and (iii) the multi-oscillatory nature of the stock-recruitment system.

Also, effects of the Total Allowed Catches (TACs) are expected to be differential as the stock-recruitment system will oscillate even while in low orbits of stability. ▪

CHAPTER 3-3.1

Further case studies to support the new framework

On the dynamics of Cod, Skipjack, the common *Octopus*
and a historical “Almadraba” trap fishery

3.1. Further case studies to support the new framework.

In Chapter 2, we put forward and discussed the new dynamical framework based on an example on stock and recruitment in Baltic cod. In the present chapter, we will address further cases. Our intentions were to find, analyse, support and validate the ideas on population dynamics we proposed in our original study (after *Solari et al., 1997*).

Although different cases may require the incorporation of further concepts into the framework (an ad hoc approach for each particular case), many of the proposed general concepts and model may be useful. The complementary case studies presented herein are as follows:

While dynamics in Baltic cod occur in a semi-enclosed environment with limited water inflow from Kattegat-Skagerrak, cod populations in Icelandic waters (Section 3.2) may be affected by different environmental conditions and show different dynamical features. We thought this case study could open up further views in our framework and serve to support our general ideas for exploited, demersal fish populations in relatively larger marine systems.

Also, we shifted our interest further onto populations in FAO Fishing Area 34 (Eastern Central Atlantic) which is an interesting zone both for fish and cephalopod dynamics: on the one hand, we selected skipjack tuna (Section 3.3) due to the migratory nature of the stock and, on the other hand, we chose the common *Octopus* (Section 3.4) as there is still a lack of predictive framework for the study and exploitation of this species. Both of these species are of high bio ecological and socio-economical values and the exploitation and management of these resources are critical for several countries in the area.

Furthermore, we approached a historical "Almadraba" trap fishery on tunas (Section 3.5) to further investigate whether our new concepts could be of use to understand the dynamics of an exploited population as neither industrial fisheries nor recruitment over fishing existed: this case study may give us an insight in the past which may allow us to better understand the role of modern, high and intense fishing mortality and how we may cope with these matters both theoretically and practically. On the grounds proposed in our theoretical framework, we may address short and medium term future situations and propose sustainable harvest ranges, adapted to several of the cofactors governing the dynamics.

In Sections 3-5, the introduction to classical models and the new framework are referred both to Chapters 1 and 2 in order to avoid repetitive theoretical background exposition.

3.1.2. Notes on methods for data analyses.

This is a brief explanation of the statistical methods we use and why we chose them:

(i) in general terms, we use statistical tests which may give us indications on whether there are periodicities, lags, dependencies and persistency or memory effect in the series (auto- and cross correlations, the Hurst exponent and spectral and wavelet analyses);

(ii) in series where raw data is neither stationary nor homogenized, they are log transformed to meet conditions for statistical normality;

(iii) also, we work on standardized data (with mean = zero) as we are interested in trends, not in absolute numbers (we assume that catches may be regarded as proxies for abundance) and to facilitate visual comparison;

(iv) data is smoothed with a five year moving average window both to denoise the series and to determine whether trends remain;

(v) we use simple regressions either to determine the “replacement line” (i.e. recruitment needed to replace the stock) or as an indicator of general equilibrium values (in which the fitted system does neither grow nor decrease);

(vi) polynomial regressions (incorporating three constants for each orbit of stability) to approximate the dynamical continuum we propose.

It should be remarked that without the proposition of a framework for population dynamics (whatever it may be), statistics per se may become a useless tool. In the present case, the statistics we use are complementary tools to the (qualitative) framework and allow us a quantitative analyses of certain aspects in the data. For instance, while the results of a spectral analyses which detects periodicities in the series will not offer any advantage to classical models (which assume equal statistical weight to all of the data points in a stock-recruitment relationship, that is no dependence or memory effect between the observations), it will be of significant value to our model to determine the frequency in which orbits of stability arise.

As the studies presented herein incorporate newer statistical approaches as our work was being developed, the "Methods" section in each of studies should be regarded as self standing.

3.1.3. Extended concept of recruitment.

The classical concept of "recruitment" refers to the influx of juveniles into the adult population. However, we have extended the concept to comprehend both (i) the number of individuals entering the area of the interest ("recruitment-to-the-area") and (ii) to the fishery ("recruitment-to-the-fishery"). All of these concepts are useful in our framework to study both local and global dynamics relative to areas of particular interest, to determine whether there is any dynamical similarity between stocks/sub-stocks and within/between areas and to address other factors such as short and medium term trends in recruitment, sustainable catch ranges, in-area dynamical features and external forcings at different spatial scales. In this way, we may incorporate both dynamical and geospatial components in the framework.

3.1.4. Extended concept of equilibrium.

In our original paper (Solari et al., 1997), we used the concepts of "equilibrium" and "steady state": these are solely theoretical ideas to describe the "mean" within discrete dynamical situations. Also, "mean" may be regarded as a human artefact as "equilibria" out in nature will permanently shift as a function of the ever changing transition scheme in the ocean. However, as our framework was further developed, we extended our nomenclature to "pseudo-equilibrium", "orbit of stability", "trajectory" and "dynamical continuum" in order to describe more accurately the dynamical nature of the population system and the temporal evolution between different situations.

3.1.5. Catches as a proxy for abundance.

Both conceptually and for management purposes, classical models rely strongly on the concept of fishing effort. As a consequence of this, we should put forward an argumentation to show that "an oscillating population system governed by wave-like forcings may retain the dynamical structure and, solely, scales of numbers change". In Appendix I, we show examples of a population which retains similar dynamical patterns under different linear and non-linear fishing mortality regimes. This is critical to understand that catch data from oscillating populations may be as useful even as no or unreliable effort data is available.

3.1.6. Previous papers.

In previous papers by Solari et al. (1997), Bas et al. (1999), Castro et al. (1999) and Solari et al. (2003), we proposed recruitment both to the population (influx of juveniles to the adult population), area (migration of cohorts/individuals into fishery areas) and fishery (dynamics of the fishery) as a system or summation of non-linear functions (multiple orbits of stability or equilibrium states) with dynamic features ranging from chaos (when external conditions are extremely benign), going through a range of relatively stable, convergent cycles (as external stress increases) to a standstill state with no clear oscillations (when the minimum viable population is being approached): the system was suggested to have the capacity to, persistently, evolve and return within a wide range of equilibrium states allowing for multiple carrying capacities as well as density-dependent (compensation and depensation due to population numbers), density-independent (compensation and depensation due to environmental fluctuations and fisheries) and inverse-density-dependent (per capita reproductive success and recruitment declines at low population levels) coupled mechanics. Our new, dynamical framework was justifiable on an ad hoc basis because of the flexibility it afforded. Also, it offered some conceptual advantages over classical approaches as it allowed for (i) multiple equilibria or stable phase states, independent but linked to each other (no mathematical interdependence between the functions due to the additive nature of the approach), (ii) either higher or lower equilibria could be incorporated into the system, (iii) transitions between equilibria due to density-dependent and density-independent oscillations could be linked and, among other features, (iv) several maxima and minima and depensatory dynamics could be described in the same relationship, allowing for simultaneous equilibrium states and dynamical similarity, at different spatio-temporal scales and substocks/local populations. All of these features may vary, depending on the particular case for each stock and, as we see it, it may provide a more realistic perspective of the structure and dynamics of fish and cephalopod populations as presented in the case studies which follow.▪

CHAPTER 3.2

On the Dynamics of Icelandic cod: LINKED EQUILIBRIA AND FISHERIES

3.2 On the dynamics of Icelandic cod: linked equilibria and fisheries.

3.2.1 Abstract.

The stock and recruitment (SR) relationship in Icelandic cod is studied: in light of the field data, it is assumed the relationship turns around three orbits of stability due to the interaction between density-dependent compensation and depensation and (b) density-independent, compensatory and depensatory transitions between equilibrium states due to external disturbances. The relationship is proposed as a multiple steady-state system, described as a summation of non-linear functions, with multiple replacement lines and ceilings-floors (variable carrying capacities) allowing for stable, periodic and chaotic dynamics. The proposed approach may both describe and link, within a dynamic continuum limited by a maximum allowable carrying capacity (or highest ceiling) and a minimum viable population (or lowest floor), all of the known population mechanics (i.e. both density dependent- and independent- compensation and depensation as well as inverse density-dependence) in a simple equation. Two base functions are proposed in the model aimed to describe stock-recruitment systems in both semi-enclosed and open areas (such as in Baltic and Icelandic cod, respectively) either governed by the environment, anthropogenic perturbations (fisheries, pollution and habitat changes) or a combination of both. The conceptual advantages of the new framework are discussed in relation to the classical Shepherd and Paulik SR approaches. Further, it is stressed that (i) linked mathematical functions are independent of each other whereas variable equilibria may be either independent or partially dependent; (ii) higher equilibria may disappear due to external medium and long term disturbances; (iii) descriptions of equilibria at several spatio-temporal scales and substocks are allowed; (iv) the minimum viable population may either allow for a logistic type of population increase (as it tends to zero while the external environment is benign), be at standstill with no clear, density-dependent oscillations or become an unstable equilibrium implying inverse density-dependence (as the intensity of external stress increases at low numbers) and (v) at extremely high levels of fishing mortality, the present model may describe persistency at low equilibria whereas the Shepherd approach predicts instability and extinction. It is suggested that the combined effect of both a meso scalar negative trend in temperature and high fishing mortality may have contributed to the settlement of the low equilibrium state observed at the present time.

3.2.2. Introduction.

The qualitative relationship between spawning stock (S) and recruitment (R), the later being considered as the influx of juveniles into the adult population or fishery, may be fundamental to the population dynamics and management of fish stocks. Early non-linear approaches by Beverton and Holt (1957) and Ricker (1954, 1975), still being widely used in fishery science, proposed extinction curves where recruitment either reaches an asymptotic maximum (Beverton-Holt) or becomes low at high spawning stock sizes (Ricker). These classical SR approaches were unified by Shepherd (1982, henceforth referred as the 'Shepherd approach') in a functional form which, when modified, could incorporate time varying parameters allowing for multiple, uncoupled equilibria, a variable carrying capacity and external disturbances, either random or in the wave like frequency domain. However, the Shepherd approach could neither incorporate multiple, coupled equilibria nor inverse density-dependence (i.e. decline of reproductive success at low population levels). Also, Myers et al. (1995) proposed an extension of the Beverton-Holt SR function modified to allow for depensatory dynamics but no multiple, stable equilibria could be described therein. Moreover, Paulik (1973, henceforth referred as the 'Paulik approach') proposed a general SR model which was formed from the concatenation of survivorship functions: this highly advanced approach could exhibit multiple, stable, coupled equilibria and complex dynamics and was the result of a multiplicative process where the initial egg production could be modified by non-linear functions specific to each life-stage and cohort- population size. However, the Paulik approach was not sufficiently flexible due to the interdependency between the concatenated functions in the multiplicative model and the inability to incorporate inverse density-dependence.

A recent paper by Cook et al. (1997) addressed the issue of potential collapses of North Sea cod stocks and the significance of the underlying SR relationship and replacement line (i.e. the recruitment needed to replace the spawning stock in the future) in relation to the sustainability of harvesting. Recruitment in most fish populations is found to vary erratically from year to year in ways that presently cannot be explained or predicted (Bakun, 1988). Studies by Jakobsen (1996) and Baldursson *et al.* (1993) showed that there is a significant uncertainty when fitting north sea and Icelandic cod SR data, respectively, to the classical functions proposed by Beverton and Holt (1957) and Ricker (1954, 1975). In our view, the difficulties to understand the SR relationship may neither rely on recruitment variability nor on the noisy series but on the theoretical framework in which observations are expected to fit: the complexity of the SR system requires the utilization of a flexible framework which may allow us to approach the specific dynamics of each particular case.

The purposes of this study were (i) to analyze Icelandic cod SR data in light of our new, non-linear approach; (ii) to discuss whether our model may have any advantages over the Paulik and Shepherd approaches for this particular case and (iii) to raise further discussion on the dynamic qualities of this SR system.

3.2.3. Data and background to the model.

Spawning stock and recruitment series in Icelandic cod (numbers-at-age), years 1956-1997, are shown in Fig. 2 (after ICES, 1997). We used the Welch method (after Oppenheim and Schafer, 1975) to estimate the spectral density of the smoothed SR series (Fig. 3.2.3): although degrees of freedom were limited, peaks corresponding to periods of approximately 10 years were detected for both of the series. Also, the SR relationship from the field data, both interpolated by a cubic spline and smoothed, is shown in Fig. 3.2.4 where the following dynamic features are proposed: the present SR system is assumed to turn around three equilibria; a high equilibrium state (A) when the spawning stock is relatively large; an intermediate equilibrium (B) as the spawning stock decreases and a low equilibrium (C), which arises during the late 1980's, with significantly lower numbers in both spawners and recruits. Furthermore, it is assumed that (i) each equilibrium state is limited by a particular carrying capacity which will variate as a function of external perturbations; (ii) oscillations, within equilibria, are due to density-dependent compensation and depensation as numbers increase and decrease, respectively; (iii) equilibria are linked through density-independent transitions due to compensatory (D) and depensatory (E) mechanisms which arise when the external environment is either benign or disturbances increase, respectively. As the spawning stock either increases (D) or decreases (E), recruitment remains relatively stable. However, as the SR relationship settles into new equilibria (A, B, C), recruitment variability becomes relatively high. Moreover, it is further assumed that (i) shifts towards lower equilibria may be induced by fishing mortality; (ii) the combined effects from both fishing mortality and environmental medium term disturbances may shift the SR system towards the low equilibrium state, observed at the present time and (iii) any additional disturbances, while depensatory mechanisms are operating, may imply further shifts towards the minimum viable population and, hence, the extinction of the commercial fishery.

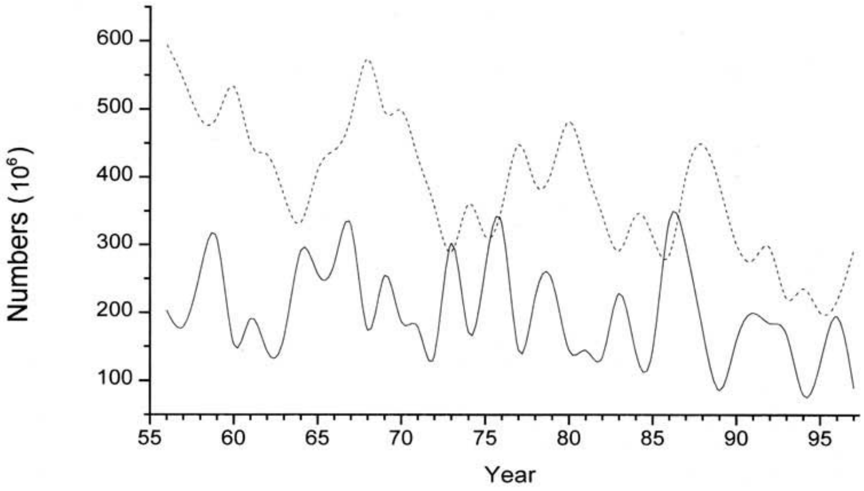

Figure 3.2.1. Spawning stock (dashed line) and recruitment (continuous line) series in Icelandic cod (numbers-at-age), years 1956-97 (after ICES, 1997).

The analyses of environmental time series from Icelandic waters is beyond the scope of this paper. However, we have attempted to gather some synoptic to discuss some of the premises we have proposed in our approach, particularly, concerning the SR shift towards the present, low equilibrium state. Reynolds and Smith (1994) developed a technique which uses blended in-situ and satellite Sea Surface Temperature data: the major advantages of this method are (i) the objective, time-dependent correction of any satellite biases relative to the in-situ data and (ii) the optimum interpolation of the available satellite and in-situ ship and buoy data on a 1° Latitude (Lat)/Longitude (Long) spatial grid as well as daily, weekly and monthly temporal resolutions. The Optimum Interpolated Sea Surface Temperature (OI SST) data presented herein was obtained from the Coupled Model Project (W/NMCx3), National Meteorological Centre (NMC) at Camp Springs (USA) through the Integrated Global Ocean

Services System (IGOSS, 1977). The OI SST series comprehend yearly means from January 1982 to January 1997. We chose a local area coverage (LAC) given by a 2º Lat/1º Long cell centred at Lat 64º 00'' and Long 25º 30''. It was, further assumed, that (i) any short and medium term tendencies detected for the LAC west of Iceland may be representative for the sea surface in the remaining of the areas where Icelandic cod spawns and juveniles are recruited and (ii) OI SST series may be related to demersal temperature and oxygen conditions which may be key factors for recruitment in cod.

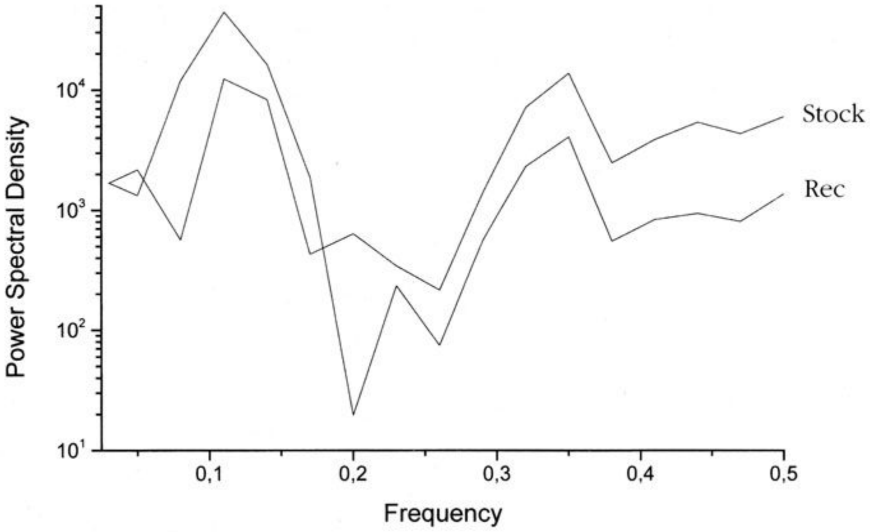

Fig 3.2.2. The spectral density of the smoothed stock-recruitment series In Icelandic cod, years 1956-1997. The highest peaks correspond to periods of approximately 10 years. Stock = spawning stock; rec = recruitment.

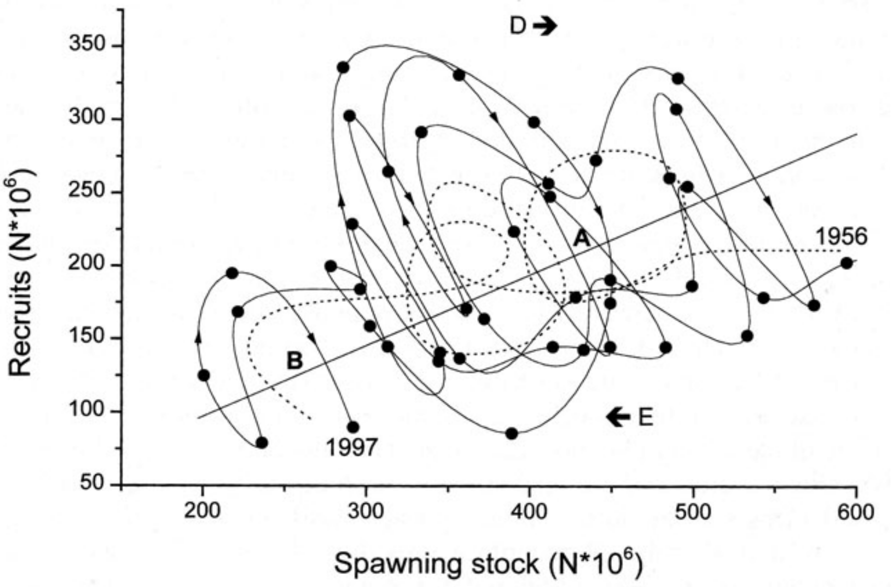

Figure 3.2.4. The stock-recruitment relationship in Icelandic cod both interpolated by a cubic spline and smoothed (dotted line). A, B and C represent a high equilibrium, an intermediate and a low equilibrium state. Density-dependent compensation and depensation are represented by the arrows on the spline. Also, D and E represent density-independent compensatory and depensatory transitions; the 1956 and 1997 labels are the start and end year of the series, respectively.

3.2.4. The model.

The SR system, in our model, is proposed to consist of two kinds of coupled, cyclic phenomena which operate similarly, within the same temporal scale, but are due to different causal mechanisms. The suggested criteria are as follows:

(i) Highly non-linear, density-dependent medium term (≅ 10 years) oscillations which may exhibit behaviour ranging from limit cycles to chaos (A-C in Fig. 3.2.4): this kind of regular fluctuation is assumed to (i) turn around stable, variable equilibria (E_i, i = 1 ... m) which are related to both variations in carrying capacity (K_i, i = 1 ... m) and mean numbers in spawning stock and recruits; (ii) keep similar geometric distances in relation to the equilibrium state SR values are turning around, making up orbits of stability and (iii) be due to the interaction between density-dependent population growth (induces compensation), mortality (induces depensation) and delays between short and medium term external disturbances and recruitment. Also, a variable minimum viable population ($0 < K_0$) is assumed under which stock and recruitment may not rehabilitate due to depensatory dynamics at low spawning stock sizes, a mechanism which may imply the extinction of commercial fishery;

(ii) Compensatory and depensatory, density-independent transitions (▪ 3-5 years on either phase) between equilibria which make up medium term, non-linear oscillations, governed by both the environment and fishing mortality (D, E in Fig. 3.2.4). As the time length of these regular variations may be shorter than that of density-dependent oscillations, different orbits of stability may overlap. Furthermore, K_i is assumed to variate due to external cyclic, quasi-cyclic or random-shock perturbations inducing such density-independent transitions: as the external environment becomes either benign or more stressed, stock and recruitment may shift towards higher and lower equilibria, respectively. Also, fishing mortality is considered as an external perturbation limiting the carrying capacity of an equilibrium: as numbers decrease due to fisheries, the SR relationship may shift towards lower equilibria with lower carrying capacities. However, any shifts towards the ceiling of an equilibrium and, hence, towards higher equilibria may be limited by fishing.

Both of the described mechanisms are coupled due to the development of the dynamic system: the SR relationship may evolve and return within a wide range of stable, variable equilibria which are dynamically linked and partially dependent on each other. Both links and dependencies between equilibria may arise due to (i) the plasticity of individuals and the cohort-population to, gradually, adjust to external perturbations within a dynamic continuum; (ii) the interaction between critical thresholds allowed in each equilibrium state and (iii) dependencies due to the effects of past disturbances. Also, as the SR relationship shifts towards the ceiling or carrying capacity (K_i) of a particular equilibrium state (E_i), the later switches from attractor to repellor allowing the shift to the upper equilibrium (E_{i+1}) which, now, becomes the new attractor. Furthermore, a similar mechanism may apply as the SR relationship shifts towards the floor of an equilibrium: as the carrying capacity (K_{i-1}) of the preceding equilibrium state is approached, E_i becomes a repellor and E_{i-1} an attractor allowing the shift towards the lower equilibrium state. Attractor-repellor switches may be caused both by the intensity and degree of external changes such as variations in K_i and levels of fishing mortality. Within our framework, the carrying capacity in each equilibrium state is regarded both as a critical threshold allowing transitions between equilibria and a link between attractors and repellors. Moreover, as the SR relationship shifts towards either higher or lower equilibria, the amplitude between maxima and minima may diverge and converge, respectively. Different orbits of stability may show different degrees of stretching (divergence) or shrinking (convergence) due to density dependence at higher and lower numbers, respectively. Stretching may be limited by K_{max} or highest allowed ceiling in the SR system, a threshold which will shift the SR relationship towards lower equilibria and shrinking may be limited by K_0 which is a critical threshold where density-dependent oscillations may cease, implying the extinction of the commercial fishery due to sustained low catches per unit of fishing effort. In the proposed framework, also K_0 is variable: while disturbances are low, it may tend to zero allowing a logistic kind of increments within the lowest equilibrium state of the SR system whereas it will increase and become an unstable equilibrium as external stress increases. Hence, at low spawning stock and recruit numbers, our approach allows a minimum viable population which may either be relatively low while the external environment is benign or high as external stress increases. Also, K_0 may become an unstable equilibrium if the intensity of external disturbances (environment and/or fisheries) increase, upon the remaining of the spawning stock, implying a shift of the SR relationship towards zero. In such a dynamic system, high and constant levels of fishing mortality may shift the SR relationship towards lower equilibria when either type of depensation is operating. Furthermore, shrinkage may be unavoidable when high levels of fishing are carried out under both types of depensation: this implies that 'surplus' yield harvest strategies may, solely, be applied when compensatory mechanisms have operated. Also, within a certain orbit of stability, high and persistent fishing may be viable during density-dependent depensation as far as it is not combined to other medium term external disturbances affecting recruitment success. Otherwise, the combined effect from both fishing mortality and environmental stress may shift the SR system towards low equilibria implying the collapse of the fishery. Solari et al. (1997) suggested that stock and recruitment in Baltic cod shifted to a low equilibrium state, nearby K_0, due to high levels of fishing mortality when both types of depensation were operating, simultaneously. Also, in 1977, when the spawning stock, in the Baltic Sea, was about to more than double, fishing mortality was higher ($F = 0.93$) than during 1984 ($F = 0.90$) when a shift to lower stock sizes followed. Hence, it was, further, suggested both that (i) delays affecting stock and recruitment should be considered; (ii) high fishing mortality may be allowed during the late stages of strong compensation and (iii) a relatively minor reduction in the level of captures might not change the SR trend under density-independent depensation.

To synthesize the proposed criteria, recruitment, R, is defined in Equation 3.2.1 as the summation of non-linear functions (f_i) of spawning stock (S_i) given by

$$R \cong \sum_{i=1}^{m} f_i^{(g)}\left(S_i\right) \qquad (3.2.1)$$

where i = 1 ... m is the number of equilibrium states in the SR relationship, being m the highest allowed equilibrium where the SR system is limited by K_{max} and g represents either of the base functions, $f_i^{(1)}$ or $f_i^{(2)}$, proposed below.

Several non-linear functions may be chosen to describe the dynamics of anyone specific SR relationship. On the one hand, we chose $f_i^{(1)}$, (Equation 3.2.2, Fig. 3.2.1) as the base function for the additive approach in order to describe SR systems which may be, mainly, controlled by variations in K_i. In this base function, given by

$$f_i^{(1)} = \frac{a_i \cdot (S)}{(S-b_i)^2 + c_i} \qquad (3.2.2)$$

the equilibrium state is controlled by the coefficients a_i (natural rate of increase), being b_i and c_i the density-dependent mortality entries. Also, values of b_i will define the ranges of spawning stock for which the equilibrium state may arise. All of these coefficients will define each equilibrium state and their values may be fixed. The summation of the $f_i^{(1)}$ type of base function may be appropriate to describe SR systems where the following is observed: (i) equilibria are clearly defined and orbits of stability do not overlap; (ii) time span of the density-independent oscillations is relatively longer than that of the density-dependent and (iii) spawning stock and recruit numbers are positively related. In our view, this base function may be fit to describe SR systems in relatively closed seas, estuaries and lakes where K_i may be the main factor controlling the system. For instance, we used $f_i^{(1)}$ in an approach to describe the SR system in Baltic cod where salinity and oxygen-temperature may be limiting factors both for recruitment success, shifts towards higher equilibria and the rehabilitation of the spawning stock (Solari et al., 1997). On the other hand, we chose $f_i^{(2)}$ (Equation 3.2.3, Fig. 3.2.5) as the base function in order to describe the SR relationship in Icelandic cod, a system whose orbits of stability, partially, overlap and appear to be, mainly, controlled by fishing mortality rather than by changes in K_i. Key features in this function are that (i) it is local and it decreases monotonically away from a central point and (ii) it is both suitable and flexible for the additive approach as it allows to describe highly complex dynamics. Hence, $f_i^{(2)}$ is given by

$$f_i^{(2)} = R_{max(i)} \cdot e^{-\varepsilon_i (S-S_i)^2} \qquad (3.2.3)$$

where $R_{\max\,(i)}$ is the maximum recruitment for the spawning stock value S_i (centre of $f_i^{(2)}$) which given by

$$S_i = S_{0i} - \Delta \qquad (3.2.4)$$

where Δ represents the difference in spawning stock numbers between the equilibrium point and the centre of the function. Furthermore, after substituting (4) into (3), the parameter ε_i is given by

$$\varepsilon_i = \frac{1}{\Delta} \cdot \log\left(\frac{R_i}{R_{0i}}\right) \qquad (3.2.5)$$

which determines the width of the symmetric function. Once the equilibrium point as well as R_i and Δ are known, $f_i^{(2)}$ may be fitted to the corresponding orbit of stability. The summation of the $f_i^{(2)}$ type of base function may be appropriate to describe SR systems where the following is observed: (i) equilibria are less clearly defined and orbits of stability may overlap; (ii) the time spans of both density-independent and density-dependent oscillations are similar and (iii) spawning stock and recruitment numbers either show a relatively weak, positive relationship or recruitment remains at similar levels across several intermediate and high spawning stock densities. However, recruitment will decrease significantly once the SR system settles onto low equilibria at low spawning stock numbers. In our view, the $f_i^{(2)}$ base function may be suitable to describe SR systems in relatively open seas where fisheries may limit shifts towards both K_i, upper equilibria and K_{max}.

3.2.5. Results and Discussion.

We have fitted the SR data to the functional form proposed by Shepherd (Sh, 1982) given by

$$R_{Sh} = \frac{\alpha \cdot S}{1+\left(\frac{S}{K_{Sh}}\right)^{\beta}} \qquad (3.2.6)$$

where R_{Sh} is recruitment, S is the spawning stock and K_{Sh} the carrying capacity or threshold abundance above which density-dependent effects dominate. The parameters α and β are referred as the slope at the origin and degree of compensation involved, respectively. This approach could unify, within a single framework, both the classical dome-shaped (for $\delta > 1$) and asymptotic (for $\delta = 1$) functional forms proposed by Ricker (1954) and Beverton-Holt (1957), respectively and it determines, through least squares, a representation of mean SR values.

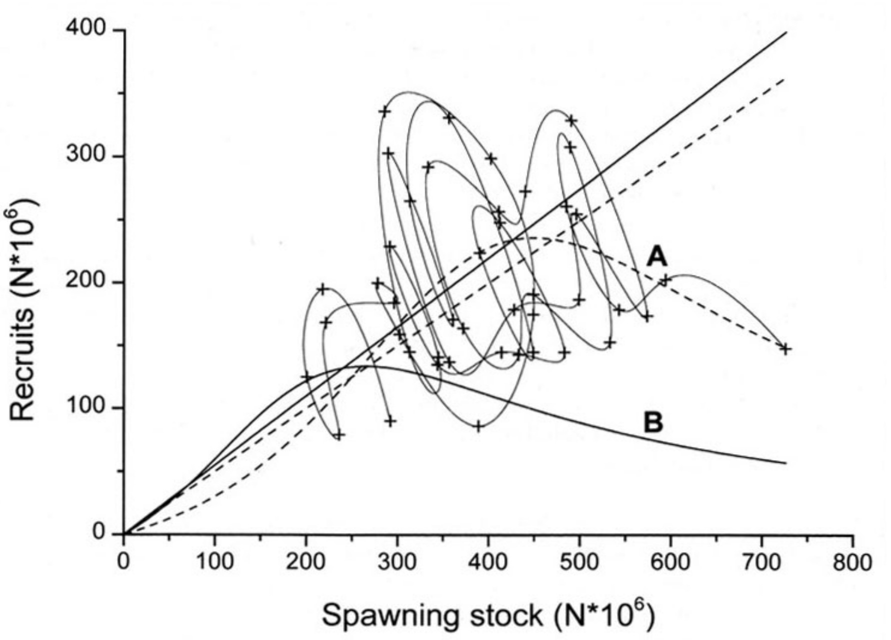

Figure 3.2.5. The stock-recruitment relationship in Icelandic cod both interpolated by a cubic spline and smoothed (dotted line). A, B and C represent a high equilibrium, an intermediate and a low equilibrium state.

The curve fittings according to both our and the Shepherd models (equations 1, with base function $f_i^{(2)}$ incorporated, and 6, respectively) as well as 4 cases of local, stability analyses for $\mu_{1...4}$ are shown in Fig. 5: after fitting the data, the Shepherd function will return mean values of α and β as well as a single K_{Sh}. All of these parameters will define a single equilibrium state (E_{sh}) which is the intersection between the fitted Shepherd curve and the replacement line: stock and recruitment is assumed to be both attracted to and limited by E_{sh} and K_{Sh}, respectively. Also, the curve fit from our approach describes the SR relationship as a relatively complex, dynamic system with multiple replacement lines and carrying capacities as well as multiple, dynamically linked, equilibrium states. The intersection between both of the curve fits is the point [R_c, S_c] which we have used as the initial equilibrium in our approach: in this way, we have considered the temporal evolution of the SR system (i.e. it developed from relatively high and stretched equilibria to a low and shrunken equilibrium state between years 1956-1997) and used the Shepherd function as a 'control' or standard to discuss whether our theoretical framework may be suitable to describe the dynamic features of this relationship. Also, the quotient between R_c and S_c (Equation 3.2.7) will be μ or slope of the replacement line which is given by

$$\mu = \frac{R_c}{S_c} \tag{3.2.7}$$

while the inverse of μ or S_c/R_c will be the spawning stock production per recruited numbers. Moreover, each orbit of stability includes a particular replacement line which may be determined by the degree of external disturbances (environmental or fisheries) affecting both recruitment and the spawning stock: multiple replacement lines are proposed due to (i) the dynamics within and between orbits of stability may range from chaos to cycles to a quasi-standstill state with no clear oscillations; (ii) disturbances may bias the structure of the population towards certain age classes whereby the quality of the reproductive output (i.e. mean egg size, floatability and offspring survival), recruitment and, hence, the spawning stock production per recruited numbers may change at different levels of numbers-at-age and (iii) environmental heterogeneity and patchiness, seen as the dynamic qualities of different spatio-temporal locations or multiple external states affecting the SR system, may change as scales and locations change. Moreover, we have included four local stability analyses for the equilibrium states E_m ... E_{m-3} in order to show how the proposed SR system may be stable at several levels of numbers and how shifts between equilibria are linked. Assuming that μ may be positively related to fishing mortality and that ceilings and floors will depend on both density dependence and external disturbances, the following features may be described: (i) for $\mu_1 = 0.3671$ and $\mu_2 = 0.55$ neither of the equilibria (E_m, E_{m-1}) show neither ceiling nor floor: these [K_m and K_{m-1}] may appear as the degree of external disturbances change affecting the stretching of the orbits. Also, although the level of exploitation or value of μ increases, recruitment remains at similar levels across a certain range of spawning stock densities; both of these cases may describe the coupled dynamics of Icelandic cod at relatively high and intermediate levels of numbers while the SR system is being governed by fishing mortality rather than by density-independent depensation mediated by variations in K_i; (ii) for $\mu_3 = 0.78$, the SR system has, further, shifted to a lower equilibrium state (E_{m-2}) where the corresponding orbit of stability shows a reduced degree of stretching with significantly lower numbers of spawners and recruits due to an increased disturbance level; in this case, external disturbances imply that the orbit of stability is limited both by a ceiling (K_{m-2}) and a floor ($K_{0\ m-2}$); (iii) for $\mu_4 =$ 1.2 which may represent an extremely high level of fishing mortality, our model describes persistency at a low and highly shrunk orbit of stability while the Shepherd approach predicts instability and extinction. Also, K_{m-3} and K_0 represent: (i) the floors of the equilibrium states E_{m-2} and E_{m-3}, respectively; (ii) the spawning stock values below which the SR relationship may shift towards lower equilibria and (iii) the carrying capacities for the immediate lower equilibrium states, respectively. Furthermore, K_{max} and K_0 are the variable, overall ceiling and floor of the SR system, respectively: on the one hand, K_{max} is the maximum allowable carrying capacity and any spawning stock values surpassing this ceiling will induce a shift towards lower equilibria; on the other hand, K_0 is the minimum viable population allowed and represents a critical value below which density-dependent oscillations may either cease or tend to zero as K_0 becomes an unstable equilibrium. Also, $R_{(K\ max)}$, is the maximum allowable recruitment and any values surpassing this ceiling will lead to lower equilibria. Furthermore, $R_{(K\ m-2)}$, $R_{(K\ m-3)}$, and $R_{(K0)}$ represent the ceiling in recruitment for their respective equilibria and the threshold above which the SR relationship may shift towards higher equilibrium states while $R_{(K\ max)}$, $< R_{max}$. Also, as maximum recruitment values approach the replacement line, the SR relationship comes into a critical stage where perturbations may induce shifts towards either higher or lower equilibria.

It should be stressed that neither $f_i^{(1)}$ nor $f_i^{(2)}$ alone but the summation of functions make up our approach: there is no evidence in the field data to assume the SR relationship is governed by a single attractor and a global carrying capacity but rather by multiple attractors-repellors which are dynamically linked by multiple carrying capacities through which stock and recruitment may, persistently, evolve and return between a wide range of equilibria allowing for stable, periodic and chaotic dynamics. Garcia (1998) and Sharp et al. (1983) suggested that the Hokkaido sardine series were characterized by loops and proposed an oscillating system consisting two strange attractors, linked by some transitional shifts, operating at two different levels of spawners and recruits. Also, Berg and Getz (1988) suggested that stock and recruitment, in a sardine-like population, moved along a path or attractor in some higher dimension coordinate system; Conan (1994) observed that lobster and snow crab landings in Atlantic Canada may follow two orbits of stability or cycles; Powers (1989) suggested chaotic behaviour for a 2 species system of fish and Tyutyunov et al. (1993) demonstrated cycles of different period and chaos in population dynamics of perch from 10 lakes. Moreover, Caddy (1998) pointed out several other cases, in semi-enclosed areas, where SR dynamics could be linked to oscillatory phenomena: (i) an apparent 9-18 year periodicity for the Bay of Fundy scallop stocks (Caddy, 1979); (ii) a 12 year, fishing-effort-independent periodicity in the landings of both hake and red mullet at the island of Mallorca in the Mediterranean Sea (Astudillo and Caddy, 1986) and (iii) a 12-13 year oscillatory pattern in the catches of the Adriatic sardine. In our view, fitting the data from SR systems with several orbits of stability to the Shepherd approach which may solely incorporate a single, stable equilibrium and value of carrying capacity might not allow us to understand the dynamics of an SR system affected by both modulated perturbations and feed-back mechanisms both operating at different spatio-temporal scales and which may show several dynamical patterns. Also, while hypothesis testing based on the Shepherd approach may be relatively robust for series with limited degrees of freedom, the classical framework has neither the capacity to describe nor link such complex dynamics: there is no support, in the field data, to assume a single equilibrium state but rather several equilibria with corresponding carrying capacities and replacement lines as well as a minimum viable population under which the extinction of the fishery occurs. Rothschild (1992) suggested that populations reduced by fishing or anthropogenic substances which compensate for reductions in vital rates may easily transit among stable, periodic and chaotic population dynamics. Also, Conrad (1986), Schaffer (1986) and Kot et al. (1988) suggested that chaotic mechanisms would serve to maintain the adaptability of the population. Hence, we may suggest there are several conceptual advantages in the proposed theoretical framework over the Paulik and Shepherd approaches. This may justify our model, on an ad hoc basis, to attempt approaching the SR system in Icelandic cod as well as other cases both in semi-enclosed and open areas. The criteria are as follows:

(i) The new framework is sufficiently flexible to (a) fit SR systems which may be governed by either changes in the environment, by anthropogenic disturbances such as fishing mortality, pollution and habitat changes or a combination of both; (b) allow for the continuity of stock and recruitment within a wide range of density-independent and density-dependent limits of variation whereby all of the known population mechanics (i.e. density-dependent, density-independent and inverse density dependence) may be dynamically linked, in a continuum, by multiple ceilings and floors all of which may be described by a relatively simple equation; (c) contribute to the understanding of the causal mechanisms behind the development of equilibria, how these may be linked to each other and how and why shifts between equilibria may arise at one or several spatio-temporal scales;

(ii) At high and intense levels of fishing mortality, our approach may still describe persistency at low and highly shrunk orbits of stability while the Shepherd approach predicts extinction. The present model allows several dynamic features at low numbers: (a) the minimum viable population is unstable and variable allowing for changes in both the environment, external mortality sources and the rehabilitation of stock and recruitment; this implies that K_0, in our framework, may either tend to zero while the external environment is benign or increase as external stress increases; also, as K_0 approaches zero, while the environment is extremely benign, the model allows for a logistic or Shepherd type of population increase; (b) orbits of stability may be stable either at a quasi-standstill with no clear, density-dependent oscillations, periodic (limit cycles) or chaotic within the limits of variation corresponding to low equilibria. These features may allow to explain why SR systems may persist at extremely low numbers;

(iii) Independent and partially-dependent equilibria. Our additive approach allows description of highly complex, coupled dynamics while the functions representing each of the orbits in the concatenation are mathematically independent. This feature allows the flexibility to describe a wide range of dynamical behaviours at several spatio-temporal scales and, while the orbits may be linked, the model is still simple. Furthermore, transitions between equilibria may be more explicitly identified, described and mathematically controlled with regard to both density-dependent and density-independent mechanisms. In a multiplicative model, such as the Paulik approach, there is a strong (mathematical) dependency in the concatenation of functions implying a lack of flexibility to represent many dynamical situations as, for instance, certain orbits of stability may shrink and disappear, temporarily or permanently;

(iv) Higher equilibria may disappear. As series evolve, higher orbits of stability may come to disappear from the SR system: due to medium and long term, negative, disturbances, the SR system may shift towards lower equilibria and be, either temporarily or permanently, settled around low orbits of stability. For instance, such cases may occur when stocks cannot rehabilitate due to recruitment failures caused by over fishing combined to environmental perturbations or due to permanent environmental changes. Malmberg and Blindheim (1994) suggested that the relative stability of temperature and salinity conditions off the northern and eastern coasts of Iceland was broken, since 1965, due to flow changes in the Irminger (warm) and East Greenland (cold) currents implying important ecological impacts over the North Icelandic Shelf which is a nursery area for the Icelandic cod population;

(v) Several maxima and minima may be incorporated, in the same relationship, allowing for description of equilibrium states at different spatio-temporal scales, substocks and/or age classes;

(vi) Inverse density-dependence is allowed. At low population levels, reproductive success may be reduced due to both internal and external factors which may affect the fecundation of spawned eggs: probabilities of encountering male sexual cells, diffusion due to hydrodynamic processes and size related qualities such as egg volume and floatability. All of these factors may become critical at low spawning stock numbers implying a shift from relatively higher equilibria towards K_0. This may imply that the SR relationship may no longer turn around stable equilibria but will be at a quasi-standstill state with no clear oscillations, implying the extinction of the commercial fishery due to sustained low catches per unit of fishing effort. In our framework, unless the intensity of disturbances increase during a near-K_0 stage, the extinction of the commercial fishery per si may imply the SR relationship will, subsequently, shift upwards to a low equilibrium state where density dependent mechanisms start operating again. This phenomenon may occur with delays of 3-6 years (in cod) while the rehabilitation of the spawning stock is underway. Hence, it may be relevant for a conceptual framework to allow for inverse density-dependence since it cannot be ruled out a-priori and may show up at some stage while there is recruitment over fishing combined to other external disturbances. Myers (1995) reported likely inverse-depensatory trends for Icelandic spring-spawning herring, Pacific salmon and sardines and Georges Bank herring and a similar trend was suggested by Solari et al. (1997) for Baltic cod. Furthermore, we put forward for consideration the question whether stock and recruitment in Icelandic cod is being affected either by meso scalar or global changes in temperature and possible derived changes in the oceanographic regimes affecting survival of young cod. Fig. 3.2.7 shows the normalized recruitment (continuous line) and OI SST (dashed line) series between years 1982-1997 where recruitment values were delayed three years to match the temperature data. Although degrees of freedom are limited, the negative trend in OI SST for the LAC we chose is highly significant ($R = 0.688$, $p < 0.005$, $df = 15$). Also, stock and recruitment shows a slight negative trend and settled into a low and highly shrunk equilibrium state during the early 1990's when temperature values were about the mean. It is our view that the combined effects from high and intense fishing mortality and a negative meso scalar trend in temperature may be two key factors for the settlement of the low equilibrium state.

3.2.6. Acknowledgements for this section.

Dr.s Gunnar Steffanson (Marine Research Institute, Reykjavik, Iceland) as well as *John Caddy* and *Serge Garcia* (FAO/Fishery Resources Div. Rome, Italy) are acknowledged for their comments and encouragement to apply our non-linear approach upon the present and other cases; *Dr. Diane Stokes* and *Dr. Richard Reynolds* from the Coupled

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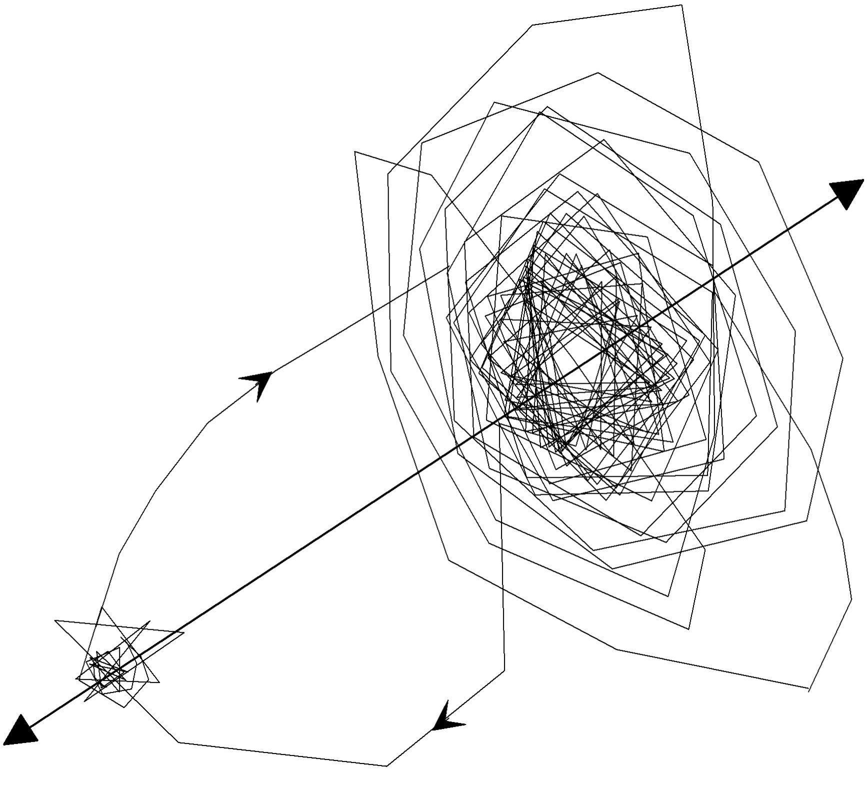
CHAPTER 3.3

On the Dynamics of Skipjack tuna: Similarity at Several Scales



3.3 On the Dynamics of Skipjack tuna: similarity at several scales.

3.3.1 Abstract.

Skipjack tuna fishery landings from three spatial scales (Port of Mogan, Canary Islands area and CECAF Division 34) are studied. Series are tested for homogeneity and auto- and cross correlated. Periods are shown through spectral densities and phase spaces are studied. It is proposed that skipjack stock and recruitment to the area consists of a two-steady state system with a high and a low equilibrium state, similar at three spatial scales. Two general equations, a multiplicative and an additive approach, are suggested to describe the system. The dynamical features of the system are related to variable carrying capacity (ceilings), minimum populations (floors), multiple stable equilibria, compensatory and depensatory dynamics, extinction of the commercial fishery and migration and recruitment through a fractal system. It is concluded that the proposed framework may allow for the description of complex processes governing migration and recruitment, link population dynamics between spatial scales and forecast recruitment to the area and overall dynamics from local series at certain spatial locations. Finally, a theoretical, self similar system is simulated and set in a dynamically referenced frame, in order to discuss the concept of similarity at several scales.

3.3.2 Introduction.

The tuna resources in the eastern Central Atlantic have been the object of both an intensive fishery for over 30 years and numerous studies conducted under the coordination of the International Commission for the Conservation of Atlantic Tunas, ICCAT (Fonteneau and Marcille, 1993).

The skipjack tuna (*Katsuwonus pelamis*, henceforth referred as "skipjack") supports an important commercial fishery across the eastern Atlantic from the Gulf of Guinea to the south-western Irish coast (ICCAT, 1986). Tag recovery studies have indicated that skipjack migration routes lie from the south-east toward the north and north-west Atlantic (Ovchinnikov et al., 1988) and catches on the highly migratory tuna stocks are due multigear fisheries (Fonteneau, 1991). Also, both the spatio-temporal distribution and abundance of skipjack tuna have been related to causes such as environmental requirements and feeding (Ramos et al., 1991), upper ocean dynamics (Ramos and Sangrá, 1992), hydro climatic factors (Pagavino and Gaertner, 1994), prey abundance (Roger, 1994; Roger and Marchal, 1994), thermal habitat (Boehlert and Mundy, 1994), schooling behaviour (Hilborn, 1991; Bayliff, 1988) mesoscale frontal ocean and upwelling dynamics (Fiedler and Bernard, 1987; Ramos et al., 1991) as well as several other aspects beyond the scope of the present paper. Skipjack tuna appears to be able to adapt the feeding strategy to environmental conditions preying upon what it encounters (Roger, 1994) and the 18 degree C isotherm and 3 ml oxygen per litre isoline are considered as lower limiting factors (Piton and Roy, 1983). The exploitation rate on most tuna stocks has been constantly increasing and assessments have been inefficient in estimating the real maximum sustainable yield of those stocks (Fonteneau, 1997). In the Atlantic, tuna catches were suggested to be both underestimated and misreported (Wise, 1985) and despite the high level of fishing effort, recruitment over fishing has never been suggested for skipjack (Fonteneau, 1987).

The aims of the present study were to: (i) analyze three independent, skipjack fishery landing series representing catches from three different spatial scales; (ii) determine whether there may be any similarity between the series and (iii) discuss new concepts to study the evolution of both recruitment-to-the-area and the dynamics and future approaches to skipjack populations in the Eastern Central Atlantic.

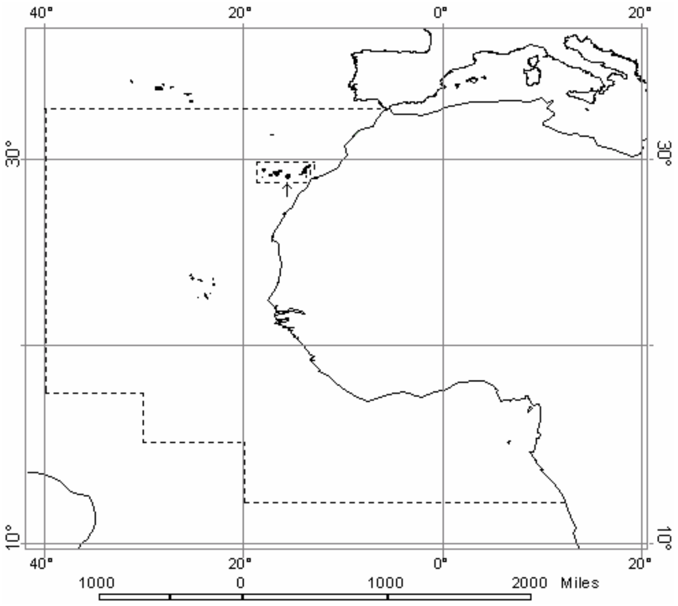


Figure 3.3.1. Three spatial scales of skipjack tuna sampling. The CECAF (Committee for Eastern Central Atlantic Fisheries) Division 34 (larger area indicated by the dashed line; from Gibraltar to the Congo river, Lat. 36°00'N-6°04'36"S, Long. 12°19'48"E-5°36'W); the Canary Islands archipelago (minor area indicated by the dashed line, Lat. 29°40'N-27°10'N, Long. 13°W-18°20'W) and the Port of Mogan (local waters off the southern shore, island of Gran Canaria, Lat. 27°55'N-Long. 15°47'W, indicated by the arrow). Map modified after FAO (2001).

3.3.3 Data.

The skipjack fishery series analyzed herein (annual catches in metric tonnes, Tn) were the following: (i) Landings due a local bait fishery at the Port of Mogan (Lat. 27°55'N-Long. 15°47'W, henceforth referred as the "Mogan series"), island of Gran Canaria (Canary Islands, Spain), years 1980-96 according to Hernández-García et al. (1998); (ii) Overall pooled landings due local bait fisheries for the whole of the Canary Islands area (Eastern Central Atlantic, Lat. 29°40'N-27°10'N, Long. 13°W-18°20'W, henceforth referred as "Canarian series"), years 1975-93 according to Ariz et al. (1995); (iii) Pooled landings due multigear (bait, long-line and purse-seine) both oceanic and coastal fisheries within the CECAF (Committee for Eastern Central Atlantic Fisheries) Division 34 (from Gibraltar to the Congo river, Lat. 36°00'N-6°04'36"S, Long. 12°19'48"E-5°36'W; henceforth referred as the "CECAF series"), years 1972-96 according to Fishstat/FAO (1999). Fig. 3.3.1 shows the aforementioned spatial scales (map modified after FAO, 2001): a point (waters off the Port of Mogan), a minor area (waters within the Canary Islands archipelago) and a relatively large ocean area (the CECAF area 34) and Fig. 3.3.2 the shows the skipjack series from each location.

3.3.4 Methods.

We standardized the series to the same scale (Z values with mean = 0) in order to facilitate both the analyses and visual comparison. We used both t-tests and autocorrelations to determine the homogeneity between the series and indications of auto similarity. Also, the Welch method (after Oppenheim and Schafer, 1975) was used to estimate the spectral density. The phase spaces (stock-in-area against recruits-to-the-area) were obtained by plotting data values from a certain year (N_t) against values the year after (N_{t+1}). Cross correlations were used to determine the degree of correspondence between the series. Furthermore, data values were fitted both by linear regressions through the origin (to determine a the "replacement line" or recruitment needed to replace the stock-at-spatial-location) and sixth order polynomials (to describe the dynamical features of the systems). To set the final, schematic example, we simulated sinusoidal waves with an arbitrary noise to represent the proposed system.

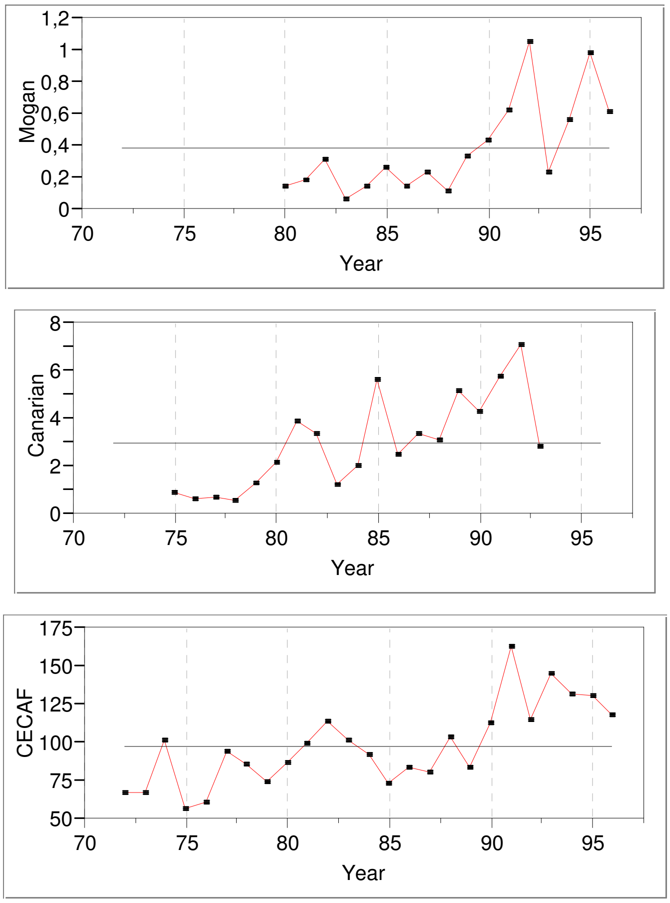


Figure 3.3.2. Skipjack tuna series (Tn*10^3) from a local bait fishery at the Port of Mogan (island of Gran Canaria, Canary Islands, years 1980-96), after Hernández-García et al. (1998); overall pooled landings due local bait fisheries for the whole of the Canary Islands area (years 1975-93), after Ariz et al. (1995) and pooled landings due multigear (bait, long-line and purse-seine) both oceanic and coastal fisheries within the CECAF Division 34 (years 1972-96), after Fishstat/FAO (1999). The catches represent sampling series from three significantly different spatial scales. The straight lines indicate the mean of the series.

3.3.5 Results.

Recruitment (R) in our framework is defined (Chapter 2, Equation 2.1.) as the summation of non-linear functions of spawning stock. This new approach can be applied to the plane N_t, N_{t+1} to describe dynamics in both migration and catches (recruitment to the area) in skipjack and link local and mesoscalar trends from different spatial scales, as well. Each equilibrium state may represent stock and recruitment to the area in a certain spatial location and link local and mesocalar dynamics. An m number of oscillatory phenomena ranging from limit cycles to chaos and inverse density-dependence are allowed in this system which may be approximated either by least squares using Equation 1 or by polynomial regressions incorporating three constants for each equilibrium state. The objective of the sixth order fittings we use is to describe in a simple way the multiple steady state cases we approach. Further aspects of this new model are well detailed in Solari et al. (1997).

We have assumed a positive relationship between the number of juveniles being recruited to the population and those entering the area of the fishery: this implies that the number of recruits-to-the-area in a migratory stock may increase as recruitment increases in the remote nursery areas. Also, we have regarded the analyzed series as statistically independent due the different sources and relatively large geographic range of the areas concerned: paired t-tests ($p < .001$ in all of the cases) showed the series may represent three significantly different levels of recruitment. Furthermore, in spite of the limited degrees of freedom in all of the series, the autocorrelation values were 0.42 ($p = 0.06$), 0.52 ($p = .01$, lag = 1) and 0.56 ($p = .003$, lag = 1) for the Mogan, Canarian and CECAF series, respectively: these results may suggest that there is a certain auto similarity or "memory" in the series implying that the skipjack stock a certain year may depend on the abundance in preceding years. Moreover, the spectral density of the series detected maxima around the periods of 3-4 years in all of three series (Fig. 3.3.5). Only fourteen years were common to all of the series and, consequently, the spectral analyses should be interpreted independently for each time series. Likewise, the cross correlations showed a certain degree of correspondence between the series: we tested for several time lags and the highest obtained values were .84 (Mogan-Canarias series, lag = 0), .56 (Canarian-CECAF series, lag = 1) and .68 (Mogan-CECAF series, lag = 1). The lag 1 between the CECAF and Canarian and Mogan series may be a consequence of the reduction of the spatial scale.

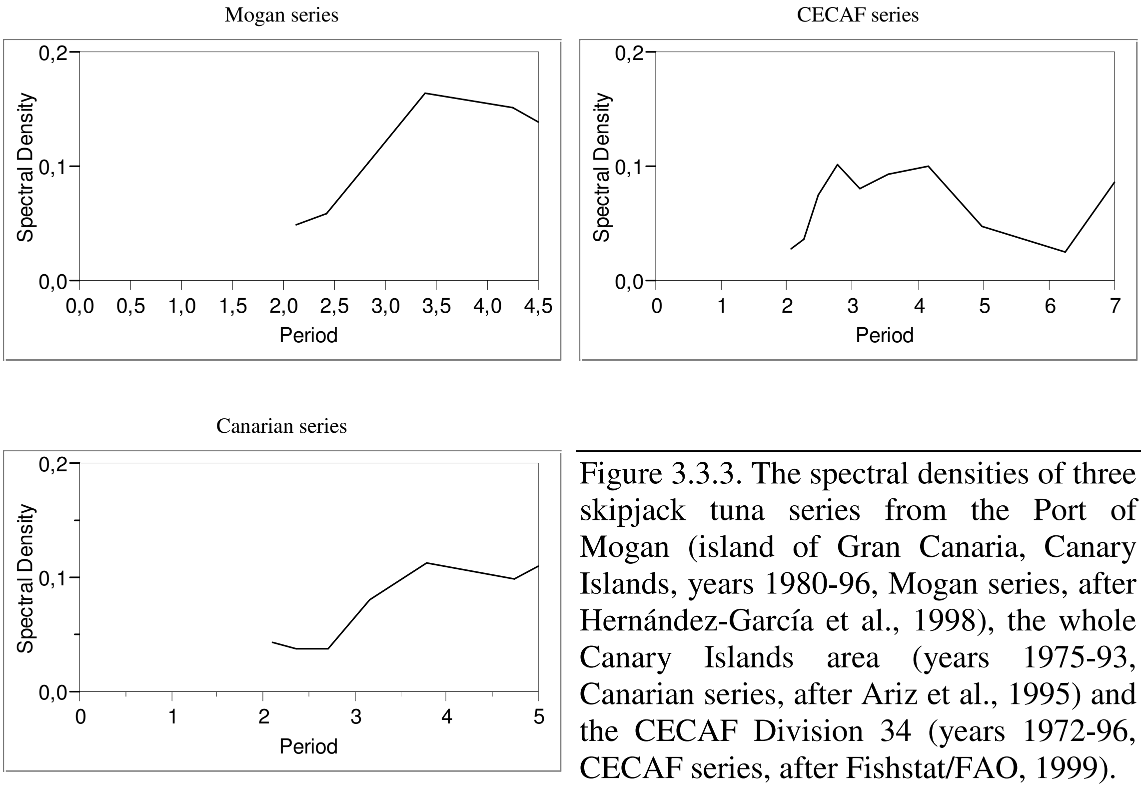


Figure 3.3.3. The spectral densities of three skipjack tuna series from the Port of Mogan (island of Gran Canaria, Canary Islands, years 1980-96, Mogan series, after Hernández-García et al., 1998), the whole Canary Islands area (years 1975-93, Canarian series, after Ariz et al., 1995) and the CECAF Division 34 (years 1972-96, CECAF series, after Fishstat/FAO, 1999).

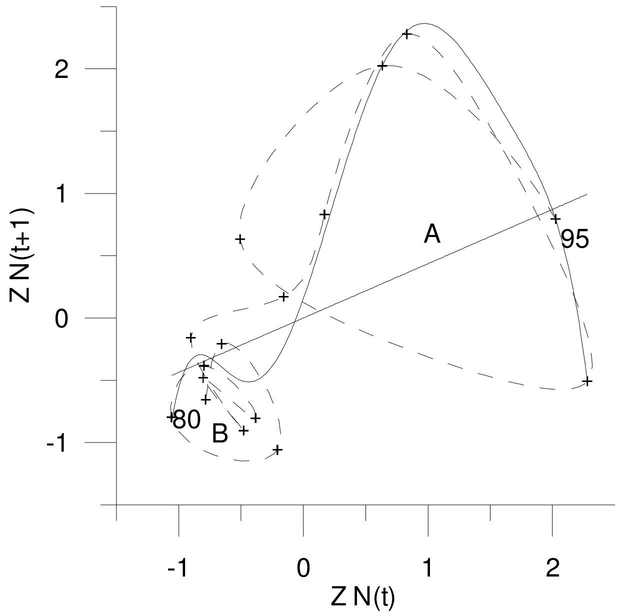


Figure 3.3.4. Phase space for the skipjack fishery landing series at the Port of Mogan (island of Gran Canaria, Canary Islands). The linear regression through the origin represents both the recruitment needed to replace the stock-at-spatial-location and overall equilibrium values. The 6th degree polynomial regression describe the evolution of the high and low steady-states indicated by "A" and "B", respectively. Z indicates standardized values and N_t and N_{t+1} the generation of the values; 80 and 95 indicate the start and end year of the plotted values.

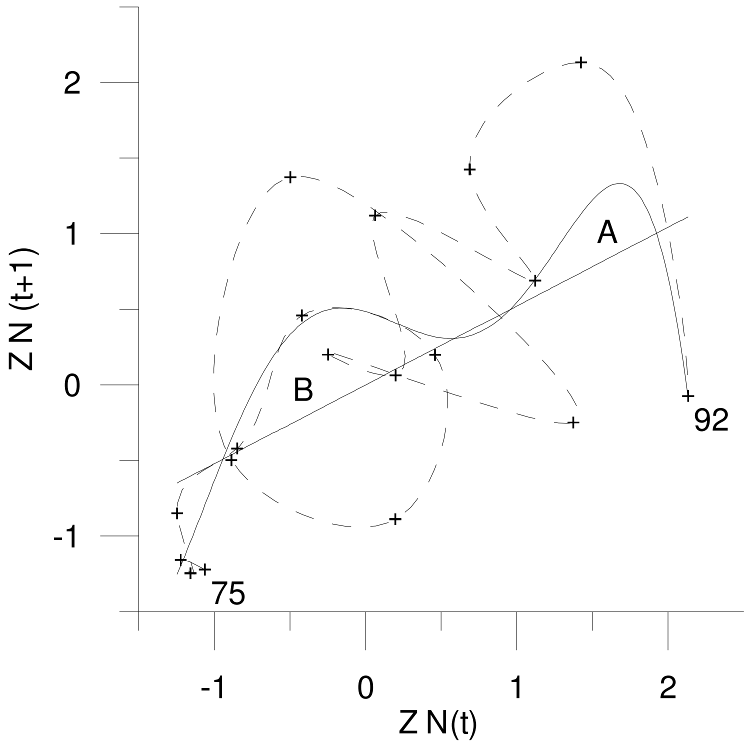


Figure 3.3.5. Phase space for the skipjack fishery landing series from the Canary Islands area (Eastern Central Atlantic). The linear regression through the origin represents both the recruitment needed to replace the stock-at-spatial-location and overall equilibrium values. The 6th degree polynomial regression describe the evolution of the high and low steady-states indicated by "A" and "B", respectively. Z indicates standardized values and N_t and N_{t+1} the generation of the values; 75 and 92 indicate the start and end year of the plotted values.

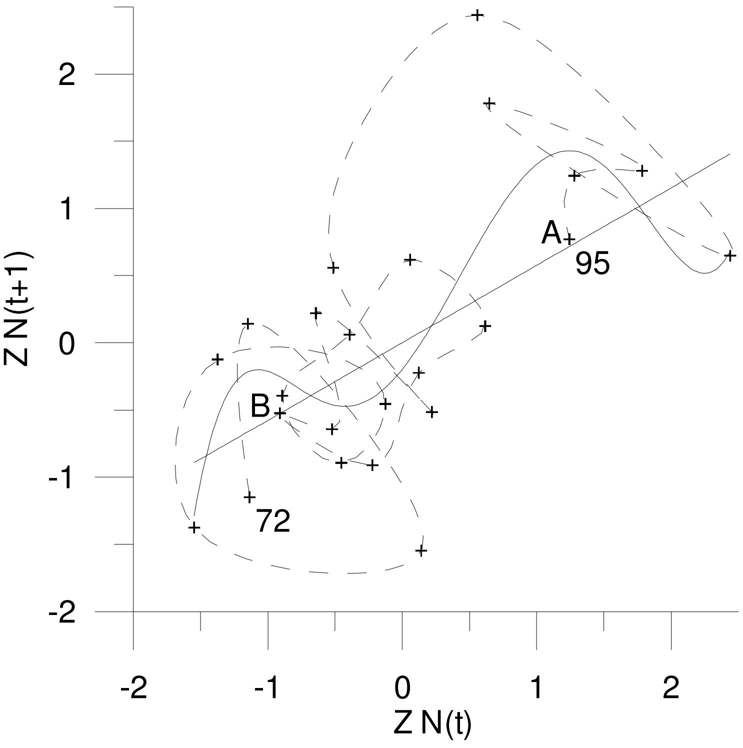


Figure 3.3.6. Phase space for the skipjack fishery landing series from the CECAF Division 34 (Eastern Central Atlantic). The linear regression through the origin represents both the recruitment needed to replace the stock-at-spatial-location and overall equilibrium values. The 6th degree polynomial regression describe the evolution of the high and low steady-states indicated by "A" and "B", respectively. Z indicates standardized values and N_t and N_{t+1} the generation of the values; 72 and 95 indicate the start and end year of the plotted values.

Fig. 3.3.6-8 show the phase spaces for the Mogan, Canarian and CECAF series, respectively. The linear regression through the origin represents both the recruitment needed to replace the stock-at-spatial-location and overall equilibrium values. Furthermore, the polynomial regressions describe the dynamical features which may be common to all of the three cases: (i) A relatively high equilibrium state (indicated by "A") with high levels of both captures and recruitment where maxima and minima diverge and (ii) a relatively low equilibrium state (indicated by

“B”) with lower levels of both captures and recruitment where maxima and minima converge. A summary of results from the linear and polynomial regressions are shown on Table 3.3.1. Also, there may be an indication of a third equilibrium state both in the cases shown in Fig. 3.3.7 (for years 75-78) and 3.3.8 (between “A” and “B”). Fig. 3.3.6-8 show the principal results in this paper. The plane N_t, N_{t+1} fitted by a third degree polynomial and a simple regression may allow us to easily understand the dynamics behind the data and both describe and link them through our multi steady-state approach. Other non-linear models may be used both to fit the data and obtain several equilibrium states. However, our approach can be used as an ad-hoc model because it allows a great flexibility and may link and explain most population dynamical phenomena (compensation, depensation, density dependence, density independence, inverse density-depensation and dynamical system behaviour) in a relatively simple framework taking into consideration different spatial scales and substocks. No references describing such a dynamical similarity at several spatial scales were found in the literature on skipjack tuna and we were able to detect this dynamical auto similarity while interpreting the data in light of our model.

	Linear trend			Polynomial (6th order)		
DF	R	F	p<	R	F	p<
15	0,44	3,35	0,09	0,92	7,77	0,01
17	0,54	6,55	0,05	0,77	2,63	0,08
23	0,59	11,62	0,01	0,70	2,66	0,06

Table 3.3.1. Summary of results from data fits upon the steady state systems proposed for the skipjack tuna series (standardized values) from three spatial scales (Port of Mogan, Canary Islands area and CECAF Divison 34). DF= degrees of freedom, R=regression value, F=F value, p=probability.

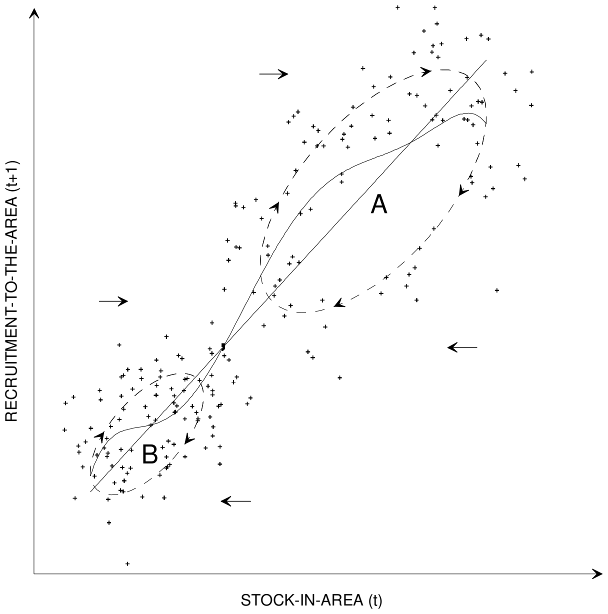


Figure 3.3.9. Theoretical in-area stock and recruitment system proposed for three spatial scales in the Eastern Central Atlantic (Port of Mogan, Canary Islands area and CECAF Division 34). The linear regression represents the replacement line and the polynomial fit describes the dynamical evolution of the system. A and B are the high and low equilibrium states, respectively. The dot represents the transition point between the steady states, being the floor of A and carrying capacity of B, respectively. Density-independent compensation and depensation are represented by the arrows → and ←, respectively. Orbits of stability are indicated by the dashed ellipses on which arrows represent density-dependent compensation and depensation. Data values are arbitrary and were generated by sinusoidal waves plus noise.

In order to illustrate the dynamical features we have proposed, we show, in Fig. 3.3.9, a schematic example on arbitrary data (sinusoidal waves plus noise) of a theoretical in-area stock and recruitment system where the following features are described:

(i) The linear regression represents an overall replacement line: while the system evolves above the linear fit, compensation operates and numbers grow (indicated by the arrow, →) whereas depensation operates under the replacement line implying that numbers decrease (indicated by the arrow, ←);

(ii) A high and a low equilibrium state represented by A and B, respectively. These orbits of stability (indicated by the dashed ellipses) are caused by oscillations due density-dependent compensatory and depensatory phases (indicated by the arrows on the ellipses). Also, the polynomial regression describes the two-steady state system, the evolution of equilibria and the shift between equilibria as both the floor of equilibrium A and the carrying capacity of equilibrium B are approached (indicated by the dot);

(iii) Also, density-independent transitions may occur due changes in the environment and fishing mortality: as the lower equilibrium state approaches the ceiling or particular carrying capacity (indicated by the dot), the system may shift towards a higher equilibrium through a density-independent compensatory phase. Moreover, while density-dependent depensation operates in the higher equilibrium state and the floor of A is approached, density independent depensation may shift the system towards the lower equilibrium state;

(iv) Maxima and minima converge as the system evolves towards the lower equilibrium and diverge as it shifts towards the higher steady state. Density-dependence may operate similarly in both equilibrium states but at different levels of numbers: on the one hand, oscillations may be larger in high equilibrium states as the systems evolves towards the maximum carrying capacity of the system (a critical value or overall ceiling above which the trajectory enters depensation, K_{max}); on the other hand, oscillations may become lower as the system evolves towards a minimum viable population (a critical value around which oscillations become small or non-existent implying the extinction of the commercial fishery).

The proposed two-steady state system may be described either by a multiplicative equation such as

$$R_a \cong f_1(S_A)\cdot f_2(S_B) \qquad (3.1)$$

or an additive model such as

$$R_a \cong f_1(S_A)+f_2(S_B) \qquad (3.2)$$

where R_a represents recruitment, $f_{1,2}$ are non-linear, three parameter functions and $S_{A,B}$ the stock-in-area for the equilibrium states A and B, respectively.

3.3.6 Discussion.

Although skipjack harvesting is subject to some form of international regulation, control is minimal and we have regarded it as an open access fishery: exploitation may be carried out in international waters on the migratory stock without any effective policy enforcement. In the present approach, recruitment-to-the-area is a key concept which describes a migrating population or stock entering the area of operation of the fishery. This concept is used, in part, due the lack of data on juveniles being recruited to the adult population and migrating from the nursery areas in the Gulf of Guinea. Also, we lack fishing effort data for all of the series.

Within the Canary Islands area, however, fishing effort may be assumed as relatively stable during the time span of the Mogan and Canarian series. Also, the largest skipjack individuals enter the area of the fishery twice a year as they return from Azores to the Gulf of Guinea passing through the Canary Islands area a second time. Furthermore, it may be argued that both the classical models and second order polynomial regressions could be more appropriate to fit the data, meeting mainstream modelling criteria. However, such classical approaches are inappropriate to describe the linked dynamics of multiple steady state systems (density-dependent and density independent compensation and depensation, orbits of stability, multiple carrying capacities and auto similarity at several scales). We need both conceptual frameworks and statistical techniques which will allow us to understand the dynamics behind the data and link changes in skipjack stocks to fluctuations in the environment. In our view, the system consists of multiple steady-states, distinct regimes, qualitatively similar which should be dynamically linked both to each other and the environment. A minimum of three constants are needed to describe each equilibrium state and allow the linkage between the steady-states. Furthermore, while the classical models and second order fittings may assume that residuals are either random or solely caused by noise, we have assumed that residuals may be a combination of both signal and noise: while dynamical structures may be an artefact of smoothing techniques (i.e. we may obtain cyclic-like patterns after several steps of smoothing upon random data), the temporal evolution and the structures observed in the phase spaces upon the standardized data showed that a multi-steady state system may be more appropriate to understand the mechanics behind the system. Also, the theoretical criteria we put forward may be useful to explain the processes governing both recruitment and stock dynamics in skipjack tuna in the

Atlantic and to develop new approaches for the preventive management of the migratory stock.

Fonteneau (1987) observed that recruitment over fishing has never been suggested for skipjack in the Atlantic. The steady states observed in the skipjack system appear to be persistent within relatively wide ranges of stability. Also, the stability of equilibrium states may be further enhanced by catch and effort oscillations as economical over fishing is being approached. However, several mechanisms could generate both recruitment over fishing and the (temporal) extinction of the fishery: on the one hand, environmental medium term disturbances in the nursery grounds may cause the skipjack system to shift towards low equilibria with decreasing amplitude between maxima and minima; on the other hand, both types of depensation combined to a relatively constant fishing mortality may imply that the skipjack system evolves towards an overall minimum viable population with no oscillations. Further aspects of the Discussion are referred to Section 3:7.

3.3.7 Migration through a fractal marine system.

While the studied time series showed quantitatively different, qualities such as dynamical similarity observed in the two-equilibrium system, memory and periodicity may be similar features to all of the cases. These results may open up an interesting field of work in the research on exploited skipjack populations in the Atlantic: the correspondence between the series and similarity in the phase spaces may suggest that stock and recruitment relationships may be caused by deterministic mechanisms with similar dynamics at several spatial scales. This may imply that we could (a) estimate complex processes governing recruitment and migration in skipjack; (b) link population processes between different spatial scales relevant to the dynamics of the migratory stock; (c) forecast recruitment in wider areas from local series at certain spatial locations and (d) estimate future recruitment in minor spatial locations from overall CECAF series taking into consideration the detected time lags. In order to, further, discuss these ideas, we simulated a self similar system through the iteration of the function $f(x) = x^2+m$. We allowed the function the random choice between two possible inverses (+1 or -1) and let the iteration run until we obtained an arbitrary number of data points (N=19851). The data was standardized and the system is shown in Fig. 3.3.10. All of the variables (R, IM), the initial value of the parameter (m) and number of iterations were arbitrary. In order to make up a dynamically referenced description of the data, we fitted the output to a linear regression, a sixth degree polynomial, a cubic spline (to show more detailed local dynamics) and 50 and 95% bivariate ellipses (also, confidence intervals), as well. Furthermore, we sampled the simulated series both randomly and sequentially to 10, 5, 1 and 0.1% of the total number of points (to resemble different spatial scales or sampling windows) and, in all of the cases, we obtained similar tendencies: as in the skipjack fishery, the simulated system showed results with similar dynamical patters at different sampling windows. While the tendencies remain similar at several scales, we may obtain different levels of numbers depending on the quadrant we carry out the sampling. As the skipjack stock migrates through the ocean, it will be affected by a multiplicity of external perturbations of dynamical nature: there is an increasing body of evidence suggesting that the upper ocean layer through which the skipjack is recruited and migrates may be both of fractal nature and affected by multifractal processes: the spatial distribution of foam and white caps (Kerman and Szeto, 1994), wind-wave breaking (Raizer et al., 1994) and breaking of waves (Kerman and Bernier, 1994), distribution of sea surface temperature (Fu, 1994; 1995), isotherm lengths and patterns of the sea surface temperature in mesoscale turbulence (Bunimovich et al., 1993) and fractal behaviour of the temperature isolines and properties of frontal regions (Marullo et al., 1993) may be examples of factors which determine recruitment patterns and spatial distributions in fishery areas. Also, such fractal structures in the ocean may explain the dynamical similarities we have proposed for the skipjack system at the three spatial scales: if a skipjack stock diffuses-advects through a fractal ocean with similar properties at several scales, we might expect the equilibrium states we observe in the skipjack system to show a certain degree of auto similarity, as well. Assuming the theoretical criteria proposed in our framework, we could develop a method based on remotely sensed data with which we could estimate the dynamics of one or several substocks of skipjack from a few spatial windows. Block et al. (2001) reported electronic, satellite tracked tag recovery data on both vertical-diagonal and transatlantic (Gulf of Mexico-Mediterranean Sea) migration of bluefin tuna. The incorporation of data which show depth boundaries in tuna migration combined to Sea Surface Temperature, recruitment-to-the-area and catches may allow for the determination of the dynamical 3-dimensional system (Latitude, Longitude, Depth) through which tuna migrates: a multi steady-state framework as proposed in our paper may incorporate all of the variables to describe this hyperspace. Such an approach could be critical both for the conservation of tuna and the preventive control of the fishery. Also, it may become the ground for the development of a formal theory for both system behaviour and migrations in skipjack and other tunas. Classical approaches assume both a single spatial scale, an equilibrium state and sole value of carrying capacity. It is critical to realize that a dynamical framework will enable us both to understand the temporal evolution of the skipjack system and the causal mechanisms behind the data.

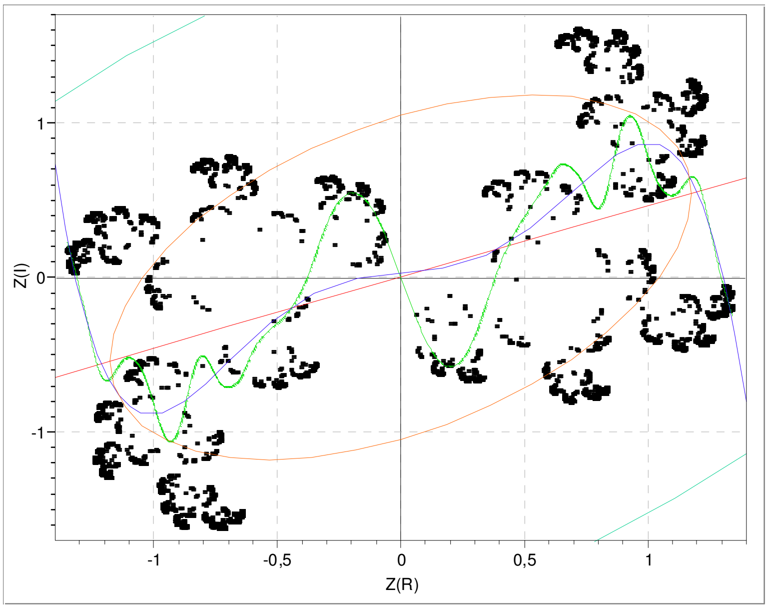


Figure 3.3.10. A theoretical self similar system resembling a stock-in-area [Z(R)] recruitment-to-the-area [Z(I)] relationship. Data values (N=19851) are dynamically referenced through linear regression, a sixth degree polynomial, a cubic spline (to show more detailed local dynamics) and 50 (inner) and 95% (outer) bivariate ellipses (also, confidence intervals). The random and sequential sampling of 10, 5, 1 and 0.1% of the total number of points (resembling captures from different spatial scales) showed similar tendencies: as in the skipjack fishery, the simulated system shows similar dynamical patters at different sampling windows. Different levels of numbers are obtained depending on the quadrant the sampling is carried out. Iteration and data, parameter values and function are arbitrary.

3.3.8 Acknowledgements for this section.

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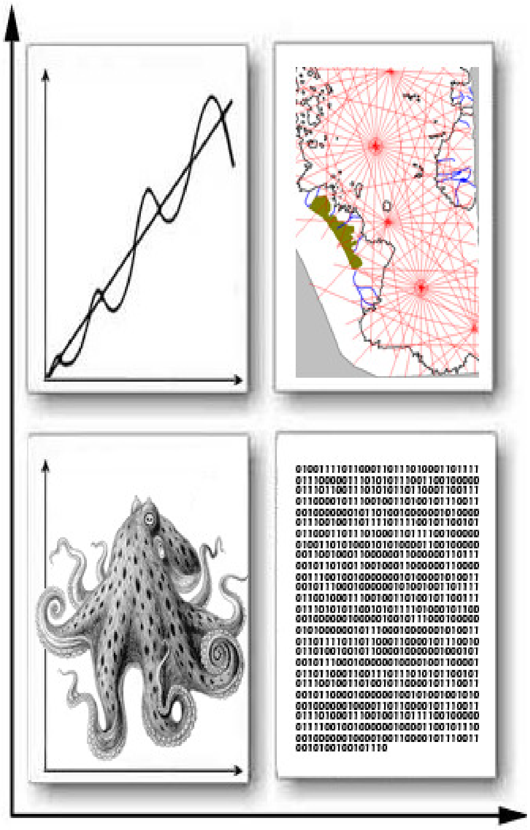
CHAPTER 3.4

On the Dynamics of the common *Octopus:* towards A NEW SYSTEM FRAMEWORK



3.4 On the dynamics of the common *Octopus*: towards a new system-framework.

3.4.1. Abstract.

This chapter takes a first step towards the proposal of an ad hoc, non-linear population system framework for the dynamics of *Octopus vulgaris* (Cuvier, 1797) in the Eastern Central Atlantic (FAO Fishing Area 34). Catches are both used as a proxy for abundance and assumed to represent population trends (recruitment to the population and fishery). The stock-recruitment (SR) relationship to the fishery is studied. Pulses in the North Atlantic Oscillation (NAO) are considered as an external forcing which may determine the temporal evolution of the population. Series are analyzed to determine memory effects, correspondences and periodicities. It is proposed that SR dynamics, during a 40 years long period, (i) consists of four orbits of stability (two global and two local equilibrium states) which may arise due to (ii) NAO pulses, an external forcing which is considered a key factor governing the temporal evolution of the population. It is put forward that the SR relationship is a multi-oscillatory dynamical continuum mediated by multiple, linked orbits of stability and governed by a variable carrying capacity: this system is described by a new model which represents a summation of non-linear functions and allows for stable, periodic and chaotic dynamics. The proposed SR system is suggested to have the capacity to, persistently, evolve and return within a wide range of orbits of stability allowing for all of the observed population mechanics coupled into the same relationship, as various stressor/promotor variables are defined. Finally, several of the proposed concepts are discussed and a modified model which may incorporate external perturbations is put forward. An example is given in Appendix I both to (i) support the use of catches as a proxy for abundance in short lived cephalopod populations and (ii) explain the persistence of dynamical trends in a multi-oscillatory population/system under two linear and two non-linear, significantly different levels of fishing effort. Finally, catch, effort and abundance series updates are provided for the Saharan and Mauritanian *Octopus* fisheries in which the proposed concepts are validated.

3.4.2. Introduction.

The Eastern Central Atlantic (FAO fishing Area 34, henceforth referred as “Area 34”, Fig. 3.4.1) and, in particular, the coast of the former Spanish Sahara (Northwest Africa, 21-26º N, FAO fishing area 34.1.3) is the fourth richest fishing ground in the world. Generally, it is considered that this is due to a combination of several geomorphologic, meteorological and oceanographic factors. The intensive upwellings taking place, along the coast, are of particular significance (Cruzado, 1974; Belveze and Urzini

1983; Bas et al., 1995). Similarly, advances in the understanding of the larger scale wind field and hydrologic cycles for the region have been linked from this region westward into the Atlantic (Gray, 1990). Also, the exploitation within the ranges of Area 34 was started by fishermen from Canary Islands (Spain), during the sixteenth century (Molina and Quesada, 1779). Historical fisheries were seasonal and followed the biological cycles of several fish species, particularly those in the Sparidae and Serranidae families.

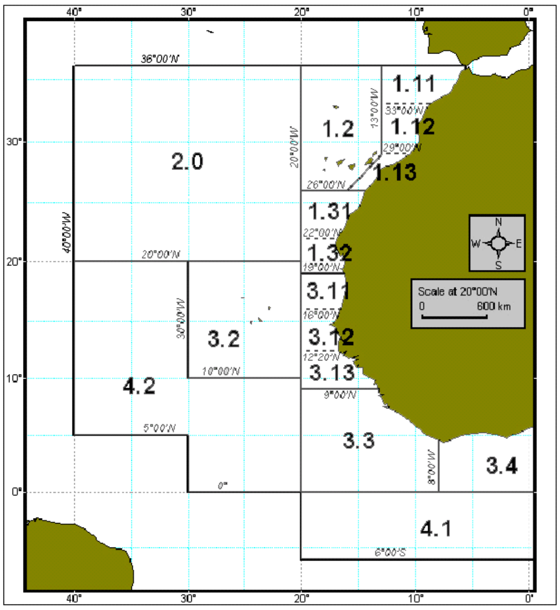


Figure 3.4.1. The FAO Fishing Area 34 (from Gibraltar to the Congo river, Lat. 36°00'N-6°04'36"S, Long. 12°19'48"E-5°36'W). Map modified after FAO (2001). Equidistant cylindrical projection.

Cephalopods are characterised by having a short life span, with fast growth rates and a relatively high metabolism (Boyle, 1983; Guerra and Pérez-Gándaras, 1983; Mangold, 1983). *Octopus vulgaris* (Cuvier, 1797; henceforth referred as "common *Octopus*") is both the most important target among cephalopod species and a key fishery resource in Area 34, particularly, in subareas 34.1.3 and 34.3.1, along the coast, from the former Spanish Sahara to Guinea Conakry, Latitude 26-9º N (García-Cabrera, 1968, Guerra and Pérez-Gándaras, 1983; Hernández and Bas, 1993). Yearly catches on the common *Octopus* have, regularly, reached over $1*10^5$ tn in Area 34 (Guerra and Pérez-Gándaras, 1983; Bravo de Laguna, 1985; FAO 1988, 1991, 1994; Bravo de Laguna and Balguerías, 1993) most of which is harvested within sub area 34.1.3: for instance, landings reported during years 1994 (137844 tn) and 1995 (156300 tn) represented 47.2 and 50% of the world catches upon this species, respectively (FAO, 1998).

The common *Octopus* may be found from the sea shore to the border of the continental shelf and the optimal temperature and salinity ranges are between 7-33 ºC and 32-40 ‰, respectively (Guerra, 1992). Depending on female size, the egg output may oscillate between 10^4 and $4*10^4$. Spawning occurs the year around and there are seasonal peaks on both spring and autumn (Hatanaka, 1979; Nigmatullin and Ostapenko, 1977; Nigmatullin and Barkowsky, 1990). Both embryonic development and the planktonic early life stages (2 to 6-7 mm of mantle length) are strongly dependent on temperature. Once the common *Octopus* settles on the sea bottom, it preys upon polychaetes, crustaceans, fish and molluscs (Mangold, 1983; Guerra, 1992). Also, reproductive migration of mature individuals to areas closer to the coast was proposed by Mangold (1983) and the size distribution is associated with depth (Sánchez and Martín, 1993). Death may occur immediately after reproduction and their life span is approximately one year long (Hernández-López et al., 2001). Moreover, the ecological role of the common *Octopus* in marine trophic webs is considered important: this cephalopod is frequently preyed upon by several fish species, particularly those in the Sparidae family (Domanevsky and Patokina, 1987), sea birds

(Guerra, 1992) and marine mammals (Hernández-García, 1995), as well. Furthermore, it has been suggested by Balguerías et al. (2000) that changes in the dynamics of the common *Octopus* may be caused by a combination of factors, including those of economic, oceanographic and ecological nature (interspecific competition for food).

Although, a relatively large body of information is available due to the industrial fishery on this species (see among others García-Cabrera, 1968; Bas, 1975; Guerra, 1975; Nigmatullin and Ostapenko, 1977; Hatanaka, 1979; Hernández and Bas, 1993; Fernández-Nuñez et al., 1996), Boyle and Boletzky (1996) observed that there was still a lack of a predictive framework to address the structure and dynamics in cephalopod populations.

The economic importance of the common *Octopus* as food for humans and its key role in marine ecosystems justify both an efficient analyses and dynamical management approaches. In our view, there is an urgent need to develop a flexible, ad hoc framework which may allow us both to ask better questions and understand causal mechanisms to dynamical patterns behind the data.

In this chapter, we aim to put forward a first, ad hoc framework for the common *Octopus* in Area 34: we shall (i) analyse the fishing and environmental data, taking into account the temporal evolution of both landing series and phase spaces, periodicities, possible correspondences and time lags, as well as fitting the data to the non-linear model; (ii) develop further ideas on recruitment both to the population and fishery as dynamical continuums mediated by multiple, linked orbits of stability, governed by variable carrying capacities and (iii) discuss some of the inferences relative to both classical models and the present approach. Finally, we will discuss some of the future developments within the framework we propose, as well.

3.4.3. Data.

The series analyzed herein were as follows: (i) yearly catches (in metric tonnes, tn) on (a) the common *Octopus* (years 1962-2001) from FAO Fisheries Area 34 (from Gibraltar to the Congo river, Lat. 36°00'N-6°04'36"S, Long. 12°19'48"E-5°36'W), after FISHSTAT/FAO (2003) and (ii) yearly means of the North Atlantic Oscillation (NAO, 1865-2000) series (pressure data for Ponta Delgada, Azores) after Hurell (1995) and Climate Research Unit (2003).

3.4.4. Methods.

We standardized to the same scale (Z values with mean = 0) and smoothed the time series in order to facilitate both the analyses and visual comparison. To analyze the data, we used (i) autocorrelations to detect persistency or memory effect; (ii) the Hurst (H) exponent (after Hurst, 1951; Auto Signal, 2002) as a quantitative measure of the underlying trends: while values of $H = 0.5$ correspond to Gaussian or true white noise (i.e. the observations are independent from preceding values), those approaching (or higher than) 0.75 will reflect a persistency or memory effect (each data value is related to some number of preceding values) in the time series; (iii) the Welch method (after Oppenheim and Schafer, 1975) to estimate the spectral density in order to establish the frequency and time length of the oscillations (different equilibrium states); (iv) cross-correlations (Pearson's correlation) to determine the degree of correspondence between the series. Also, the trajectory obtained by plotting catch values in each phase plane N_t against N_{t+1} (i.e. the value from a certain year against that the year after) was assumed to reflect dynamical features of the Stock-Recruitment (SR) system: considering catches as a proxy for abundance, their trajectory may reflect SR trends. Also, the spawning stock, any one year, will replace itself due to the generation length in this species. Furthermore, the SR system was fitted both by a linear regression through the origin (to determine the "replacement line" or recruitment needed to replace the stock) and a sixth order polynomial (three constants for each equilibrium).

3.4.5. Results.

In order to analyse the data on the common *Octopus* in light of our framework, we will briefly overview both the classical approaches and our new, non-linear model.

On the one hand, the Shepherd (1982) functional form is given by

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

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 α and δ are referred as the slope at the origin and degree of compensation involved, respectively. This approach could unify, within a single framework, both the classical dome-shaped (for $\delta > 1$) and asymptotic (for $\delta = 1$) functional forms proposed by Ricker (1954) and Beverton-Holt (1957), respectively. An arbitrary example for each of the models is shown in Fig. 3.4. 2.

On the other hand, recruitment (R) in our framework is defined (Equation 3.4.2) as the system or summation of non-linear functions of spawning stock, S, given by

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

where the entries $i = 1 \ldots m$ represent the number of equilibrium states in the stock-recruitment (SR) system, being m the highest equilibrium where the SR relationship reaches the ceiling or maximum allowable carrying capacity. equilibrium states 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 spawning stock for which equilibrium states may arise.

Graphical representations of both a single steady state and a multiple equilibrium system, according to our framework, are shown in Fig. 3.4.3 and 4, respectively. This new approach can be applied to the phase plane (N_t, N_{t+1}) to describe both the SR system and fishery dynamics of the common *Octopus*. An m number of oscillatory phenomena ranging from limit cycles to chaos and inverse density-dependence are allowed in this system which may be approximated either by least squares using Equation 3.4.2 or by polynomial regressions incorporating three constants for each equilibrium state. Further aspects of this new model are extensively detailed in Solari et al. (1997).

We have assumed a positive relationship between the number of juveniles being recruited to the population and those entering the fishery and, in order to discuss the SR system in the common *Octopus*, we offer the following results:

Fig. 3.4.5 shows the series on both catches and the NAO oscillation: (a) autocorrelations (acorr) showed significant decays of 4 years for the common *Octopus* catches (acorr was 0.91 for time lag = 1, N = 40) and 3 years for the NAO (acorr was 0.82 for time lag = 1, N = 48). Also, the correspondence between both of the series was highly significant (cross correlation was 0.63, p<.001, N = 40): pulses in NAO are clearly reflected in the level of catches on the common *Octopus*; (ii) also, the Hurst exponent (values on the raw series between parenthesis) was 1.08 (0.98) and 1.09 (0.75) on catches and the NAO, respectively, showed a marked persistency and were well beyond the value for series due to a random process or a true white noise (H=0.5); (iii) furthermore, the spectral analyses (Fig. 3.4.6) detected 5 peaks for each of the series: while these values (in years) were 33.5, 8, 4.33, 3.03 and 2.47 for the common *Octopus* series, those for the NAO were 21.06, 9.96, 5.68, 3.64 and 2.64. These results are interesting as they show similar short (4 years) and medium term (8-9 years) oscillations (equilibrium states) for the SR system within a 40 year long attractor trajectory. Also, it appears that both short and medium term oscillations in the SR system are embedded in the oscillations shown by the NAO (i.e. equilibrium states in the dynamics of the common *Octopus* are slightly shorter than those shown by the NAO).

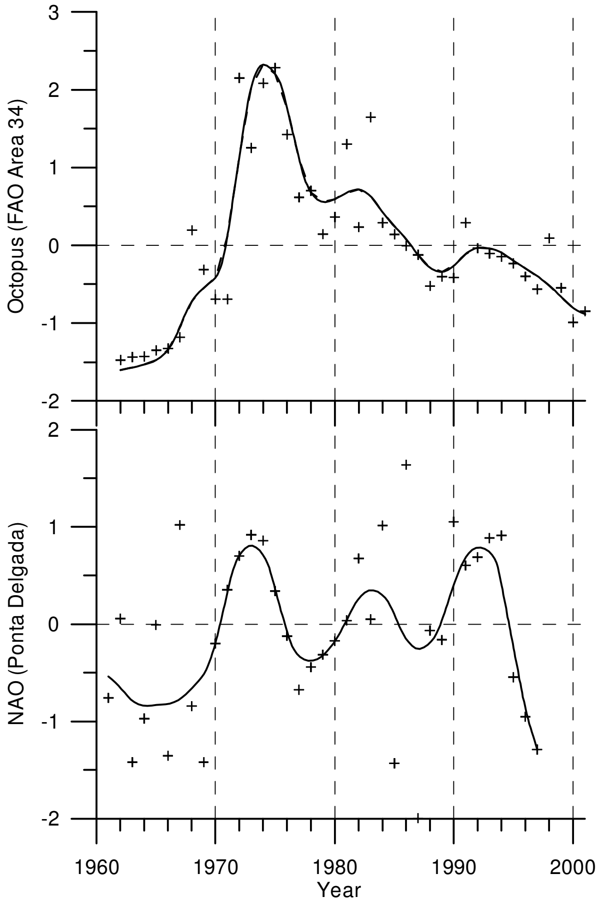


Figure 3.4.5. The North Atlantic Oscillation (NAO; at Ponta Delgada, years 1961-97) and common Octopus (FAO Fishing Area 34, years 1962-2001) standardized (yearly means) raw (+) and smoothed (shown by the cubic spline) series.

Fig. 3.4.7 shows the proposed SR system in the common *Octopus*: (i) Raw values (+) are plotted and the smoothed series is fitted by a cubic spline which represents the dynamical trajectory of the SR system; (ii) a 6th degree polynomial describes the proposed dynamical continuum and transitions between equilibria, as the carrying capacity changes and (iii) a linear regression through the origin represents both the recruitment needed to replace the stock and overall equilibrium values: the system grows and decreases as trajectory values are above and below the replacement line, respectively. Within the 40 year long trajectory, there are four orbits of stability (equilibrium states): (i) each equilibrium state implies an oscillation due to both density-dependent compensation and depensation. The transition between equilibrium states is due to either density-independent compensation (➤) or depensation (➤, indicated by the filled arrows on the trajectory) and occurs as either the carrying capacity or the minimum viable population is reached, respectively; (ii) E_1 and E_2 are global, medium term equilibria one of which is relatively low (E_1) while the other is relatively high (E_2).

Low equilibria imply relatively lower levels of numbers and maxima and minima converge whereas high equilibria imply relatively high levels of numbers and maxima and minima diverge. The density-independent transition between both of these orbits of stability may have arisen due to a positive NAO trend during years 1964-72 after which density-independent depensation started due to the NAO negative trend between years 1973-78; (iii) E_3 and E_4 are local, short term equilibria (indicated by the simple arrows): these orbits of stability may have arisen due to pulses in the NAO, during years 1979-87 and 1988-94, respectively.

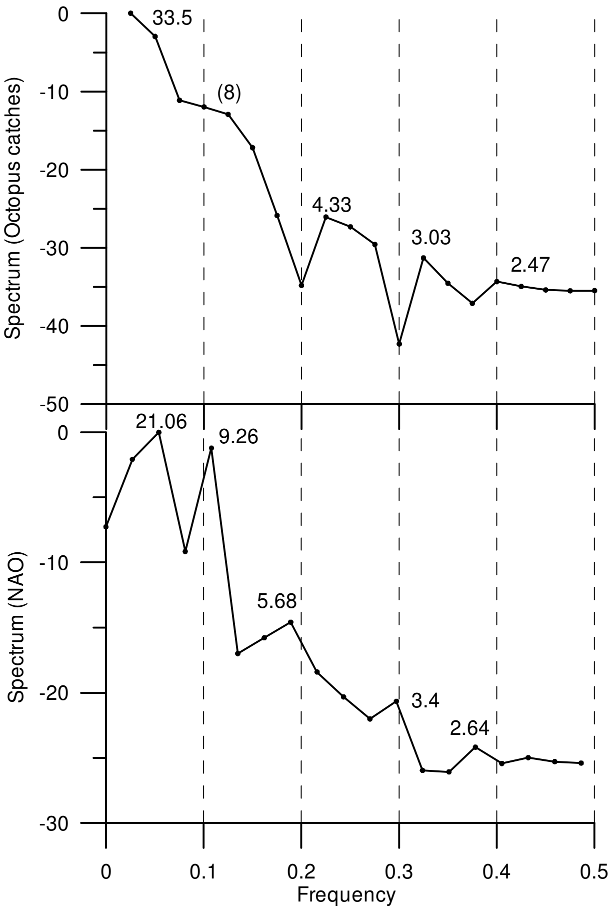


Figure 3.4.6. Spectral analyses on both the North Atlantic Oscillation (NAO; at Ponta Delgada, years 1961-97) and common *Octopus* (FAO Fishing Area 34, years 1962-2001) standardized and smoothed series. Numerals over the peaks refer to number of years.

3.4.6. Discussion.

One of the main assumptions in the present study is that catches may be used as a proxy for abundance to infer trends in the dynamics of the common *Octopus*: to support this assumption, we show in Appendix I an arbitrary example in which an initial population is affected by four different fishing mortality regimes (two linear and two non-linear) where similar trends persist at different scales of numbers under four levels of exploitation. This implies that we may be able to analyze and estimate population trends in the short and medium terms even as no or unreliable effort data is available.

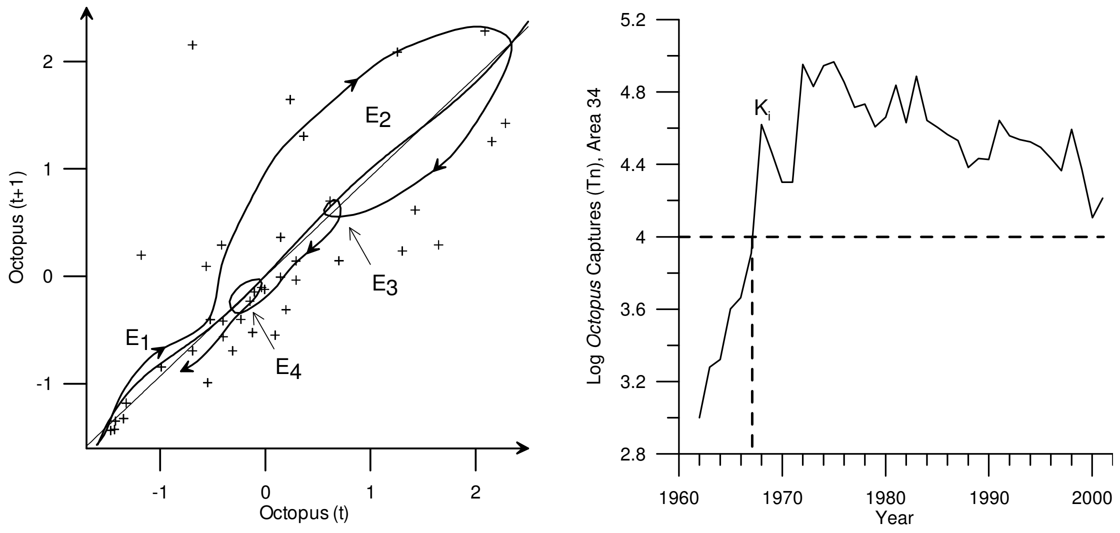


Figure 3.4.7. Above, left: the Stock-Recruitment (SR) system (plane N_t, N_{t+1}) for the *Octopus vulgaris* in FAO Fishing Area 34 (years 1962-2001). Raw (+) and smoothed (shown by the cubic spline) standardized series describe the dynamical trajectory. Global and local dynamics are indicated by the equilibrium states E_1-E_2 and E_3-E_4, respectively. Filled arrows on the trajectory indicate compensation (➤) and depensation (◀). The memory effect is highly significant (Hurst exponent >1). Oscillations in the SR system may arise due pulses in both the North Atlantic Oscillation (NAO) which may control the variable carrying capacity. According to our theoretical criteria, a new compensatory trend for the SR system is expected, during the coming 4-8 years, as the NAO turns into a positive trend. Above, right: data was log transformed to determine both the "build-up" of the fishery, during the 1960's, and the approximate year (1967) as the fishery system started to oscillate (indicated by the dashed lines). The first peak of the series should reflect the first carrying capacity (K_i) of the system reached (in part, due to high and intense fishing) after which the population system kept oscillating due the combined effects from the environment and fishing mortality.

Stock and recruitment either to the population or the fishery in the common *Octopus* is a complex system whose dynamics makes up a system which may be determined both by (i) density dependent and density independent processes, (ii) the combined effects from environmental factors and fishing mortality and (iii) several dynamical features such as correspondence between variables, persistency at the variable and system levels, time lags, periodical oscillations and a relatively high degree of non-linear behaviour (memory effects, possible feed-back mechanisms and a relatively high sensitivity to external pulses).

Although we have analyzed series with limited degrees of freedom, it is clear from the combined results we report here that the SR system in the common *Octopus* is affected by a multiplicity of factors: (i) the turnover speed (seen as the generation time) of the SR system is approximately one year and the number of recruits (either to the population or fishery), any one year, appears to be strongly dependent on spawner abundance during the preceding 3 to 5 years: there is a clear persistency or memory effect which links the dynamics of the common *Octopus*, longer than the time length for any single spawning stock replacement. This may be related to both changes in distribution, and local abundance changes. Also, the weight of data values change during the evolution of the series being most significant approximately five years before anyone value (i.e. the temporal evolution in the data should be considered in a modelling effort). These fundamental concepts are well supported by the results from the auto-correlations and the Hurst exponent: the dependency on preceding values and non-white-noise/non-random, deterministic nature of the data (i.e. data is the result of a signal which depends on preceding values, with some noise) were well established; (ii) also, the effect of the NAO is complex as it showed an overall positive, linear relationship but further analyses revealed a marked non-linearity: similar NAO pulses may imply similar responses on the SR system but at different levels of numbers (different orbits of stability; an schematic example is shown in Fig. 3.4.8 a., b.). While the positive trends in the NAO pulses may imply density-dependent and density-independent compensation, the negative trends in the pulses may also imply density-dependent and density-independent depensation.

Also, we have been able to obtain the common Octopus and NAO series up to years 2001 and 1997, respectively. However, if our framework is theoretically correct, during the coming (4-8) years, we expect the SR system to respond with higher recruitment: the NAO showed a relatively long, negative trend during the 1990's and reached, in 1997, one of the lowest values of the series, since 1865 (there are just six significantly lower values than that for year 1997, in the long time series). We may thus expect both that (i) a positive NAO trend within the next coming years whose length and slope will positively change the carrying capacity of the SR system and (ii) a correspondent density-independent compensation in recruitment of the common *Octopus*. Both of these factors may cause the settlement of the SR system in lower or intermediate equilibria, during the next 4-8 years.

As we see it, the variable carrying capacity and transition between equilibrium states of the SR system may be governed, either directly or indirectly, by NAO pulses (or other variables, operating from a mesoscalar spatial range, such as upwelling, and Sea Surface Temperature or the combination of upwelling-related production and SST which may be governed by the NAO). Also, the SR system appears to be sensitive even to minor NAO pulses which may imply the occurrence of both global (due to major pulses) and local (due to minor pulses) dynamics. This latter observation is important to stress as we might expect that local dynamics (E_3 and E_4 in Fig. 3.4.7) could arise due to increases in fishing effort while they appear to be determined by relatively minor NAO pulses, during a global, density-independent depensation phase. Furthermore, it is clear that we may use data from a minor spatial scale (Ponta Delgada) to analyze the dynamics of a SR system operating at a significantly larger scale. Moreover, we could expect a dynamical auto-similarity, at several spatial scales, particularly in those FAO subareas (or localized sub-stocks) where the abundance of the common *Octopus* is high; (iii) the spectral analyses supported the ideas, as set forth by our framework, that (a) the carrying capacity of the SR system is variable and mediated by an external forcing, (b) there are several equilibrium states, during the 40 years of the trajectory and (c) we may expect a dynamical continuum which evolves towards a complex attractor with global and local dynamics, as long time series become available. For instance, the NAO long time series (1865-1997) showed several oscillations which may range between 2-5, 7-13, 15-30 and 35-70 years with a clear non-white noise nature (H = 1.04 and 0.82 on the smoothed and raw data, respectively): these pulses could be linked to the SR system in the common *Octopus* implying a dynamical, multi-oscillatory continuum governed by a variable carrying capacity.

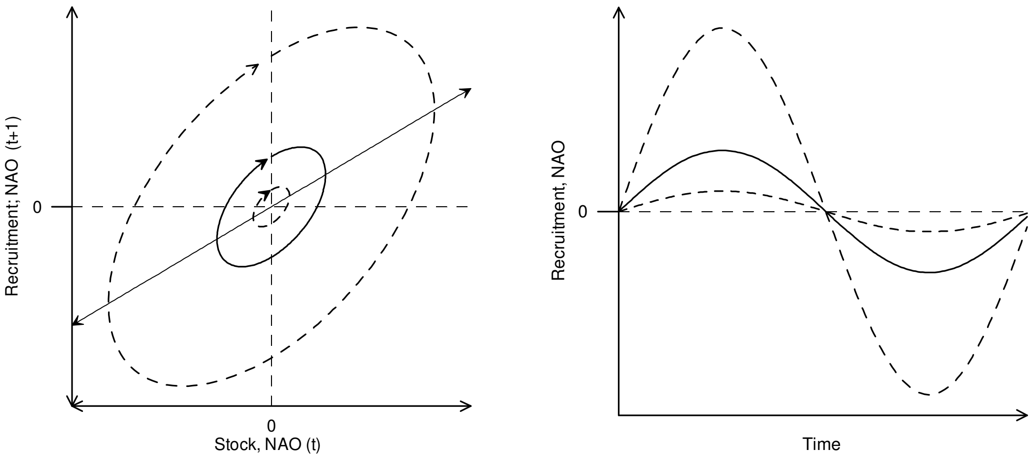


Figure 3.4.8 a (above, left) and b. An arbitrary example (values are standardized) of the effect of a North Atlantic Oscillation (NAO) pulse (continuous line) on the recruitment (either to the population or the fishery) in *Octopus vulgaris* (FAO Fishing Area 34): a similar external perturbation may lead either to a relatively higher (outer dashed line) or lower (inner dashed line) equilibrium depending on the level of numbers and carrying capacity during prior years and length and slope of the perturbation, as well. The phase plane is shown above (a) and time series below (b).

The plane N_t, N_{t+1} fitted by a polynomial incorporating three constants for each equilibrium and a simple regression through the origin is embedded as a simple method in our framework and may allow us both to more readily comprehend the dynamics behind the population catch and abundance data and describe the SR system. In general, the trajectory of the data in the plan SR from year to year is significant, which means that the temporal evolution and independent, external forces must be considered to fully understand the process. In our new, non-linear model, the system can include different orbits of stability or equilibria whose number and shape will depend both on the studied stocks and the external variables affecting the SR system.

The flexibility in our approach is given by the additive nature of the model which may describe a wide range of dynamical situations linking several, mathematically independent, functions in a simple Equation. This is necessary to understand the stock recruitment system under the studied period and it may serve for the future predictions. Our approach can be used as an ad hoc model because it allows the explanation and linking of most population dynamical phenomena (compensation, depensation, density dependence, density independence, inverse density-dependence or "Allé effect", oscillations which may range from chaos to cycles to a near-standstill dynamical state with no clear oscillations, transitions between equilibria, temporal evolution of a variable carrying capacity and dynamical system behaviour) in a relatively simple framework, taking into consideration different spatial scales and substocks. No references describing such an approach on cephalopod dynamics was found in the literature. However, recent studies of pelagic fisheries comprising multiple species by Norton and Mason (2003, 2004) and the major world production fisheries by Sharp et al. (2001 a-b, 2002) provide impetus to follow-up on our progress, and extension to the FAO Area 34 fisheries, and beyond.

Other non-linear models (such as those of multiplicative nature) may be used both to fit the data and obtain several equilibrium states: however, such approaches incorporate an interdependence between the functions which is a serious shortcoming both as (i) equilibria approach extremely low values; (ii) as stock and recruitment converges towards the minimum allowed population; (iii) fishing mortality reaches the unity in some sub-areas/sub-stocks and, among other factors, (iv) whenever other inputs are near-zero (or zero) may affect the model.

3.4.7. Acknowledgements for this section.

We would like to acknowledge the key contributions -in the review of this ad hoc framework- of senior scientists Dr. Gary Sharp (Centre for Climate/Ocean Resources Study, Monterey, California), Dr. Serge García (Director, Fisheries Department (FIRD), FAO) and Dr. Jorge Csirke (Chief, Marine Resources Service, FAO). This study was funded by the Agriculture and Fisheries Ministry (Consejería) of the Canarian Autonomous Government.

3.4.8. Series update (August, 2007).

In this chapter, we took a step forward to propose the first ad hoc population framework for the common *Octopus* in FAO fishing area 34. The approach was based on 39 years (1962-2001) worth of pooled catch data from the Eastern Central Atlantic, after FAO (2003). The main proposed ideas were that catches (a) may be used as a proxy for abundance and (b) assumed to represent population trends in recruitment both to the population and fishery; (c) there were four orbits of stability (arising from two local and two global equilibria) in the nearly four decades represented by the series and (d) that such oscillations could arise (directly or indirectly) due to pulses from an external forcing such as the North Atlantic Oscillation.

The series are now updated with catch and effort (unpublished, after IEO, 2007) and abundance index data (after FAO, 2006; published in late 2007) from both the Saharan (Spanish fleet) and Mauritanian fisheries, respectively, in order to further validate the model proposed by Solari et al. (1997). Also, we use Optimum Interpolated Sea Surface Temperature, SST, and SST Anomaly (selected over an arbitrary geographical range between

Lat 24.5-26.5°N, Long 14.5-16.5°W, yearly maxima, means and minima for years 1981-2005 with resolution 2° Lat/Long; after Reynolds and Smith, 1994; IGOSS, 2007) as proxies (which may, in part, reflect upwelling and NAO effects) to further explain part of the external forcings which may govern the variable carrying capacity and stock dynamics.

It should be noticed that the Western Saharan and Mauritanian *Octopus* stock nucleii are both (a) genetically different and (b) oceanographically isolated from one another: on the one hand, genetic studies (Murphy et al., 2002) established genotypic differences between both of the stocks and, on the other hand, the populations (measured by georeferenced catches, after Balguerías et al., 2002) are isolated due to the eddies arising from the upwelling (a phenomenon which can be observed through both SST and Altimeter data). These aspects may be of significance as we observe similarities in the dynamics of both stocks and fisheries and find that external forcings may be sufficiently powerful to cause (dynamical) auto-similarities at mesoscalar (hundreds to thousands of kilometres wide areas) spatial ranges upon genetically and biogeographically distinct stocks.

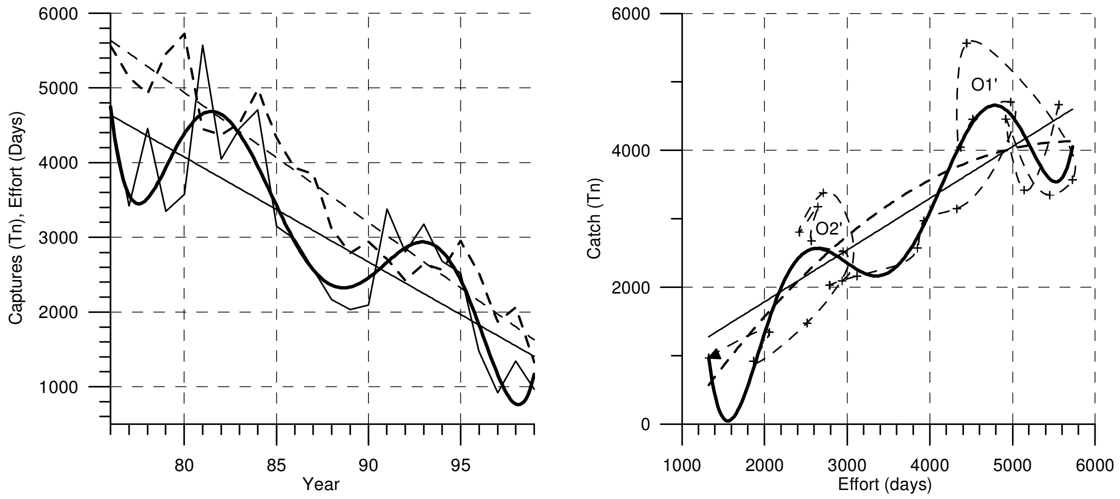


Figure 3.4.9 a-b. Above left (a), Catch (Tn; thicker, continuous line) and Effort (days; dashed line) of the Spanish *Octopus* fishery within the Saharan upwelling zone for years 1976-1999 (after IEO, 2007); above right (b), Catch-Effort relationship fitted by a simple regression (straight line), a classical 2^{nd} order approach (dashed line) and a polynomial approximation to our dynamical model. O1' and O2' orbits of stability.

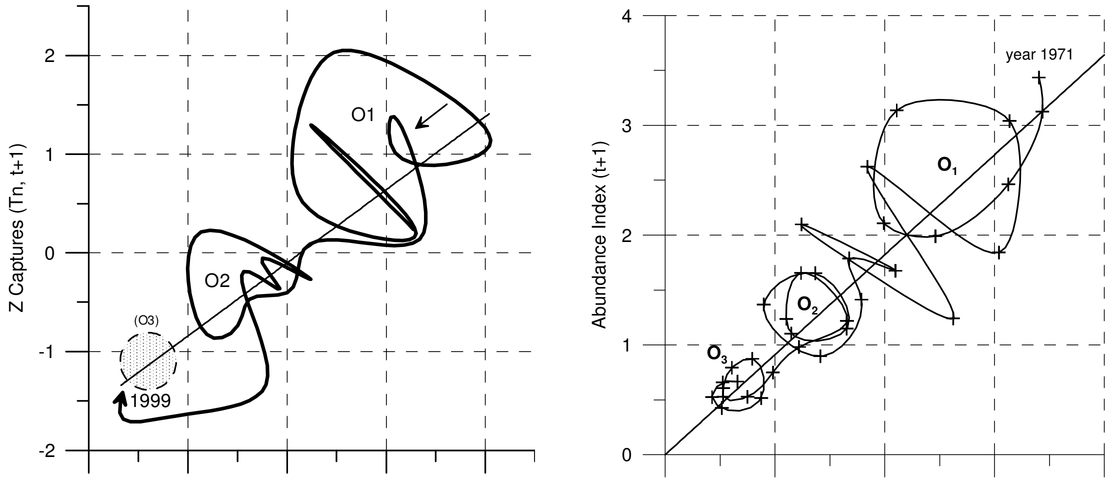


Figure 3.4.10 a-b. Above left (a), the phase plane of catches (considered to approximate the Stock-Recruitment system). O1 and O2 are orbits of stability. O3 (dotted area) is the future expected range of oscillation from year 2000. Arrow indicates an example of local dynamics. Above right (b), phase plane of the Mauritanian *Octopus* Abundance Index series (1971-2005, after FAO, 2006). O_1-O_3 indicate the orbits of stability as explained in our multi-oscillatory framework. This data clearly validates the dynamical model we have proposed and is similar to the Catch-Effort relationship we have shown for the Spanish *Octopus* fishery in the Saharan upwelling zone (after IEO, 2007).

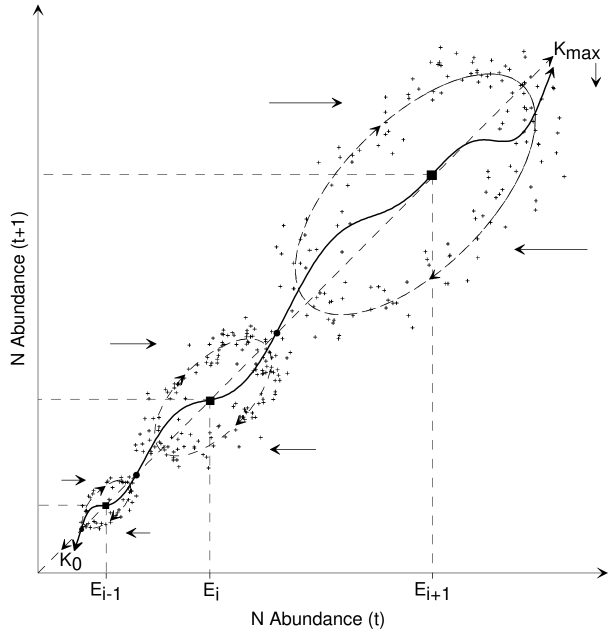


Figure 3.4.11. A (preliminary) model (based on our framework) on the *Octopus* off the Saharan upwelling zone. Three orbits of stability with corresponding “steady states” (E_i), maximum carrying capacity (K_{max}) and minimum viable population (K_0). Also, every orbits will be limited by a local ceiling (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 show the population positive and negative growth. This reconstruction may be useful for the Mauritanian case, as well (to be addressed in the second half of the project by the Multi-oscillatory System Approach). Ground theoretical model after Solari et al. (1997).

The Mauritanian *Octopus* Abundance Index series (1971-2005) showed (i) three periods of approximately 3-4, 6-7 and 12 years which may be related to the density-dependent (interaction between compensation-depensation in the population) and density independent (compensation-depensation due to the combined effects from environmental inputs and fishing mortality) processes; (ii) an autocorrelation which detected a clear “memory effect” of up to 7 years (data is highly significantly different from a white noise or random walk) and (iii) the Mauritanian *Octopus* abundance index (1971-2005) was highly correlated to Maximum ($p<.01$) and mean

($p<.05$) SST series which appear to be the inverse of each other. Similarly, the Spanish *Octopus* fishery in the Saharan upwelling zone showed (i) a memory effect of three and four years for catches and effort, respectively and (ii) highly significant cross correlations ($p<.01$ for both catches and effort) with the Mauritanian Octopus Abundance Index and SST series. Also periodicities (peaks from spectral analysis) in the Octopus catches, Southern component of NAO and Sea Surface Temperature Anomaly fall into similar frequencies.

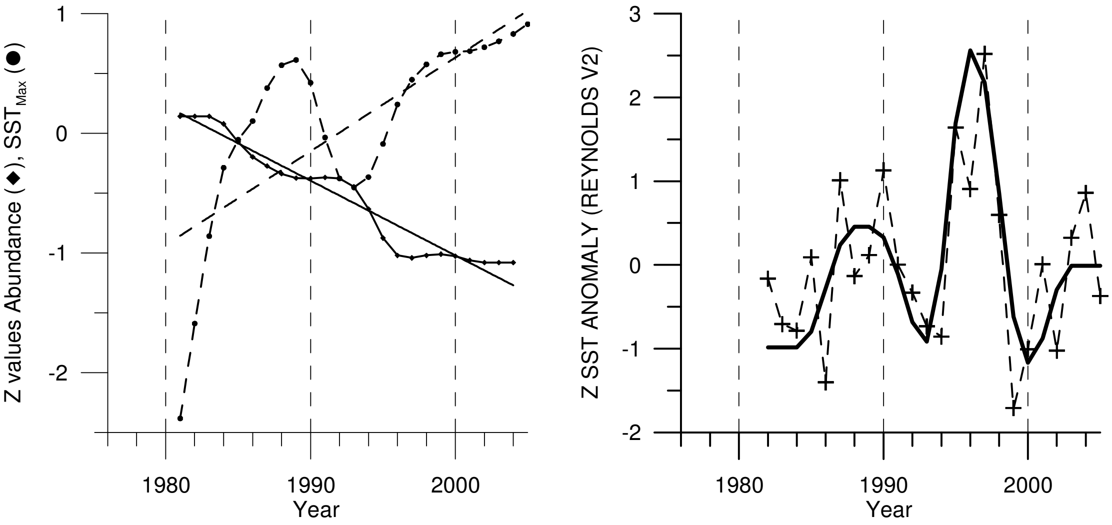


Figure 3.4.12 a-b. Above left (a), the Optimum Interpolated Sea Surface Temperature (SST, after Reynolds and Smith, 1994) series (yearly maxima) for the area (data was used as a proxy) Long. 17.5-19.5° W – Lat 19.5-21.5° N and Abundance Index series (after FAO, 2006) on *Octopus* off Mauritania. Cross correlations between the series are highly significant and periodicities (peaks from Spectral analysis) fall into similar frequencies. The variables appear to be the inverse of each other (Pearson correlation, $p<.01$) from which we may infer that trends in SST maxima are a co-factor determining abundance (year class strength) in *Octopus* stock nucleii. Above right (b), trends (raw and smoothed data) in Sea Surface Temperature Anomaly (SSTA, after IGOSS, 2007) appears as one of the best descriptors for trends in the *Octopus* populations in FAO Area 34. Z values are standardized (mean = 0) to facilitate visual comparison.

3.4.9. *Octopus* off Mauritania: proposed sub-models for SST-Abundance.

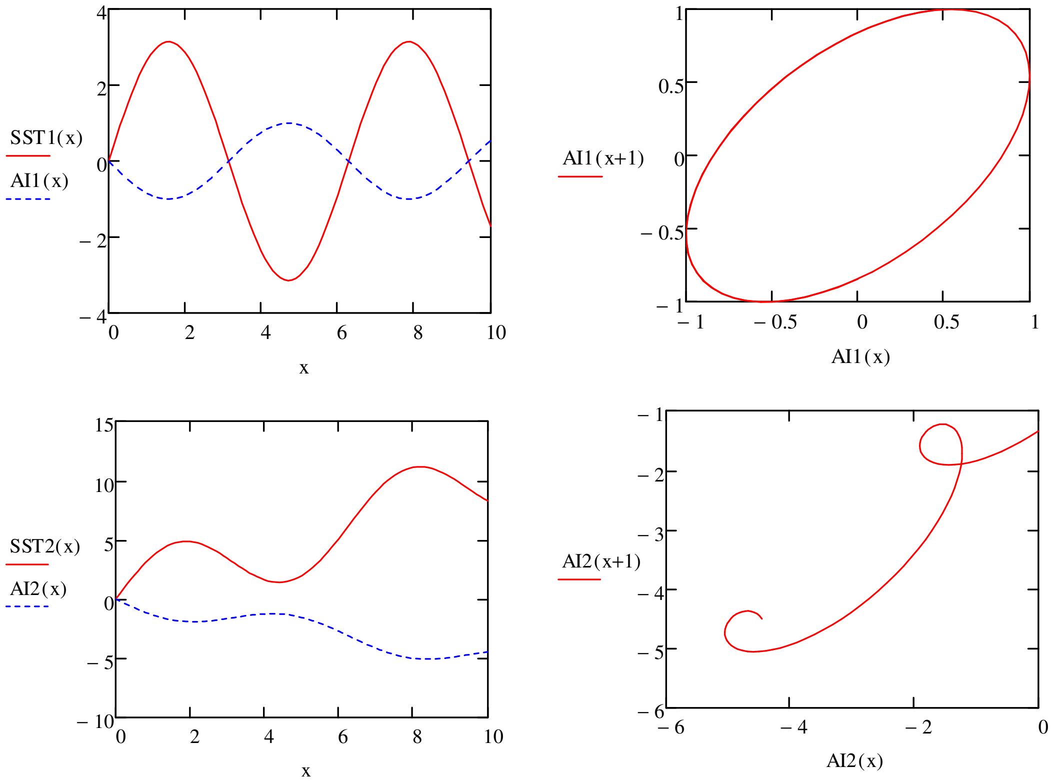


Figure 3.4.13 a-d. Proposed theoretical sub-models for the relationship between Optimum Interpolated Sea Surface Temperature (SST, after Reynolds and Smith, 1994) series (yearly maxima) for the arbitrary area (used as a proxy) ranging between Long. 17.5-19.5° W – Lat 19.5-21.5° N and the Abundance Index series (after FAO, 2006) on *Octopus* off Mauritania: (a) above left, SST and AI [SST1(x), $AI1_{x+1}$] (no medium term linear trend) series as inverses with different amplitudes and (b) above right, the corresponding limit cycle [AI1(x), $AI1_{x+1}$]; (c) below left, SST2(x) and AI2(x), a medium term linear trend is considered and amplitudes and slopes of the trends variate; (d) below right, phase plane of the abundance [AI2(x), $AI2_{x+1}$] taking into account amplitudes and linear trends particular to each variable. Time is *x* (10 years).

3.4.10. Discussion (series updates).

The availability of the catch and effort and abundance index series from both the Saharan and Mauritanian cases was instrumental both to show that (i) catches may be used as a proxy for abundance in fisheries with no available effort data in order to estimate short and medium term trends in recruitment: we were able to estimate the dynamics of the population out of the catches and, later on, validated this knowledge having recent access to effort and abundance data; (ii) to further validate the multi-oscillatory/dynamical continuum/variable carrying capacity nature of stock dynamics proposed by Solari et al. (1997).

Although both of the *Octopus* population systems off Sahara and Mauritania are both genetically and biogeographically distinct, the following is suggested, according to our framework:

(i) the dynamics of the populations are similar (auto-similar) with two orbits of stability and a third becoming established at low levels of numbers (Spanish case) and three clear orbits for the Mauritanian case: the oscillations are clearly detected upon the raw and transformed data and memory effects and dependencies between variables appear to be strong;

(ii) dynamical similarity occurs at several spatial scales and for different regimes of fishing mortality/effort (trends remain similar, scales of numbers change); also, while the Spanish fleet was being gradually withdrawn from the Saharan upwelling zone in the mid 1990's, the reduced both catches and effort reflected the depensatory trend in abundance: such a "gradient" in fishing effort upon more reduced areas validates further the "dynamical auto-similarity" concept we have proposed (also, validated for tunas from three spatial scales in FAO Area 34, after Solari et al., 2003 and for the common *Octopus* from data from the Port of Mogán, Canary Islands, after Hernández-García et al. 1998); this implies that we may estimate trends in wider areas and more powerful fleets following the temporal evolution of stock nucleii in minor areas.

(iii) the compensatory-depensatory (forward and backwards bending) nature in the effort-catch relationship and fishing effort phase planes at several scales of numbers (i.e. it may occur within the number ranges of every orbit of stability) due to oscillations in abundance, environmental variables and net value of the fishery, reflected by fishing effort (which turns backwards as the fishery starts to tend to the zero net value);

(iv) the differential effects of fishing mortality upon density-dependent and density-independent compensations and depensations and the shifts towards low and very low orbits of stability as a consequence of the combined types of depensation;

(v) the relative importance of the slope and time length of the density-independent (external) inputs in causing negative and positive trends in recruitment to the population/area and fishery and speed of rehabilitation of stock nucleii from very low orbits of stability.

(vi) "backward dependency" or memory effect in a short lived stock: it was not understood that the memory effect can go longer backwards than one year (the time length for the stock to be replaced). This dependency which can go several years backwards is mediated by through recruitment numbers. Offspring mediate some of the parameters which affected the life history of preceding generations beyond the time length for which the stock is replaced.

Also, we further observed (i) a negative medium term (20-30 years) trend with environmental and fishing mortality control components and (ii) oscillations (even under Total Allowed Catches, TACs) occur due to density-dependent processes (4-8 years time scale) and environmental (density-independent) inputs.

Furthermore, the external variables which, so far, we may consider as "best descriptors" are SST Anomaly and Sea Level Pressure (Southern component of the NAO) at Ponta Delgada (Azores): during early 90's, these variables could explain positive trends (compensation) in catches (and recruitment to the population, area and fishery) whereas, during the late 90's, negative trends (depensation) may have been the result from the combined effects from the environment and relatively high fishing mortality during simultaneous density-independent and density dependent depensations. This may have resulted in the low orbits of stability observed at the present time due to a slight compensation after year 2000.

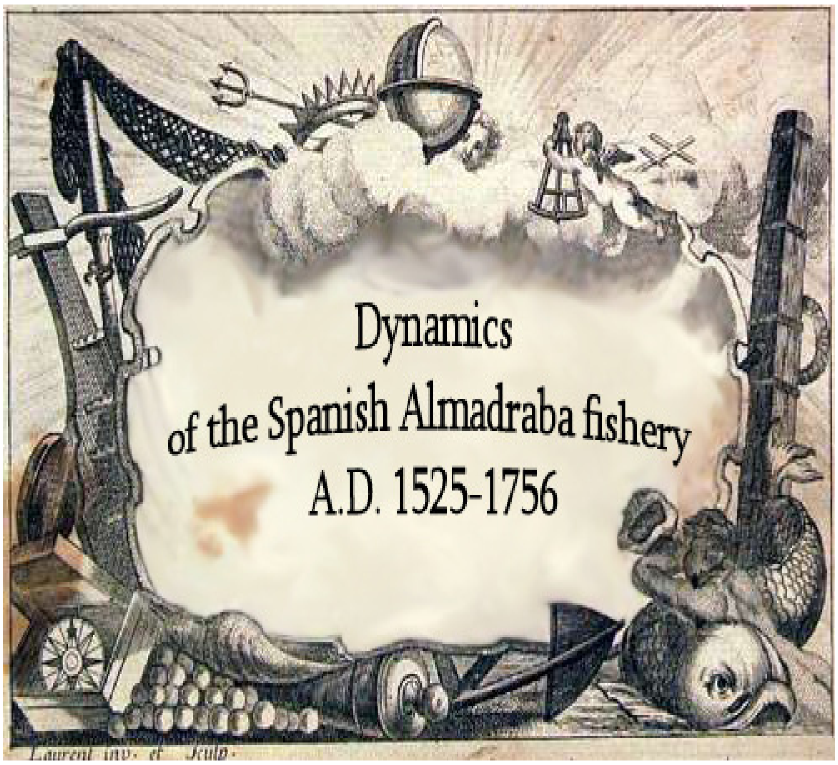
Although the variable carrying capacity of the population systems are assumed in our framework to be multivariate, our results show that we may estimate compensatory and depensatory trends in recruitment for the common *Octopus* in the studied areas by using SST both as a single external variable or as the difference between temperature within and outside the eddy generated by the upwelling: it is assumed that there may be an optimum singular (pseudo-equilibrium) point between temperature and recruitment which may be described both by linear and non-linear relationships.▪

CHAPTER 3.5

Dynamics of the Spanish “Almadraba” fishery

(1525-1756)

Approaching the past to understand the future



3.5 Dynamics of the Spanish "Almadraba" fishery (1525-1756): approaching the past to understand the future.

3.5.1 Abstract.

This chapter addresses the dynamics of the (bluefin) tuna oriented Spanish "Almadraba" trap fishery (1525-1756) after a compilation of captures published by the monk Martin Sarmiento in 1757. Pooled data from the Conil and Zahara almadrabas with over 95% of the total captures, during the 231 years of the series was analyzed in light of a new, non-linear model proposed by Solari et al. (1997) in which recruitment to the population, area and fishery is considered as a dynamical continuum (with local dynamics) governed by a variable carrying capacity. Catches are both considered as a proxy for abundance and related to reconstructed series of annual temperature for the Northern hemisphere which is used as a climatic proxy. Dependency on preceding values, lags, correspondences, periods and orbits of stability between the (log transformed) variables are shown by auto- and cross correlations, spectral and wavelets analysis and linear and non-linear curve fitting procedures. The Hurst exponent is used as a quantitative measure of the deterministic nature of the underlying trends. A strong multi-oscillatory (with three areas of stability) relationship is proposed between for the catches-temperature relationship. The fishery system is suggested to be controlled by trends both in maxima (as temperature is above the mean) and minima (as temperature is below the mean) during a "mini" ice age starting in the mid 1600's which implied an environmental induced collapse on the fishery. A theoretical representation of a multi-oscillatory attractor is proposed for the fishery. Finally, it is suggested that contemporary (20th century) data for the bluefin tuna fishery shows a similar response to Sea Surface Temperature Anomaly in the Northern hemisphere.

3.5.2. Introduction.

In the Spanish Atlantic coast, the "Almadraba" (from Arabic "fighting ground"; RAE, 2007) trap fishery (henceforth, also, referred as "almadraba fishery") consisted either of a beach seine or fixed trap nets set off shore: both fishing grounds and methods (Fig. 3.5.1 a-b) remained similar for over two thousand years (López-Capont, 1997) and the main target species of this fishery were tunas, particularly bluefin tuna in their eastward spawning migration (Rodríguez-Roda, 1983; Agudo, 1991; Regueira and Regueira, 1993). Out of the fourteen operational almadrabas along the Spanish Atlantic coast between years 1525-1756, the main were

"Conil" and "Zahara" which consisted of nets 400 mt in length, 42 mt in depth and each required over 300 men to be operated.

Figure 3.5.1 a. Geographic localization and names of eight out of the fourteen almadrabas along the Atlantic coast of Spain, during years 1525-1756. The Conil and Zahara almadrabas were the most productive with over 95% of the total captures, during the 231 years of the series (after López-Capont, 1997).

Figure 3.5.1 b. Above, the "Hercules" almadraba with a purse-seine net, 400 mt in length, 42 mt in depth, an operation which required over 300 men (after Medina Sidonia Foundation, 2005).

There are several aspects which make the catch series from the Spanish Almadraba fishery scientifically interesting:

(i) in Spain, the declaration of fish catches was compulsory until September, 1767, and the yearly landing series compiled by the monk Martín Sarmiento (due to a request from the fishery consigner, the Duke of Medina Sidonia, in 1757; López-Capont, 1997) makes the longest available time series of tuna oriented catches in the Atlantic;

(ii) it is assumed that fishing power was relatively constant in the Atlantic coast of Spain between 1525-1756, during the years comprehended by the series (Ravier and Formentin, 2001);

(iii) catches were samples from the migrating tuna cohorts/stock and occurred in absence of either industrial fisheries or recruitment over fishing;

(iv) the relative effects of environmental fluctuations and climatic change on the dynamics of the fishery could be reflected more clearly than in modern series;

(v) reported catches may give us an indication of trends in recruitment both to the area/fishery and adult population, during over two centuries.

In previous papers by Solari et al. (1997), Bas et al. (1999), Castro et al. (1999) and Solari et al. (2003), we proposed recruitment to the population, area (migration of cohorts/individuals into fishery areas) and fishery (dynamics of the fishery) as a system or summation of non-linear functions (multiple orbits of stability or equilibrium states) with dynamic features ranging from chaos (when external conditions are extremely benign), going through a range of relatively stable, convergent cycles (as external stress increases) to a standstill state with no clear oscillations (when the minimum viable population is being approached): the system was suggested to have the capacity to, persistently, evolve and return within a wide range of equilibrium states (orbits of stability) allowing for multiple carrying capacities as well as density-dependent (compensation and depensation due to population numbers), density-independent (compensation and depensation due to environmental fluctuations and fisheries) and inverse-density-dependent (per capita reproductive success and recruitment declines at low population levels) coupled mechanics. However, this framework was developed for the dynamics of populations under high exploitation regimes in which (i) maxima diverged as environmental conditions allowed higher recruitment and (ii) minima converged as a response to the combined effects from high fishing mortality during density independent depensatory trends (induced by environmental stress).

In this chapter, we will attempt to address the dynamics of the historical fishery and the aims are to (i) analyse the catch and (reconstructed) temperature data; (ii) show the phase planes representing the relationships between trends in recruitment-to-the-area (or fishery) and stock-at-location and temperature as independent variables; (iii) propose a general model for the dynamics of the fishery and (iv) discuss possible implications of exploited tuna populations either governed by the environment (historical case; climatic change) or the combined effects from the environment and high and intense fishing mortality (contemporary cases). The core in our discussion will be based on the new, non-linear framework we have developed (after Solari et al., 1997). Further historical or other aspects of this fishery are beyond the scope of the present chapter and may be reviewed elsewhere in the literature.

3.5.3. Data and methods.

The yearly landing series (N individuals) between 1525-1756 from the Almadraba fishery were compiled by the monk Martín Sarmiento and sent to –as per request of- the Duke of Medina Sidonia in 1757. A facsimile of the letter was reproduced by López-Capont (1997). We used the pooled series from the two main almadrabas which were operational over the 231 years and made up 95.2% of the total captures (the "Conil" and "Zahara" represented 41.58 and 53.64% of the total catches from all of the fourteen almadrabas, respectively). Out of the 231 years, the original series from the Conil and Sahara almadrabas had 22.4 (N=52) and 31.9% (N=74) missing values, respectively. Each of the series were linearly interpolated prior to pooling them.

To match the catch data, the temperature series used herein are reconstructions of annual global air temperature patterns from 1400 AD to 1995 (after Mann et al., 1998; NOAA, 2007): this data is based on the multivariate calibration of widely distributed high-resolution proxy climate indicators and provide insight into both the spatial and temporal nature of climatic variations during the past six centuries.

Furthermore, we used modern bluefin tuna capture (after FAO, 2005) and Sea Surface Temperature Anomaly (after Kaplan et al., 1997, 1998;

IRI/LDEO, 2007) series in order to further investigate on these matters: on the one hand, it was interesting to know whether there could be similar contemporary patterns of population response to environmental perturbations and, on the other hand, whether such responses (if any) could be similar both in the past (in absence of industrial fisheries and recruitment over fishing) and the 20th century (industrial fisheries and possible overexploitation/recruitment over fishing).

Moreover, we have considered both the catch and temperature series as proxies for abundance and climatic change, respectively.

The series were further (i) log transformed to make them stationary; (ii) standardized to the same scale (Z values with mean = 0) and (iii) smoothed, using a 5-year moving average window, in order to facilitate both the analyses and visual comparison.

The data analyses was carried out using (i) autocorrelation, to detect persistency or memory effect; (ii) the Hurst (H) exponent (after Hurst, 1951; Auto Signal, 2002), as a quantitative measure of the deterministic nature of the underlying trends: while values of $H = 0.5$ correspond to Gaussian or true white noise (i.e. the observations are independent from preceding values), values of $H \geq 0.75$ will reflect a persistency or memory effect (each data value is related to some number of preceding values) in the time series; (iii) the Welch method (Oppenheim and Schafer, 1975) to estimate the spectral density, in order to establish the frequency and time length of the oscillations and (iv) the Pearson correlation, to determine the degree of correspondence between the series.

Furthermore, we used the Time Frequency Analyses of the Wavelet Transform, WT, (after Percival and Walden, 2000; Insightful *S+8*, 2007) in order to study the catch series in different frequency domains. The WT decomposes a series into time-scale or time-frequency domains and it is a powerful tool suited for the analysis of time-frequency localization and non-stationary behaviour of time series: this method allows for the identification of temporal changes of dominant modes of variability while the classical Fourier Transform processes the contents of the whole series.

The data was fitted both by linear and polynomial regressions to determine both overall equilibrium values and the evolution of the dynamical trajectory, respectively. Each pseudo-equilibrium and orbit of stability requires three constants in order to approximate the system of linked functions we propose.

3.5.4. Results.

The log transformed and standardized catch and temperature series are shown in Fig. 3.5.2. The capture series was stationary after log transformation (Kolmogorov-Smirnov Normality test, d = 0,06465, NS) and showed a multi-oscillatory nature of the "Almadraba" fishery: (i) on the one hand, the autocorrelation showed a dependency or memory of approximately 33 years (using 95% confidence intervals); (ii) on the other hand, the spectral analyses showed peaks for 80 (58-77) and 20 (14-25) years periods (Fig. 3.5.3). Furthermore, we addressed processes of 2 (assumed as noise), 4-8 (assumed as density-dependent) and 16 (assumed as a consequence of solar activity cycles plus a lag of 4 which is a common recruitment delay in tunas) years using the Wavelet analyses (Fig. 3.5.4): A5 shows the denoised series in which we observe the medium and longer term periodicities in the catches. Also, while there are shorter term oscillations in the catches, the longer term trend for the whole of the series is negative. D2 to D4 show the 2, 4, 8 and 16 years processes and there are three common discrete zones starting approximately at years 1570, 1640 and 1687. We will show that this fishery may have been governed by a minor ice-age (climatic change) starting approximately around the year 1640 and reaching the maximum stress point between 1687-1705. An interesting factor in the capture series is the temporal evolution of noisy processes (D1): differences in noise are clear between the marked zones and it increases with time. Also, density-dependent processes (assumed as recruitment to the population and fishery; D2 and D3) show a clear divergence (maxima and minima diverge) starting at year 1640. Moreover, 16 year processes appear to be more stable.

The temperature series showed memories (autocorrelation) of approximately 5 and 50-60 years in the positive and negative ranges, respectively. Also, the spectral analyses (Fig. 3.5.3) showed peaks for periods of 10, 20, 40, 80 and 116 years. However, as we used the Pearson bivariate correlation matrix and partial correlations with time as the control variable on the log transformed raw, smoothed and detrended series, we detected similar results in which the significance in the correspondence between both of the variables ranged from $p< .01$ to .001 (summarized on Table 3.5.1).

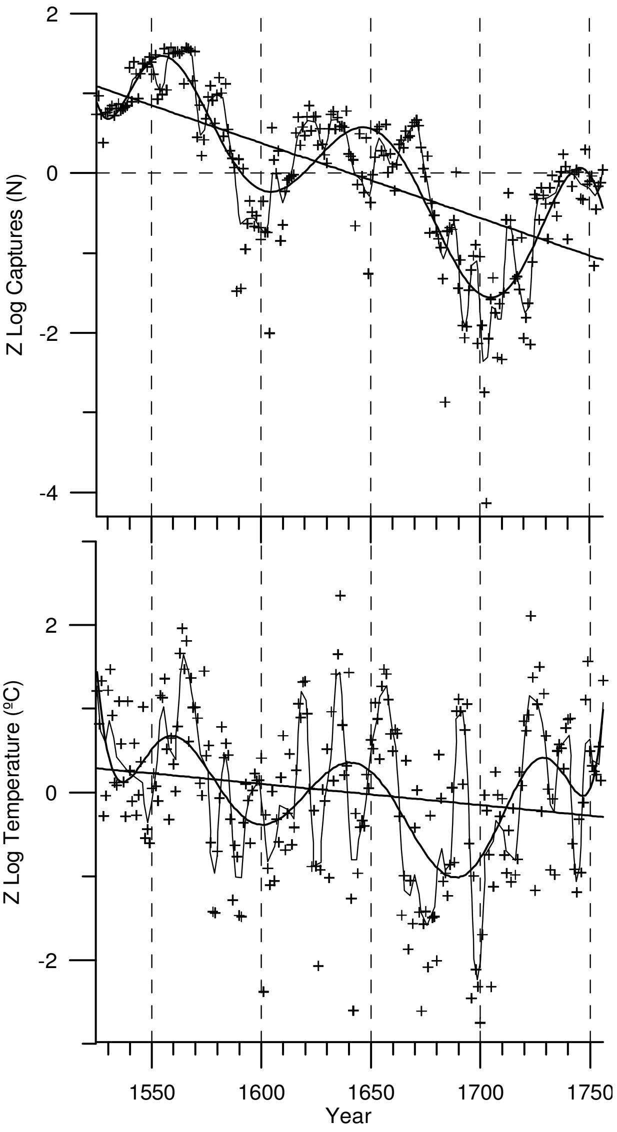


Figure 3.5.2. The log transformed and standardized (Z) Spanish "Almadraba" trap fishery (1525-1756, above) and annual global air temperature patterns (Northern hemisphere; after Mann et al., 1998; NOAA, 2007).

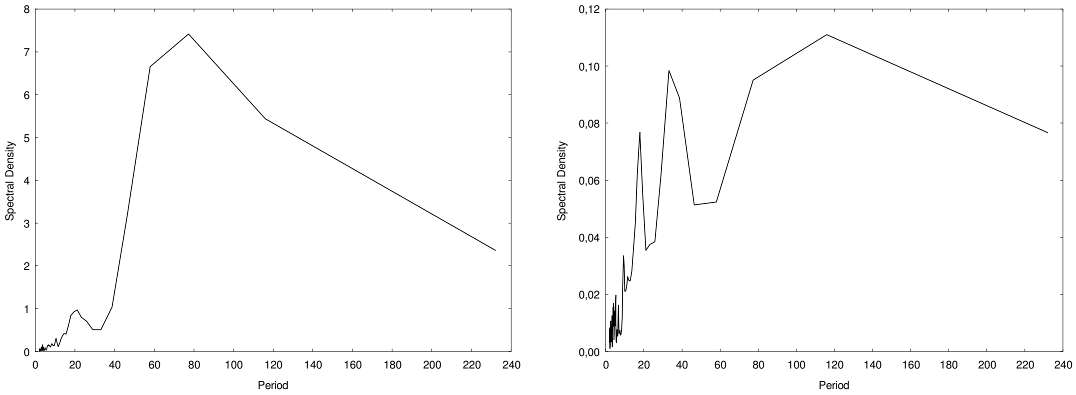


Figure 3.5.3. Spectral analyses on the series of the Spanish "Almadraba" trap fishery (1525-1756, left caption) and annual global air temperature patterns (after Mann et al., 1998) over the Northern hemisphere (right caption).

Correlation	p<	Partial corr.	p<	Series
.256	.001	.196	.01	Raw
.331	.001	.270	.001	Smoothed
.196	.01	.196	.01	Detrended

Table 3.5.1. Results from the Pearson bivariate cross correlation and Partial cross correlation with time a the control variable on the log transformed raw, smoothed and detrended from the Spanish "Almadraba" fishery (years 1525-1756, after López-Capont, 1997) and Temperature Anomaly series (Northern hemisphere, after Mann et al. 1998).

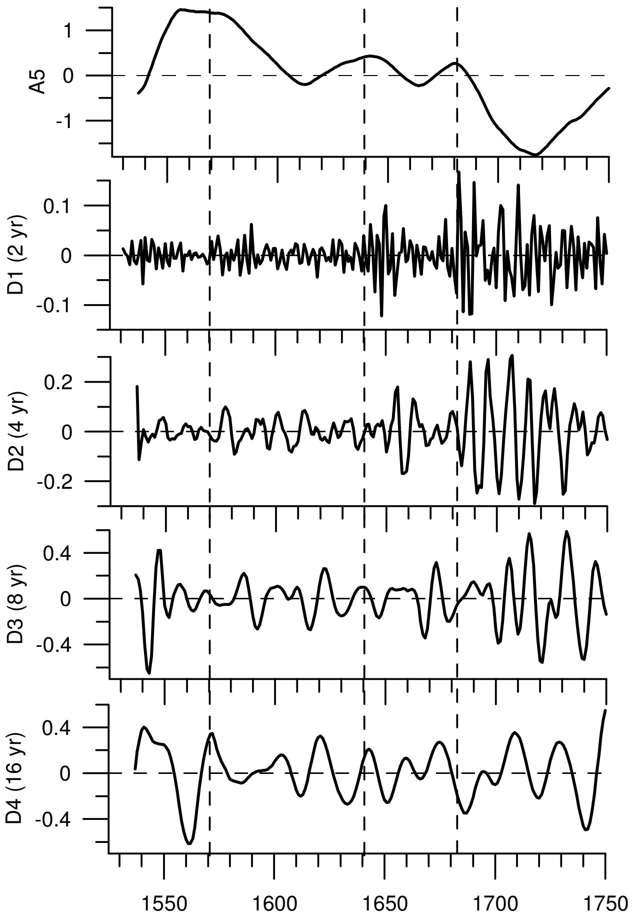


Figure 3.5.4. The wavelet analyses on the capture series from the Spanish "Almadraba" fishery (years 1525-1756). A5 shows the denoised series in which we observe the medium and longer term periodicities in the catches. While there are shorter term oscillations, the longer overall trend is negative. D2 to D4 show the 2, 4, 8 and 16 years processes and there are three discrete zones (indicated by the dashed lines) starting approximately at years 1570, 1640 and 1687. The fishery may have been governed by a relatively minor climatic change (a "mini" ice age) starting approximately around the year 1640 and reaching the maximum stress point between 1687-1705. The temporal evolution of noisy processes (D1) show clear differences between the marked zones and noise increases with time as the sampled populations reached the highest environmental stress. Also, density-dependent processes (assumed as recruitment to the population and fishery; D2 and D3) show a clear divergence (maxima and minima diverge) starting at year 1640. Also, oscillations of about 16 years (assumed as a consequence of solar activity cycles plus a lag of 4 which is a common recruitment delay in tunas) appear to be more stable.

In Fig. 3.5.5, we show the phase plane (Z Log Captures N_t, N_{t+4}) which, according to our framework, may reflect the trends in stock and recruitment in-area and, assuming catches as a proxy for abundance (Appendix I), recruitment to the population, as well. This relationship which may reflect trends in recruitment to the population, area and fishery is of multi-oscillatory nature. The attractor shows three distinct areas of stability (A-C) with local dynamics (oscillations of different shorter periods) and an overall negative trend (assumed to be controlled by a "mini" ice age which started around the year 1640 and determined the carrying capacity of the system). There are three distinct periods (P1-P3) in which noise increases as the system evolves towards the maximum temperature stress (P3). Data was fitted by a simple regression through the origin (straight line) and a cubic spline. Two outliers were excluded from the series.

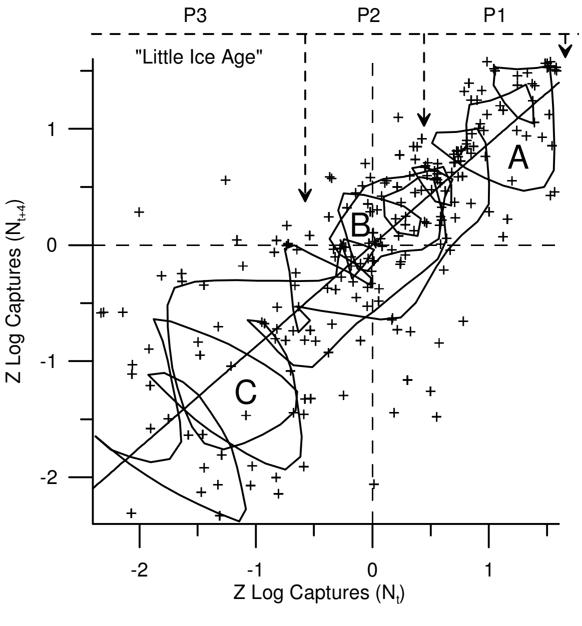


Figure 3.5.5. The phase plane (Z Log Captures N_t, N_{t+4}) on the series from the Spanish "Almadraba" fishery (years 1525-1756). Data was fitted by a simple regression through the origin (straight line) and a cubic spline. Two outliers were excluded from the series.

Fig. 3.5.6 shows the temperature and captures relationship (values were standardized, Z, log transformed and lagged 4 years which is the approximated time lag for recruitment in tunas) on the series from the Spanish "Almadraba" fishery (years 1525-1756). A'-C' indicate three distinct multi-oscillatory areas of stability and K_i the carrying capacity of the fishery (considered as the maximum possible effort the manpower of the almadrabas could carry out). The outlier from year 1703 (British invasion of Gibraltar) may show the relative effect of a conflict on the fishery the value is compared to the range of other minima (M_i) in the series. Data was fitted by a simple regression through the origin (straight line) and a 9th degree polynomial (three constants for each orbit of stability). The dots are the singular points for each area of stability.

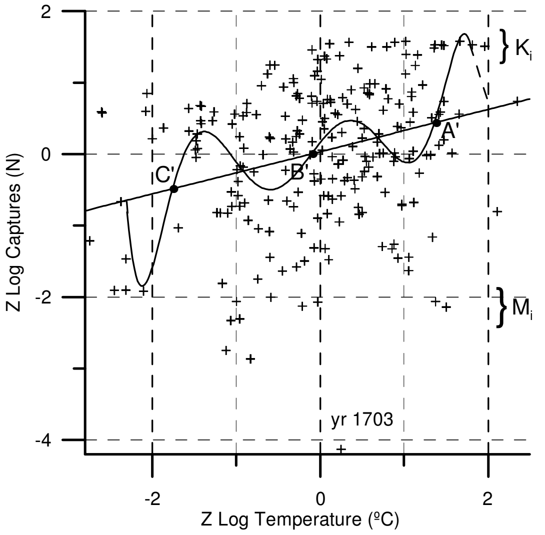


Figure 3.5.6. The temperature (after Mann et al. 1998; NOAA, 2007) vs. captures relationship (values were standardized, Z, log transformed and lagged 4 years) on the series from the Spanish "Almadraba" fishery (years 1525-1756). A'-C' indicate three multi-oscillatory areas of stability and K_i the carrying capacity of the fishery. The outlier from year 1703 may show the relative effect of a war on the fishery as the value is compared to the range of other minima (M_i) in the catch series. Data was fitted by a simple regression through the origin and a polynomial. The dots are the singular points (pseudo-equilibria) for each area of stability. The fishery system appears to be controlled by maxima in temperature (for the higher temperature range above the mean) and by minima and "mini" ice age (for the lower temperature range below the mean).

3.5.5. Discussion.

Although the exact composition of the captures may still remain unknown and we are not certain as to the relative frequencies of the tuna species in the Almadraba fishery, we have assumed the following: (i) the core of the catches was biased towards bluefin tuna as the fishery started to operate to match the timing of the reproductive migration of this species; De Buen (1924) observed that Atlantic almadrabas targeted bluefin tuna and they were more productive than their Mediterranean counterparts; (ii) historical records show that bluefin tuna was the targeted species by the fishery consigner due to the economical or market value; again, we still do not know the exact market value of the product of such a fishery; however, we believe that the value would be relatively high in order to allow the logistics of the operations; the manpower of both of the almadraba operations was over 600 individuals; (iii) the remaining of the species (Frigate and Albacore tunas and Atlantic bonito) may have had marginal abundance impacts over the catches. In the "worst case scenario" (i.e. the composition of captures was not biased by bluefin tunas), the theoretical argumentation presented herein would still apply for a mixed, multispecific tuna oriented trap fishery.

Also, the Almadraba raw series were highly non-stationary. However, once the series are log transformed (stationary), the compiled data by the monk Martín Sarmiento makes sense in a dynamical context if analyzed in light of an additive model which may incorporate a summation of non-linear functions and allow for several, linked areas/orbits of stability: in our framework (after Solari et al., 1997), we proposed the population and fishery as multi-oscillatory system consisting of a dynamical continuum with local dynamics, governed by a variable carrying capacity. Classical population models such as those derived from the logistic equation are unable to resolve/explain the mechanics behind several, linked orbits of stability: under the assumptions of classical models, the data from the Almadraba fishery would appear as a cluster of unexplainable points which should be considered the result of a process close to a random walk.

We have considered both the catch and temperature series as proxies for abundance and climatic change, respectively and even if the series may be noisy, the relationships are clear and strong and this is shown by all of the combined results. Furthermore, in Appendix I, we put forward two arbitrary examples which address the dynamics of an oscillatory population under two linear and two non-linear fishing mortality regimes in order to show that catches may be used (i) as a proxy for abundance and (ii) to infer the dynamics of stock and recruitment to the population and fishery while effort data is either unavailable or unreliable. A sinusoidal fishery or population system governed by wave-like forcings may retain the original dynamical features while scales of numbers change

Also, the ranges of catches around the carrying capacity, or ceiling, and minima, or floor, (K_i and M_i in Fig. 3.5.6) are clear and may depend on several factors: (i) the manpower of the fishery was limited and such limitations could be reflected by the catches under maximum recruitment to the fishery (the K_i of the fishery is highly clear under the higher temperature ranges and becomes lower as temperature reaches the mean and below); (ii) the minimum catches are found across most of the temperature range; this may pose the question on whether the relative effect of trends in temperature maxima or minima can be the best descriptor. In other case studies based on contemporary data (case study on the common *Octopus* off Mauritania in Chapter 3.4 of this thesis and ongoing projects), we have found that trends in Sea Surface Temperature (SST) maxima can be considered a better descriptor (or control variable) relative to trends in minimum SST; (iii) although there is a certain clear range for minimum catches across which shows across the whole of the temperature range, the spatial distribution of tunas (changes of migration patterns) due to the "mini" ice age cannot be excluded. As a curiosity, the outlier from year 1703 may show the relative effect of a war (British invasion of Gibraltar) on the fishery: this may show that political-military, socio-economic, and public health factors (wars, epidemics) may have influenced the manpower available for the fishery.

Moreover, if the fishery or population system was mainly governed by the "mini" ice age in the 232 years period, it could be interpreted as colinearity in the data (correlation is strong but the non-linear and the overall linear trends are negative). However, we run the Spearman R (a non-parametric rank order correlation; Siegel and Castellan, 1988) which assumes that the variables were measured on at least a rank order scale and the individual observations can be ranked into two-ordered series and we obtained a highly significant relationship, as well (R=0.29, p<.001). The temperature-catches relationship and effect of the "mini" ice age are strong.

In summary, the Almadraba fishery showed a multi-oscillatory system with temporal lags, different oscillation periods and an environmentally induced collapse (after which the stock recovered): this phenomenon may reflect a system which fits within the assumptions on dynamical continuum with local dynamics (multiple orbits of stability), governed by a variable carrying capacity as set forth in Chapter 2 of this thesis (after Solari et al., 1997). In this way, we may describe the system by an attractor consisting of simultaneous multiperiodic oscillations with a certain degree of noise represented by a set of functions in a system of equations which is assumed to be auto-similar at several scales: in Fig. 3.5.7 we put forward an arbitrary example of such a ground attractor for the Spanish "Almadraba" fishery (years 1525-1756).

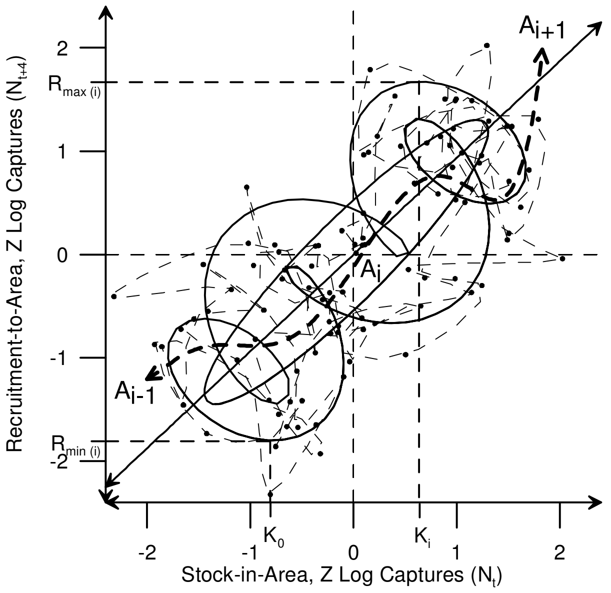


Figure 3.5.7. A theoretical representation of an attractor (Stock-in-area vs Recruitment-to-area or fishery) proposed for the Spanish "Almadraba" 231 year series (1525-1756). The superimposed trajectories represent the longer term cycle within the attractor (ellipse or limit cycle), the intermediate showing the local, shorter term oscillations and the outer which is the interpolation of data points (dots) with a certain white noise. Noise in this context is considered the differences between data values and their closest points from the intermediate trajectory. The dashed line is the dynamical continuum which may evolve (from pseudo-equilibrium A_i) either towards the carrying capacity of the system (K_i) and an upper orbit of stability (A_{i+1}) or the minimum viable population (K_0) and a lower orbit (A_{i-1}). The system is auto-similar and operates at different scales of numbers. R is recruitment to area, fishery and population.

Furthermore, it was interesting to find out whether a similar catch-temperature relationship could exist for bluefin tuna in the 20th century. Fig. 3.5.8 shows the North East Atlantic plus the Mediterranean (after FishStat/FAO, 2003) bluefin tuna captures and SST Anomaly (after

Kaplan, 1998; IRI/LDEO, 2007) raw, smoothed, 4 years lagged and fitted series (years 1950-2005). The cross correlation between the log transformed series is highly significant (p<.01). This may be a strong indication that bluefin populations may respond to trends in temperature in a similar way as we observed in the Almadraba fishery during the 16th-17th centuries. Also, this contemporary data may validate the quality of the compilation carried out by the monk Martín Sarmiento whom we may assume did neither know about population dynamics nor on dynamical systems.

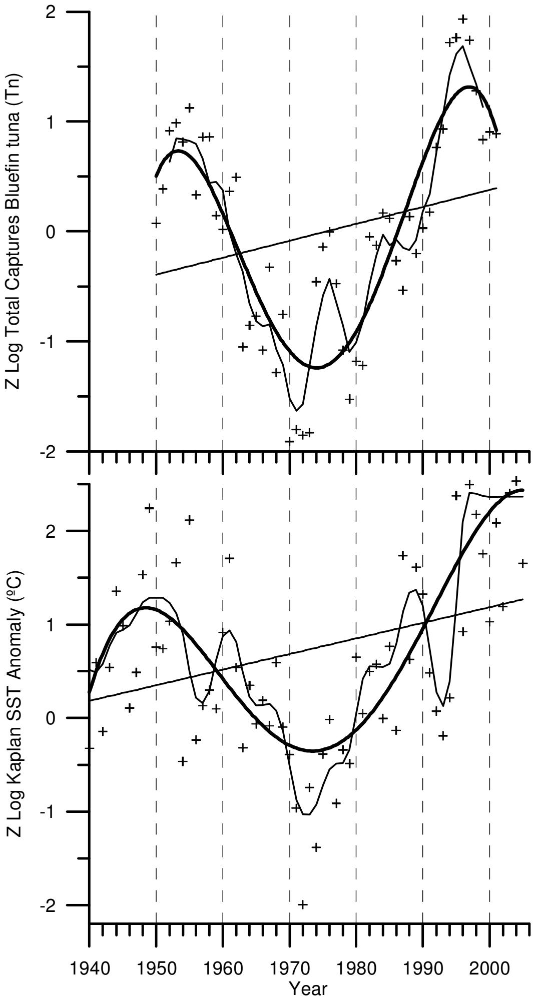


Figure 3.5.8. Captures North East Atlantic + Mediterranean (1950 2002, after FishStat/FAO, 2003) y SST Anomaly (after Kaplan, 1998; IRI/LDEO, 2007). Cross correlation between the 4 year lagged series is highly significant (p<.01).

Finally, we show in Fig. 3.5.9 the multi-oscillatory system proposed for bluefin tuna catches in the North East Atlantic/Mediterranean (1950-2002, after FishStat/FAO, 2003) and SST Anomaly (after Kaplan, 1998; IRI/LDEO, 2007): there are three clear orbits of stability (O_a-O_c) during the 52 years of the series both shown by the cubic spline (dashed line) and polynomial fitting.

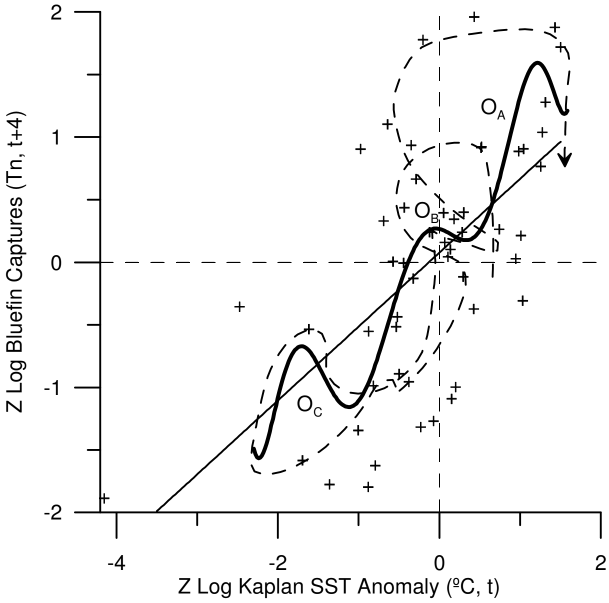


Figure 3.5.9. The multi-oscillatory system proposed for bluefin tuna catches in the North East Atlantic plus the Mediterranean (1950 2002, after FishStat/FAO, 2003) and SST Anomaly (after Kaplan, 1998; IRI/LDEO, 2007).

It would be worth to note both that (i) the contemporary bluefin tuna fishery system shows divergent maxima and minima as the dynamical continuum evolves towards the maximum carrying capacity; this phenomenon is observed in other systems which appear to be controlled both by the environment and fishing mortality and (ii) on the contrary, the

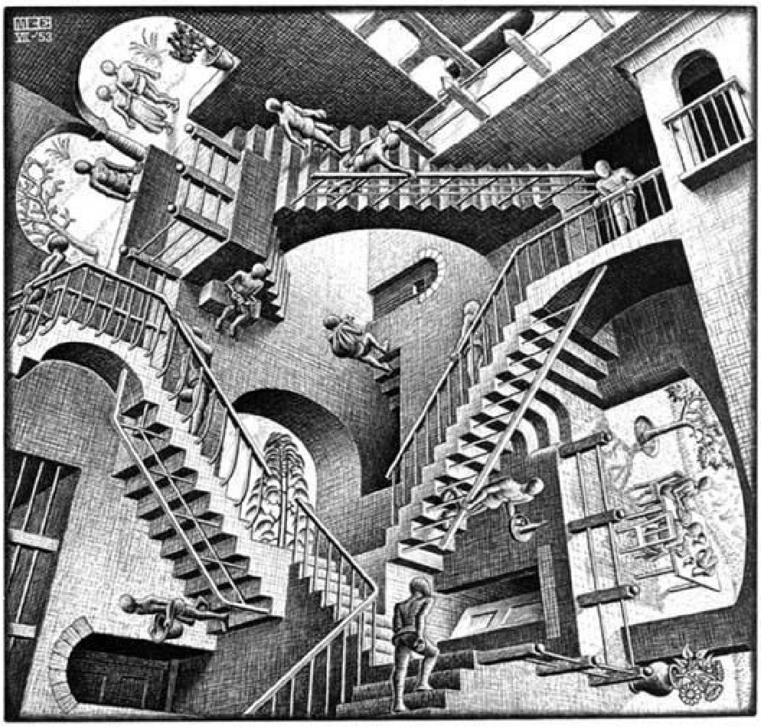
Almadraba fishery which could be assumed to be controlled solely by the environment, maxima and minima diverged as the continuum evolved toward the maximum environmental stress periods.

3.5.6. Acknowledgements for this section.

This investigation was financed by the Ministry of Agriculture and Fisheries of the Canarian Autonomous Government. Collaboration from the Fundación Medina Sidonia is acknowledged. The chapter is dedicated to our friend and colleague *Patrick Nikolaus* (In Memoriam).▪

CHAPTER 3.6

Case Studies:
DISCUSSION



3.6. Case studies: Discussion.

In this section, we discuss several of the concepts of our framework which may be common both to the case studies presented herein and useful to study other exploited stocks worldwide. The discussion is rather extensive as we address several of the key concepts, nomenclature and other aspects of the new framework.

The proposed framework offers several conceptual and practical advantages over the classical models and it may be considered a first step towards the more realistic analyses and explanation of, among others, the following aspects in the dynamics of the studied populations:

(i) the ecological persistency of the SR system: the ability of the stock to withstand both environmental perturbations and relatively high and intense fishing mortality and rehabilitate from low and extremely low equilibria;

(ii) the determination of the combined environmental and fishing effects which may lead either to collapses of the spawning stock, establishment of the SR system around low equilibria and extinction of the commercial fishery;

(iii) the short and medium term forecasting (approximately 4-8 and 9-18 years, respectively) of recruitment: expected time length of short and medium term oscillations in order to adjust exploitation levels, size selectivity and other fishing parameters;

(iv) the explanation of the high variability in the data and determination of how combined, multivariate correspondences, memory effects, time lags, periodic oscillations, noise and sensivity to external conditions affect the SR system;

(v) the preventive control of the population by the study of how fishing mortality affects the SR system both during density-dependent and density-independent compensations and depensations (that is, the differential effects of fishing mortality);

(vi) the retro-calculation and determination of whether population collapses or low to extremely low orbits of stability (near the overall minimum viable population) occurred in the past when neither industrial fisheries nor recruitment over fishing existed;

(vii) the existence of dynamical auto-similarity at several spatio-temporal scales and extrapolation of trends between different spatial scales;

(viii) the multi-dimensional determination of the SR system as function of time, latitude and longitude and how external variables shape the temporal evolution of the "3D structure" which may the population.

This thesis proposed a dynamical framework which may be useful to contribute to the understanding and, hopefully, the management of the fishery resources in the North Atlantic and FAO Fishing Area 34. In our view, the new framework allows the proposition of more realistic and better questions to study complex population dynamics which may be governed both by intrinsic and external, multivariate causal mechanisms.

3.6.1. The proposed Equations

On the one hand, a multiplicative approach formed from a concatenation of functions (Paulik, 1972) could exhibit multiple (stable) equilibria and complex dynamics: stock and recruitment may be described by the result of a multiplicative process where the initial number of recruits could be modified by non-linear functions specific to each sub stock at a certain spatial location. Such an approach could be an extension of the model proposed by Paulik (1972) for an overall spawner-recruit system. However, the drawback of the multiplicative approach is the interdependence between the functions which would imply the collapse of the system once any "near-zero" recruitment occurs or whenever "outliers" or extreme fluctuations appear to control anyone of the steady states, any one year. On the other hand, an additive approach such as the model proposed by Solari et al. (1997), where the stock-recruitment system is described as a summation of non-linear functions, is extremely flexible and may show complex dynamics for each of the steady states: while equilibria are linked they are mathematically independent and the model may describe a wide range of dynamical situations (chaos, cycles, quasi-cycles, standstills). Both of these approaches may be approximated by sixth order polynomial regressions for a two-steady-state system.

3.6.2. The phase planes.

These relationships may be assumed to describe the dynamics of the exploited skipjack population irrespective of the fishing effort assuming the following criteria: fishing mortality may either (a) become asymptotic as the fishery approaches the so called “zero net value” (i.e. economic over fishing resulting in benefits reduced to zero followed by a stabilizing reduction in the fishing effort, as suggested by Clark, 1976) or (b) cycle due a backward bending (depensatory) yield against effort relationship due either biological over fishing (as described by Pitcher and Parrish, 1993) or reductions in recruitment due either environmental perturbations or the combined effect between the environment and fishing mortality during depensatory trends (as described by Solari et al., 1997). Both of these assumptions imply that fishing mortality may reach a ceiling which may either be asymptotic during periods of relative environmental stability or follow depensatory trends towards lower equilibrium states as the external environment becomes less benign.

3.6.3. Variable carrying capacity (ceilings, K_i).

This is a central concept in our criteria and we were first to formalize it. While carrying capacity is considered as a single value in the classical approaches, we assume (a) it may be multiple and a threshold between equilibrium states; (b) it will link different equilibria and each particular steady state will show a particular ceiling or value of carrying capacity and (c) it may be quantitatively different at different spatial scales while it will remain similar, qualitatively. In our view, it may be more realistic to consider a population parameter such as K_i as variable: on the one hand, the skipjack population migrates through relatively large geographic ranges where it will encounter a continuous transition scheme with a multiplicity of external perturbations; on the other hand, density independent inputs will determine different levels of numbers recruited implying a particular K_i for each orbit of stability.

3.6.4. Minimum populations (floors, P_i).

As numbers decrease either due fishing mortality, external perturbations or the combined effects from both of these factors, each steady state may, gradually, shift towards a critical value or unstable equilibrium under which stock and recruitment will “jump” onto a lower, relatively stable equilibrium state. Also, the per-capita reproductive success may decline at lower population levels implying that reduced numbers of individuals are recruited to the area of the fishery. Floors may be approached through either density-dependent or density-independent depensation; both of these depensations combined may generate rapid shifts towards lower equilibria. Furthermore, the proposed system may contain an overall minimum viable population under which (a) no oscillations in stock and recruitment will be detected and (b) the commercial fishery may cease.

3.6.5. Multiple (stable) equilibria and pseudo-equilibria (E_i).

There is no evidence in the field data to assume the dynamics of the population systems are governed by a single attractor and a global, invariant carrying capacity and that residuals could solely be a consequence of either random processes or noise. The observed structures and temporal evolution in the data may rather suggest that population systems are governed by multiple attractors (and repellors) which are dynamically linked by multiple carrying capacities and minimum populations through which stock and recruitment may, persistently, evolve and return between a wide range of orbits/pseudo-equilibria allowing for stable, periodic and chaotic dynamics. The trajectories may turn in orbits of stability determined both by density-dependent compensatory and depensatory phases. These pseudo-equilibria may be linked through floors (or minimum threshold values) and ceilings (or maximum threshold values) which appear during transitions determined by the combined effects from fishing mortality and environmental fluctuations: these critical values may be regarded as the minimum population for the higher equilibrium state and the carrying capacity for the lower equilibrium. As recruitment reaches K_i, the system will "jump" onto the higher equilibrium whereas it will enter the lower equilibrium as P_i is approached. Also, we may observe that pseudo-equilibria (a) converge as they tend either to zero or to an overall minimum viable population (K_0) and (b) diverge as they tend to the overall ceiling of the system or maximum carrying capacity (K_{max}). Multiple, linked orbits of stability both within and between relevant spatial scales may describe the dynamics substocks, stock nucleii or local populations. Also, classical approaches may describe different unlinked regimes but will not explain the complex dynamics behind the data. The idea of a dynamic continuum is appealing to describe the phase-space and temporal evolution of a persistent system. Rothschild (1992) suggested that populations reduced by fishing or anthropogenic substances which compensate for reductions in vital rates may easily transit among stable, periodic and chaotic population dynamics. Garcia (1998) and Sharp et al. (1983) suggested that the Hokkaido sardine series were characterized by loops and proposed an oscillating system consisting two strange attractors, linked by some transitional shifts, operating at two different levels of spawners and recruits. Furthermore, Berg and Getz (1988) suggested that stock and recruitment, in a sardine-like population, moved along a path or attractor in some higher dimension coordinate system; Conan (1994) observed that lobster and snow crab landings in Atlantic Canada may follow two orbits of stability or cycles; Powers (1989) suggested chaotic behaviour for a 2 species system of fish and Tyutyunov et al. (1993) demonstrated cycles of different period and chaos in population dynamics of perch from 10 lakes. Moreover, Caddy (1998) pointed out several other cases, in semi-enclosed areas, where stock and recruitment dynamics could be linked to oscillatory phenomena: (i) an apparent 9-18 year periodicity for the Bay of Fundy scallop stocks (Caddy, 1979); (ii) a 12 year, fishing-effort-independent periodicity in the landings of both hake and red mullet at the island of Mallorca in the Mediterranean Sea (Astudillo and Caddy, 1986) and (iii) a 12-13 year oscillatory pattern in the catches of the Adriatic sardine.

Further key aspects in our approach, such as (i) the equation and matters concerning both the (ii) replacement line, (iii) equilibria/orbits of stability, (iv) variable carrying capacity or “ceilings” (K_i), (v) maximum allowable carrying capacity (K_{max}), (vi) minimum viable populations or “floors” ($K0_i$) and (vii) minimum allowable population (K_0) are extensively discussed in our earlier papers by Solari et al. (1997), Bas et al. (1999), Castro et al. (1999) and Solari et al. (2003).

3.6.6. Compensatory and depensatory dynamics.

In each steady state, oscillations may be due both density-dependent compensation (numbers increase) and depensation (numbers decrease): stock and recruitment will be affected by short and medium term external perturbations, oceanographic diffusion-advection processes, migration between schools, availability of food items, fishing mortality and catch-effort oscillations as well as several other both internal (population) and external (environmental, fishing related) factors which will determine the temporal evolution of an equilibrium state. Also, transitions between equilibria may be caused either by density-independent compensation (as the environment becomes more benign and recruitment increases) or density-independent depensation (as external stress increases). While fishing mortality may be incremented during density-independent compensation, reductions may not be enough while density-independent depensation is operating. Also, the combined effects of fishing mortality during both density-dependent and independent depensation may imply the rapid shift towards both the floor of an equilibrium and, hence, a lower steady state.

3.6.7. Dynamical continuum.

The SR trajectory may follow a transition patterning caused both by intrinsic (due to density-dependent processes) and extrinsic (due to density-independence; environment and fisheries) forcings: we may assume that all processes can be linked to a dynamical continuum which is mediated by (i) a range of orbits of stability which operate between the overall minimum viable population (K_0) and the maximum allowable carrying capacity (K_{max}) and (ii) a constantly changing carrying capacity which will govern system trends. Transitions towards different orbits of stability may occur as some threshold values ($K0_i$ and K_i) are reached. The idea of a dynamical continuum can be investigated, to better understand and, thus, determine the temporal evolution of the SR system and interactions of two or several multi-oscillatory phenomena (stock and recruitment under environmental and fishing influences). Garcia (2004, Serge.Garcia@fao.org, personal communication) suggested both that (i) smooth shifts in stock response may arise due to continuous changes in climate, that is multiple state responses of the spawning stock in the case of multiple states of the environment and (ii) the multiple-oscillatory system could be a "one-state-only" with continuous shifts between levels of numbers and no level being a "stable state" in any way due to the ever changing nature of the carrying capacity. The idea of dynamical continuum can be interesting both to determine and understand the temporal evolution of the SR system. Also, it may induce us to ask better questions as to why the trajectory of the population is shaped in different ways. Sharp et al. (1988, 1997, 1998 and 2002) suggested that the present state of world fisheries can be attributed to the denial of the importance of system dynamics.

3.6.8. Global and local dynamics.

Global dynamics may arise as a consequence of density-independent transitions between different orbits of stability and it can be the result from both major (medium/longer term) environmental pulses and an oscillating carrying capacity which allows the SR system to evolve and return between higher and lower phase states. Also, local dynamics (minor orbits of stability within the overall trajectory) could be the result of relatively minor external pulses: these changes may either occur due to a short term externally forced compensation trends combined to an increase in the fishing effort or due to minor environmental pulses alone such as we show in the present paper. The concept of local dynamics is interesting and it is the first time we detect such a phenomenon in our analyses on several populations. If a SR system is sufficiently sensitive to external pulses to show local dynamics, this feature may contribute both to the overall stability and persistency of the population.

3.6.9. Residuals: signal, noise and variability.

While classical models assumed that residuals were fully the result of a random process, we propose herein that these values, to a high degree, comprise signals which incorporate noise due to sampling errors and dispersion/contraction processes within the marine ecosystem itself. This assumption is based on results from the correlations and detected memory effects in the series. In general, classical models could explain up to 20-40% of the variability in the data. It is unrealistic to assume that 60-80% of the variability is caused by unidentifiable random processes. Also, as the temporal evolution of the series is considered, and information time series grow, this source of error becomes of lesser importance to the interpretation of the data. In our approach, residuals to a smoothing equivalent to a moving average with a 5 years window are considered as noise. Issues which may require more investigation are whether (i) noise, as part of a diffusion/advection process, contributes to persistency at the system level and (ii) whether it varies significantly depending on the nature of the external pulses affecting the SR system. Furthermore, we assumed that noise may be variable as it may increase as the SR system shifts towards higher population levels or K_{max}: this could be explained by the divergence between maxima an minima and density-dependence conditions in higher orbits of stability. As we see it, the concept of variability which arises from premises such as equal statistical weight for all of the data values and a 2^{nd} order fitting (classical models, "hockey stick" approach and the logistic equation) may be a human artefacts.

While some authors still rely on assumptions from classical (logistic derived) population models would argue that residuals are both independent of each other and a result of a random process, series of normal random numbers, plotted in the phase plane, may in some cases show single (but not multiple) orbits of stability and (from the 500 series that were tested) in no case showed significant results (auto and cross correlations, spectral and Hurst analysis and different curve fitting approaches) that could be similar to the population and environmental series we have studied.

Auto correlated residuals is another factor which we should carefully analyzed while dealing with data from highly non-linear systems with strong dependency between population and environmental or anthropogenic variables. In case this factor is considered of relevance, a trends subtraction such as $(x=x-(k_1+k_2*t)$ where t is the case number and k_1, k_2 are user defined constants could be computed. In this way, the values of the series can be transformed to remove the trend over time. However, it may be assumed that auto correlated residuals may be intrinsic to the nature of population and fishery processes.

3.6.10. Differential effects of fishing mortality.

The effects of fishing mortality are differential, according to our framework: (i) during density-independent compensation, fishing mortality may not affect the positive trend significantly (unless the orbits of stability are extremely low); this implies that fishing effort may be increased without perturbing negatively the SR system; (ii) however, as the trajectory reaches K_i and it turns into density-independent depensation, the effects of fishing mortality may contribute both to speed up the negative trend (the rate of increase becomes lower than otherwise) and shift the trajectory to lower equilibria; (iii) also, during density-dependent compensation, fishing mortality could be maintained relatively constant (unless numbers are extremely low) until a depensatory phase starts operating (after which the fishing pressure should be decreased); (iv) furthermore, during density-dependent depensation, the effects of fishing mortality may be negative if a similar fishing pressure is maintained as during the preceding compensatory trend; in such a case, fishing should be decreased, particularly, as both types of depensation start operating simultaneously. Each orbit of stability may allow a particular level of fishing effort, differentiated due to both the different stages of the oscillation, the level of numbers and the operating K_i.

3.6.11 Harvesting on multiple equilibrium systems.

As opposed to single equilibrium systems such as those described by the classical models, systems with multiple orbits of stability may retain their dynamical structure even as fishing effort increases linearly: on the one hand, fishing mortality may increase until an oscillation reaches K_i after which it will drop during depensations; on the other hand, if fishing effort is further increased, during the depensatory phase of an oscillation, the SR trajectory may rapidly shift towards lower equilibria and, consequently, fishing mortality will be lower. This stabilizing mechanism with memory effects and time lags may be the cause of the ecological persistency of the system.

3.6.12 Extinction of the commercial fishery.

There are several aspects which may be interesting to discuss concerning possible extinctions of the commercial fisheries on the studied populations. Several mechanisms may operate either alone or combined:

(i) economical over fishing may imply that fishing mortality becomes asymptotic as the fishery approaches the so called "zero net value" (i.e. economic over fishing resulting in benefits reduced to zero followed by a stabilizing reduction in the fishing effort) as suggested by Clark (1976);

(ii) recruitment over fishing may occur due to a backward bending (depensatory) yield against effort relationship due to biological over fishing (as described by Pitcher and Parrish, 1993);

(iii) establishment of the SR system around extremely low equilibria, near K_0, due to either erratic environmental perturbations or the combined effect from the environment and fishing mortality during depensatory trends (as described by Solari et al., 1997);

(iv) furthermore, inverse-density-dependence (Allé effect) will cause the extinction of the fishery as recruitment may tend to zero as the trajectory evolves below K_0.

3.6.13 Incorporating external perturbations.

Finally, we put forward a modified equation of our model which may be used to further analyse the SR system in the studied populations.

Let consider the SR system as a relationship consisting of *m* equilibrium states for which the parameters a_i, b_i and c_i are fixed and determine their stability limits. In this way, the spawning stock at the beginning of any particular year, S_{t+1}, is given by

$$S_{t+1} = \sigma \cdot S_t + R\left(S_{t-\tau}\right) \qquad (3.6.1)$$

where σ is the survivorship coefficient affecting the spawning stock, S_t, and recruitment (R) is a function of the existing parental stock τ years before (equal to the age-at-maturity). Hence, recruitment is given by

$$R\left(S_{t+1}\right) \cong \sum_{i=1}^{m} \frac{a_i \cdot P_t \cdot (S_{t-\tau})}{(S_{t-\tau} - b_i)^2 + c_i} \qquad (3.6.2)$$

where the entries a_i, b_i, c_i are those defined for Eq. 1 and τ is a fixed delay of one year.

P_t is a the perturbation term which may incorporate values from standardized, smoothed variables ($V_1 \ldots V_n$) as a summation and becomes

$$P_t = \sum_{t=1}^{n} V_{t-T} \qquad (3.6.3)$$

where T is the delay or time lag for which the cross correlation with the recruitment (to the population or fishery) series is the highest.

There are several aspects of further relevance for the perturbation term: (i) each variable should multiply a factor (α) depending on the relative effect upon the SR system; (ii) time lags can be varied both as different, partially overlapping cohorts are considered, sub-stocks from different areas are analyzed (there may be a positive relationship between sub-stock size and lag) and areas of different size are considered and (iii) the impact of the external variables upon size classes may be differential. These factors remain to be investigated.

3.6.14. Curve fitting multi-oscillatory, dynamical systems.

In general, curve fitting multi-oscillatory systems require computer based, non-linear methods. Also, it may be necessary to use several methods simultaneously on the raw, smoothed and (log and square root) transformed series.

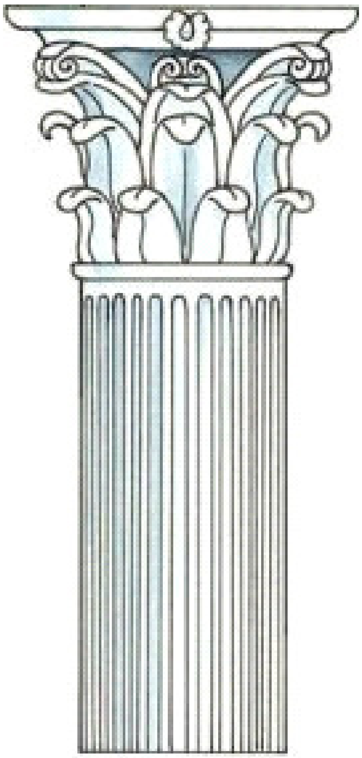
The framework we propose can be approximated through least squares, linear and non-linear regressions, lowess and smoothing techniques (cubic splines, running averages with different windows and similar approaches). For instance, the orbits of stability can be approximated by cubic splines, bivariate ellipses and smoothing using a 5 year window while the dynamical continuum in the system can be approximated by polynomial, lowess and other types of non-linear methods. The critical factor to analyse such complex systems is the ground theoretical population model without which statistics per si may become less useful tools.

3.6.15. Critique.

There are several aspects which should be mentioned in a critique on the present study: (i) we have further developed the concepts of steady-state and equilibrium state to both orbit of stability and pseudo-equilibrium which may be more realistic: the carrying capacity of the system (either seen as K_i and/or K_{max}) will shift permanently. This implies that orbits of stability will oscillate around pseudo-equilibria; (ii) we have used catch series as a proxy for abundance: while some authors may argue that rising fishing effort will make catch data overestimate biomass increases and underestimate biomass decreases, we showed in Solari et al. (2003) dynamical auto similarity in recruitment to the fishery of the skipjack (*K. pelamis*) for three significantly different spatial ranges with different fleets, fishing gears and, hence, different efforts; (iii) Garcia (2004, Serge.Garcia@fao.org, personal communication) suggested both that if effort data could be added onto the analyses of *(Octopus)* abundance (as reflected by catch) and NAO index, correlations could explain most of the variance in the data set and (iv) global dynamics could be linked to economical, market cycles; during years 2008, we have started to incorporate macro-economic and market variables into the approach; for instance, we have started to use oil barrel price evolution, local currency values relative to the Euro and inflation, factors which may be of high impact to the economies and fisheries in developing countries; (iv) although it may be argued that cross-correlation between population and NAO series could be "inflated", we might exclude a significant bias as both of the variables are not from a same composite (they respond to different processes) and the difference of the correlation on the raw and smoothed data is one degree in statistical significance.▪

CHAPTER 4

CONCLUSIONS



and

Future Work

4. Conclusions.

In this section, we shall briefly review some of the aspects which may be of relevance both to our further developments and for a wider application of our approaches in fishery science. New models in population dynamics are rare due to the difficulties and challenges associated to the proposal of scientific theories.

4.1 This thesis contributes with a new theoretical framework (that is, a new population model which has been further developed into a theory) for the study and exploitation of fishery resources.

4.2 In the model, recruitment (to the population, area and fishery) is regarded as a system or summation of non-linear functions 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).

4.2 It is proposed a population system and fishery which consist of a dynamical continuum governed by a variable carrying capacity.

4.3 Local dynamics are described for different orbits of stability each of which show a particular carrying capacity and minimum population.

4.4 It is the first time that the concepts of variable carrying capacity, multiple, linked orbits of stability and pseudo-equilibria, and dynamical similarity at several spatio-temporal scales are formalized.

4.5 Also, it is the first time that in a single model all of the known population mechanics (that is, density-dependent, density-independent and inverse-density-dependence processes) have been linked in a relatively simple equation.

4.6 The proposed model which is limited by a maximum carrying capacity and an overall minimum viable population is highly flexible as it has the capacity to, persistently, evolve and return within a 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 dynamics.

4.7 The proposed framework offers several conceptual and practical advantages over the classical models and it may allow to ask better questions and do a more realistic assessment in stock dynamics.

4.8 Some of the key concepts spinning off the model are as follows:

4.8.1 The persistency/plasticity of the population system, that is the ability of the stock to withstand both environmental perturbations and high fishing mortality and rehabilitate from low orbits of stability.

4.8.2 The differential effects of fishing mortality during density-dependent and density-independent compensations and depensations.

4.8.3 The understanding of (a) population collapses due to the effects from density-independent depensations combined to high fishing mortality and

(b) density-dependent and density-independent mechanisms may induce the rehabilitation of the stock towards higher orbits of stability.

4.8.4 The short and medium term estimation of recruitment due to trends (slopes and temporal evolution) in external "best descriptor" variables (such as SST, SSTA, NAO, upwelling strength, among others).

4.8.5 The explanation of the high variability in the data and determination of how combined, multivariate correspondences, memory effects, time lags, periodic oscillations, noise and sensivity to external conditions may affect the population system.

4.8.6 The existence of dynamical similarity at several spatio-temporal scales and extrapolation of trends between different scales.

4.8.7 The orbits of stability can be described as an attractor; the coefficient *b* can be of fractal nature and all of the features proposed by the classical models are comprehended by this new approach.

4.9 The work nurtures a wealth of new concepts, nomenclature and ways of approaching old and new aspects of population/stock dynamics: we propose new concepts on (a) global and local dynamics; (b) residuals, signal, noise and dispersion in the data; (c) harvesting in systems with multiple orbits of stability; (d) conditions which may lead to the extinction of the commercial fishery; (e) forward and backwards bending nature of catches, fishing effort, and abundance; (f) incorporation of multivariate perturbations into the model and (g) approximations to the multi-oscillatory model by different curve fitting methods and the matter on auto correlated residuals and population systems with strong dependencies on wave-like external variables.

4.10 A relatively high amount of information comes out of the five cases of validation of the new model:

4.10.1 In all of the cases studies it is shown that the dynamical patterns in the different cases consist systems with multiple orbits of stability and that population trends are due to the combined effects from internal population mechanics as well as the external environment and fishing mortality.

4.10.2 The study on Baltic cod showed (on data until 1993) two orbits of stability and, according to our theoretical criteria, we were able to estimate future trends in the population system:

4.10.3 In a previous study (Solari et al., 1993), it was estimated that Baltic cod was nearby the minimum viable population due to the combined effects from high fishing mortality and negative effects from external perturbations. However, a rehabilitation towards a low equilibrium state was expected due to likely positive trends in external perturbations. An update of the series until year 2006 showed that this estimation was correct, that is, the stock-recruitment system established itself onto a low orbit of stability in which it still remains.

4.10.4 The Icelandic cod case was determined to turn around either two or, alternatively, three orbits of stability. In this study, were found validated that at high levels of fishing mortality, the proposed model may describe persistency at low equilibria (whereas the Shepherd approach predicts instability and extinction).

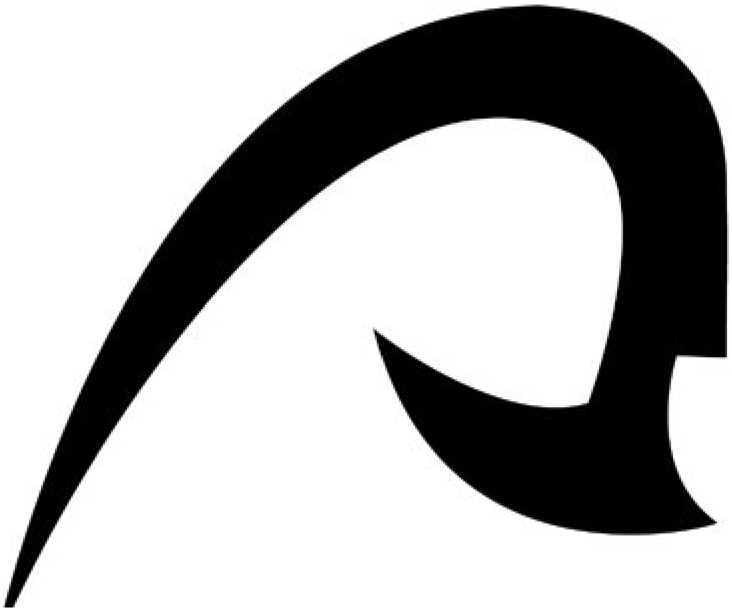
4.10.5 The skipjack tuna study contributed information to further validate several aspects of the proposed framework: (a) in order to analyse data on this species, SST was sampled at several spatial scales and similar trends were found which led us to search for dynamical similarity in skipjack dynamics; (b) two orbits of stability were clearly defined and (c) it was found that catches from different fleets, applying different fishing efforts showed similarity at three spatial scales, as well. It supported the assumptions on the differential effects of fishing mortality, the forward-backwards bending nature of fishing effort, the use of catches as a proxy for abundance and the potential ability to estimate trends in recruitment from smaller to wider areas.

4.10.6 A theoretical, self similar system was proposed in order to discuss the concept of similarity at several scales and migration of the tuna stocks.

4.10.7 The study on the common *Octopus* contributed with the following: (a) a first step towards the first population framework for cephalopods in FAO fishing Area 34; (b) catches were used as a proxy for abundance and three orbits of stability were identified; (c) population trends were related NAO pulses which was considered an external forcing determining the variable carrying capacity of the system; (d) a sub-model for the NAO effect upon the fishery system is proposed in which a similar pulse from an external variable may imply two different responses in the population. Also, we updated the data to catch and effort (and abundance) series from the Saharan and Mauritanian upwelling zones to find striking similarities in the multi-oscillatory nature of the systems, validate the use of catches as a proxy for abundance, again and determine that Octopus dynamics in both of the upwelling areas may be similar. It was shown, again, that different fleets applying different efforts may reflect similar trends in recruitment to the fishery. Finally, the study contributes further with a 3-orbit of stability variation of the original model and another on the relationship between SST and *Octopus* abundance off Mauritania.

4.10.8 The almadraba fishery was an historical incursion aimed at investigating the past in order to understand both the present and future. This study contributed with knowledge on climate change and the dynamics of tunas (biased towards bluefin) in absence of industrial fisheries or recruitment over fishing (years 1525-1756): (a) the fishery system showed three main areas of stability with local dynamics and was suggested to be controlled by trends both in maxima (as temperature is above the mean) and minima (as temperature is below the mean) during *The Little Ice Age* starting in the early 1600's which implied an environmental induced collapse on the fishery; (b) a theoretical representation of a multi-oscillatory attractor is proposed for the fishery system and (c) it is suggested that contemporary (20th century) data for the bluefin tuna fishery shows a similar response to Sea Surface Temperature Anomaly in the Northern hemisphere.▪

CHAPTER 4.1



FUTURE WORK

4.1 Future work.

The new framework (after Solari et al., 1997) opened up a new research line. There are several further developments spinning off the original work. In this section, we address some of the topics on the ongoing and future work:

(i) A multi-specific/community structure framework based (a) on 2D-3D georeferenced data from cephalopod/fish and benthic assemblages (associated clusters) and (b) described by systems of non-linear functions/equations [as shown in Appendix 1] based on concepts such as "variable carrying capacity", "dynamical continuum" and "indicator species" (as set forth in our earlier studies), "biodiversity erosion/conservation" and "fishing down the web".

(ii) Further development of a (free for academic, educational and non-profit use) GUI software package (in C#SHARP) aimed for data analysis, (classical and alternative) model fitting and fisheries management for both scientists and non-mathematically/technically oriented fishery managers. The ulterior aim of all of this theoretical work is to produce a "push button" computer based technology which will allow both fishery scientists and managers to (a) process (near) real time, georeferenced data to study the dynamics of fish and cephalopod stocks and their environmental and anthropogenic forcings; (b) estimate short and medium term trends in recruitment (to the population, area and fishery) and correspondences with external variables in several spatial and temporal scales and (c) manage both their exploitation and conservation estimating sustainable catch ranges as function of the transition scheme in the ocean.

(iii) Development of an exploitation methodology for the common *Octopus* based on the MOSA, assuming exclusion zones (stock-recruitment reserve areas) and differential effects of fishing mortality. This approach is aimed at the sustainability of the fishery, mainly during low to very low orbits of stability in recruitment.

We put forward an overview of the equation systems which may serve as a ground to our approach within a framework of community structure, species assemblages and cluster dynamics.

We consider the system

$$C_{1(t+1)} \cong \begin{bmatrix} f_1(E_{1(t-T)}) \\ f_2(E_{2(t-T)}) \\ f_3(E_{3(t-T)}) \\ \vdots \\ f_n(E_{n(t-T)}) \end{bmatrix}$$

where $C_1(t)$ is a description of the community or assemblage in time t and the abundance of each species (E_i) is described by the functions $f_1 \ldots f_n$, taking into account delays (T), dependencies and correspondences.

The functions can be linear and non-linear, assume classical population models (logistic, Beverton-Holt, Ricker, Shepherd, Schaffer, and others) but include more advanced, alternative approaches (Paulik, 1972; Solari, 1997 among others).

Also, the functions are related on the basis of concepts such as “best descriptor” or “indicator species” abundances and processes of which may be used as “system indicators”.

With such theoretical basis, we may describe the assemblage of communities or “global community” $(C_{G(t)})$ by using a matrix or system of equations as expressed below

$$C_{G(t+1)} \cong \begin{bmatrix} \begin{bmatrix} f_1(E_{1(t-T)}) \\ f_2(E_{2(t-T)}) \\ f_3(E_{3(t-T)}) \\ \vdots \\ f_n(E_{n(t-T)}) \end{bmatrix} & \begin{bmatrix} f_7(E_{1(t-T)}) \\ f_8(E_{2(t-T)}) \\ f_9(E_{3(t-T)}) \\ \vdots \\ f_{n2}(E_{n(t-T)}) \end{bmatrix} \\ \begin{bmatrix} f_4(E_{1(t-T)}) \\ f_5(E_{2(t-T)}) \\ f_6(E_{3(t-T)}) \\ \vdots \\ f_{n1}(E_{n(t-T)}) \end{bmatrix} & \begin{bmatrix} f_{10}(E_{1(t-T)}) \\ f_{11}(E_{2(t-T)}) \\ f_{12}(E_{3(t-T)}) \\ \vdots \\ f_{n3}(E_{n(t-T)}) \end{bmatrix} \end{bmatrix}$$

One of the ulterior aims of all of this work is to produce a multiple-tool which on a near-real-time data feed will allow us to (a) continuously monitor external variables and fishing mortality, (b) estimate trends in recruitment and manage the fishery.▪

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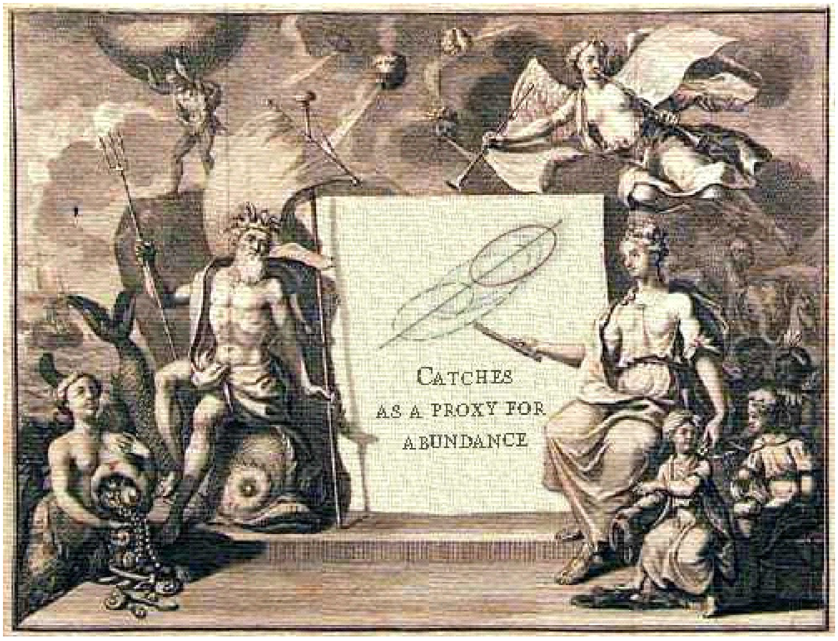
APPENDIX I

CATCHES AS A PROXY FOR ABUNDANCE



Appendix I. Catches as proxy for abundance.

In this section, we show two arbitrary examples which address the dynamics of an oscillatory population under two linear and two non-linear fishing mortality regimes. The aim is to show that catches may be used (i) as a proxy for abundance; (ii) to infer the dynamics, to estimate short and medium term trends in stock and recruitment and (iii) to manage the fishery while effort data is either unavailable or unreliable, mainly but not limited to short lived populations such as in *Octopus vulgaris* (Cuvier 1797) and other cephalopods, as well.

We assumed that trends in both (i) population numbers (density dependent and density independent compensations and depensations) and (ii) recruitment (i.e. influx of juveniles into the adult population) may oscillate due the environment alone or a combination between environmental perturbations and fishing mortality; (iii) relationships between fishing mortality and effort may be linear (positive and negative) and non-linear (of 2nd degree); and (iv) a time lag of 1 (year) between immediate neighbouring (i.e. at times t_{n-1}, t_n and t_{n+1}), non-overlapping generations (i.e. such as that between the parental and recruiting generations in *Octopus vulgaris*): this implies that the phase plane representing the trend between the stock at times t_n and t_{n+1} may reflect a stock-recruitment relationship. Furthermore, as our interest is to estimate trends, values represented are normalized (mean = 0) and while scales of numbers may change, similar dynamical trends are easily compared.

We describe spawning stock at the beginning of any particular year, S_{t+1}, as given by

$$S_{t+1} = \sigma \cdot S_t + R\left(S_{t-\tau}\right) \qquad (1)$$

where σ is the survivorship coefficient affecting the spawning stock, S_t, and recruitment (R) is a function of the existing parental stock τ years before ($\tau = 1$ in the common *Octopus* as age-at-maturity is approximately one year).

Also, the survivorship in the spawning stock is described as

$$\sigma \cdot S_t = S_t - H(S_t) - M_t \qquad (2)$$

where $H(S_t)$ and M_t are the harvest and natural mortality, respectively. In the examples below, for simplicity, we will further assume that both recruitment and natural mortality are constant.

Example 1.

An oscillatory (2-equilibrium) population under two linearly increasing, fishing mortality regimes. We let the initial population function (S_0) be a sinusoidal, two generations cycle. The remaining Stock, $S_1 \ldots S_2$, will be determined by the fishing mortality regime $F_n(x)$ upon the initial population, where n represents the number of each regime (1, 2). The higher fishing mortality regime, $F_2(x)$, doubles the lower, $F_1(x)$.

Example 2.

An oscillatory (2-equilibrium) population under two non-linear fishing mortality regimes. In this example, we proceeded analogously to Example 1 but let the fishing mortality $F_3(x)$ *and* $F_4(x)$ regimes –which double one another- be non-linear (of 2nd degree).

Both of the examples are graphically represented in Figures 1 a-d and 2 a-d in which we show the following results:

Figure 1a. shows the temporal evolution of trends both in the initial population, S0(x), under two linearly increasing fishing mortality regimes, F1(x) and F2(x), and the resulting stock (even proxies for abundance), S1(x) and S2(x). Although fishing mortality may increase both linearly and doubles from the lower to the higher regime, the following is observed: (i) both compensations and depensations which make up the oscillations are persistent; (ii) there may be oscillations within the negative phases of the trends and (iii) an initial population may be exploited in increasing rates and still retain similar dynamics while scales of numbers may change.

Figure 1b. shows the phase plane of trends for the unexploited population [S0(x), S0(x+1)] and those of the resulting stocks under a relatively lower [S1(x), S1(x+1)] and higher [S2(x), S2(x+1)], linear fishing mortality regimes, F1(x) and F2(x), which double one another. This figure reflects a stock-recruitment relationship which cycles twice and how these oscillations (compensations and depensations) may shift from one another as fishing mortality increases. Also, in this case, scales of numbers will change and dynamical patterns will be persistent.

Figure 1c. shows the (positive and negative) linear relationships between fishing mortality (x) and effort, E1(x) and E2(x).

Figure 1d. shows the temporal evolution of the Catch per Unit Effort (CPUE) as function of a negative, CPUE1(x), and a positive, CPUE2(x), linear relationship between fishing mortality and effort. Either of positive or negative nature, the catch per effort relationship will result in a forward and backward bending trend, mediated by the oscillations in the initial population.

Figure 1e. shows the phase plane of the Catch Per Unit Effort (CPUE) as function of a negative [CPUE1(x), CPUE1(x+1)], and a positive, [CPUE2(x), CPUE2(x+1)], linear relationship between fishing mortality and effort. The trends are the inverse of each other and keep similar dynamics.

Figure 2a. shows the temporal evolution of trends both for the initial population, S0(x), under two non-linear fishing mortality regimes, F3(x) and F4(x), and the resulting stocks, S3(x) and S4(x). Analogous to the case shown in Fig. 1a., although fishing mortality may be non-linear and double from one regime to the other, the dynamical patterns in the resulting catches are similar to that of the initial population.

Figure 2b. shows the phase plane of trends in the unexploited population [S0(x), S0(x+1)] and those of the resulting stocks under a relatively lower [S3(x), S3(x+1)] and higher [S4(x), S4(x+1)], non-linear fishing mortality regimes, F3(x) and F4(x), which double one another. Analogous to the case shown in Fig. 1b., this stock-recruitment relationship shows similar dynamical patterns under both of the non-linear fishing mortality regimes.

Figure 2c. shows the non-linear relationships between fishing mortality (x) and effort, E3(x) and E4(x).

Figure 2d. shows the temporal evolution of the Catch per Unit Effort, CPUE3(x) and CPUE4(x), as function two non-linear relationships between fishing mortality and effort.

Figure 2e. shows the phase plane of the Catch Per Unit Effort [CPUE3(x), CPUE3(x+1); CPUE4(x), CPUE4(x+1)] as function two non-linear relationships between fishing mortality and effort.

Discussion.

The examples shown herein may be analogous to a harvesting or fishery upon an oscillating population. We chose an initial population which cycles as a ground example. However, natural populations may show multi-periodic oscillations adapted to trends from external forcings such as the environment and fishing regimes. Also, we assumed for simplicity both constant recruitment and natural mortality: in “real world” cases, these two variables may oscillate. However, the oscillations may not change the ground dynamics of the system if there are autocorrelations (i.e. “memory effect”), dependencies between some of the variables and other dynamical features we have observed in field data. Furthermore, the functions representing oscillating recruitment and external forcings will not change the ground patterns in the dynamics but the amplitudes or scales or numbers.

The cases we put forward are clear in that: (i) Catches are useful as proxies for abundance as they will reflect the oscillations and trends in the initial population whether the fishing mortality regimes increase linearly, are positive or negative or non-linear (of 2nd degree). The dynamics of the population will reflect the forward (compensatory) and backward (depensatory) bending trends, irrespective of the fishing mortality or effort applied: this system behaviour is mediated by a matrix of external forcings in which the fishing strategy is solely a cofactor. Natural populations will oscillate due the combined effects of the environment and fishing mortality and collapses may come about due the combined effect from both density-dependent and density-independent depensations under a high fishing mortality. Also, the use of catches as proxy for abundance may be more straightforward in short lived populations with non-overlapping generations such as in *Octopus vulgaris*; (ii) the compensatory-depensatory nature (similar dynamics) of all of the phase planes (in Catches and CPUE) may persist as this is mainly mediated by the oscillations in the exploited population: as far as we can determine the main external forcings which induce density-independent compensations and depensations, we may estimate short and medium term trends in stock and recruitment and, thus, manage the fishery without effort data and (iii) the CPUE will turn in a backwards bending trend as depensatory trends arise in the population, no matter the fishing regime or catch-effort relationship.

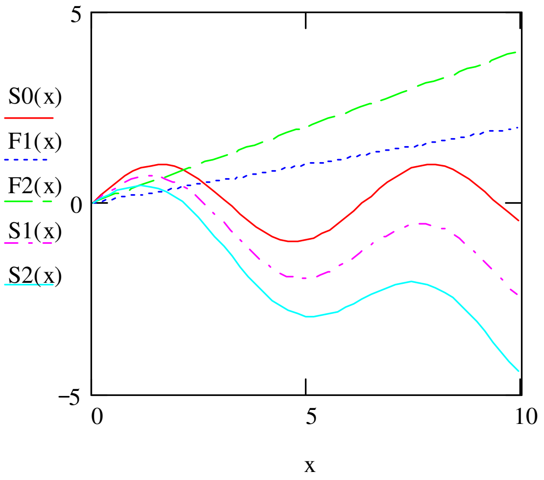


Fig. 1a. The temporal evolution of trends both in the initial population, S0(x), under two linearly increasing fishing mortality regimes, F1(x) and F2(x), and resulting stocks after catches, S1(x) and S2(x).

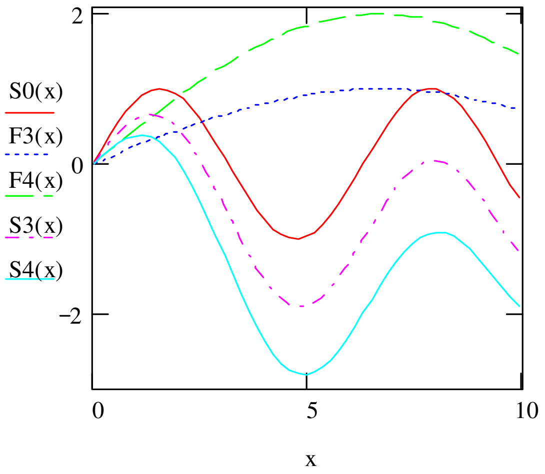


Fig. 2a. The temporal evolution of trends both in the initial population, S0(x), under two non-linear fishing mortality regimes, F3(x) and F4(x), and resulting stocks after catches, S3(x) and S4(x).

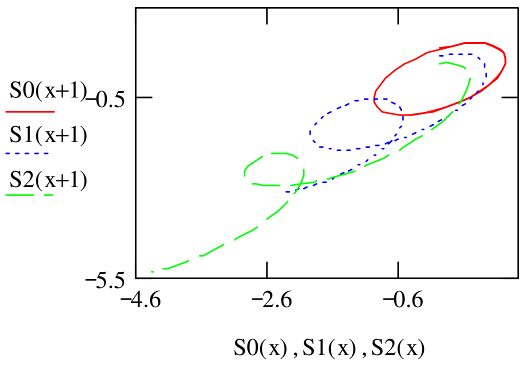


Fig. 1b. The phase plane of trends in the unexploited population [S0(x), S0(x+1)] and those of the exploited population under a relatively lower [S1(x), S1(x+1)] and higher [S2(x), S2(x+1)], linear fishing mortality regimes, F1(x) and F2(x), which double one another.

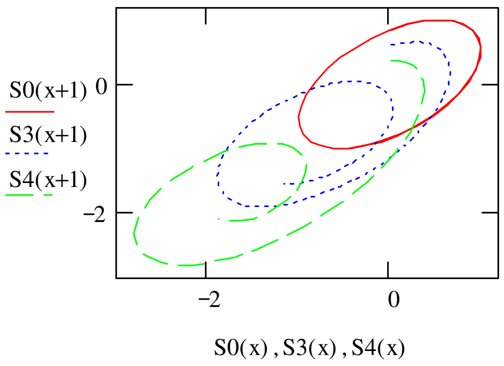


Fig. 2b. The phase plane of trends in the unexploited population [S0(x), S0(x+1)] and those of the exploited population under a relatively lower [S3(x), S3(x+1)] and higher [S4(x), S4(x+1)], non-linear fishing mortality regimes, F3(x) and F4(x), which double one another.

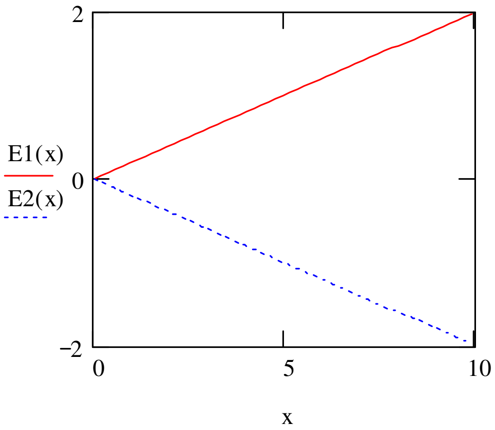


Fig. 1c. The (positive and negative) linear relationships between fishing mortality (x) and effort, E1(x) and E2(x).

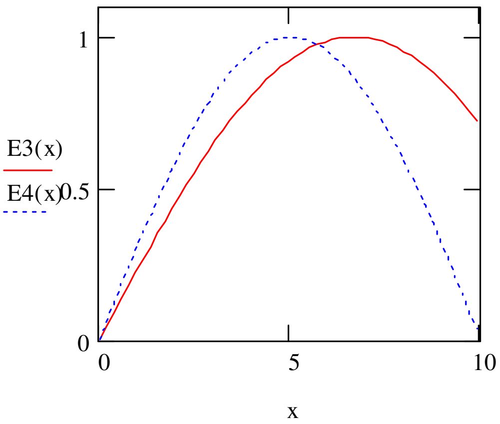


Fig. 2c. The non-linear relationships between fishing mortality (x) and effort, E3(x) and E4(x).

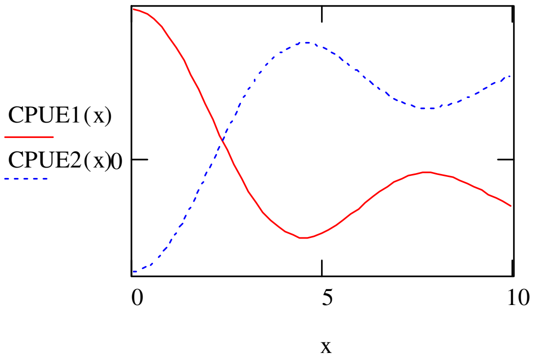


Fig. 1d. The temporal evolution of the Catch per Unit Effort (CPUE) as function of a negative, CPUE1(x), and a positive, CPUE2(x), linear relationship between fishing mortality and effort.

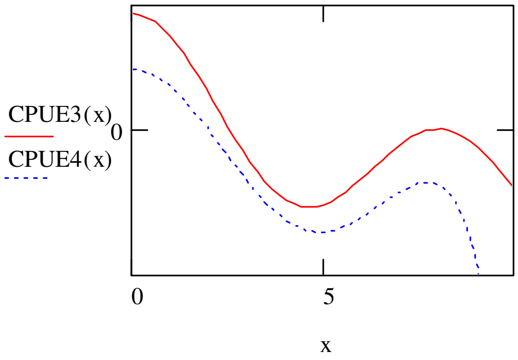


Fig. 2d. The temporal evolution of the Catch per Unit Effort, CPUE3(x) and CPUE4(x), as function two non-linear relationships between fishing mortality and effort.

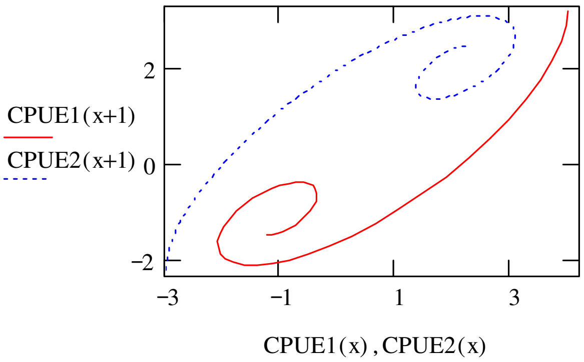


Fig. 1e. The phase plane of the Catch Per Unit Effort (CPUE) as function of a negative [CPUE1(x), CPUE1(x+1)], and a positive, [CPUE2(x), CPUE2(x+1)], linear relationship between fishing mortality and effort.

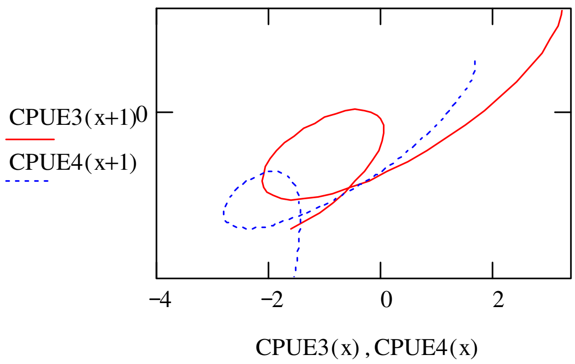
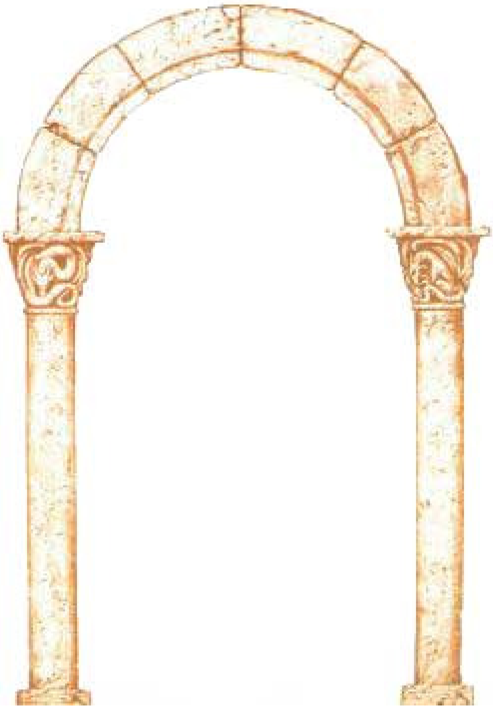


Fig. 2e. The phase plane of the Catch Per Unit Effort [CPUE3(x), CPUE3(x+1); CPUE4(x), CPUE4(x+1)] as function two non-linear relationships between fishing mortality and effort.

EPILOGUE

FINAL NOTE



We Few,
We Happy Few,
We Band of Brothers.
W. Shakespeare

Nuevo modelo no–lineal para el estudio y la explotación de recursos pesqueros

Memoria de la tésis doctoral presentada por

Aldo P. Solari

– Sumario en Castellano –

UNIVERSIDAD DE LAS PALMAS DE GRAN CANARIA
AD 2008

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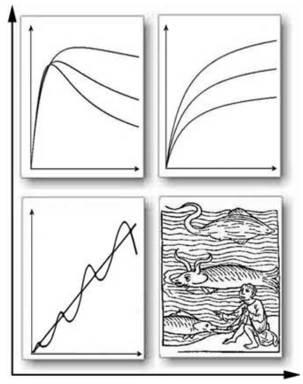

En esta sección, se presenta un breve sumario de cada uno de los capítulos (Cap.) de la tesis con sus figuras principales: (i) modelos Clásicos (Cap. 1) y crítica; (ii) el nuevo marco teórico (Cap. 2); (iii) casos de estudio que apoyan el nuevo marco teórico (Cap. 3) con ejemplos sobre las dinámicas del (a) bacalao de Islandia, equilibrios enlazados y pesca (Cap. 3.2); atún bonito listado y la similaridad dinámica en varias escalas (Cap. 3.3); pulpo común, hacia un nuevo marco teórico (Cap. 3.4), así como la pesca en Almadrabas españolas durante los años 1525-1756 (Cap. 3.5). También, se incluye una breve mención sobre los conceptos tratados en la discusión general para los casos de estudio (Cap. 3.6), las conclusiones de la tésis, el trabajo presente y futuro (Cap. 4) y, finalmente, la argumentación teórica sobre el uso de las capturas como "proxy" de abundancia (Appendix I). Para los detalles sobre el desarrollo del trabajo, metodología, argumentación e inferencia el lector deberá recurrir a la tésis propiamente dicha (en Inglés).

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(i)
Modelos Clásicos
(Cap. 1)

En general, la dinámica de poblaciones y relación Stock-Reclutamiento (SR) son estudiadas a la luz de modelos (de ahora, en adelante, referidos como “modelos clásicos”) propuestos por Beverton y Holt (1957) y Ricker (1954) los cuales, aún, se utilizan para la gestión pesquera (Gulland, 1989; Solari *et al.*, 1997). Estos modelos proponen curvas de extinción donde el reclutamiento alcanza un máximo asintótico (Beverton-Holt) o se reduce a bajos niveles cuando el stock adulto alcanza números altos (Ricker). Ambos modelos clásicos fueron desarrollados con el mismo objetivo: la identificación de la mejor parametrización de la relación SR (Stock-Reclutamiento) y la tarea principal era la determinación de la mejor función matemática (forma de la curva y número de parámetros) que permitiera el incremento de los coeficientes de determinación (explicación de los datos) con el menor número de parámetros.

Shepherd (1982) pudo unificar, dentro de un único marco, las funciones clásicas de “campana” y asintótica, propuestas por Ricker (1954; para valores de $\delta > 1$) y Beverton-Holt (1957; para valores de $\delta = 1$), respectivamente y se expresa como

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

donde R es el reclutamiento, S es el stock adulto y K el valor crítico, en la población por encima del cual los efectos de la denso-dependencia dominan (eso es, la capacidad de carga). Los parámetros α y δ son referidos como la pendiente en el origen y grado de compensación, respectivamente. El modelo propuesto por Shepherd (1982) no podía incorporar múltiples equilibrios ni dinámica depensatoria: la Fig. 1 muestra dos ejemplos arbitrarios del mencionado modelo.

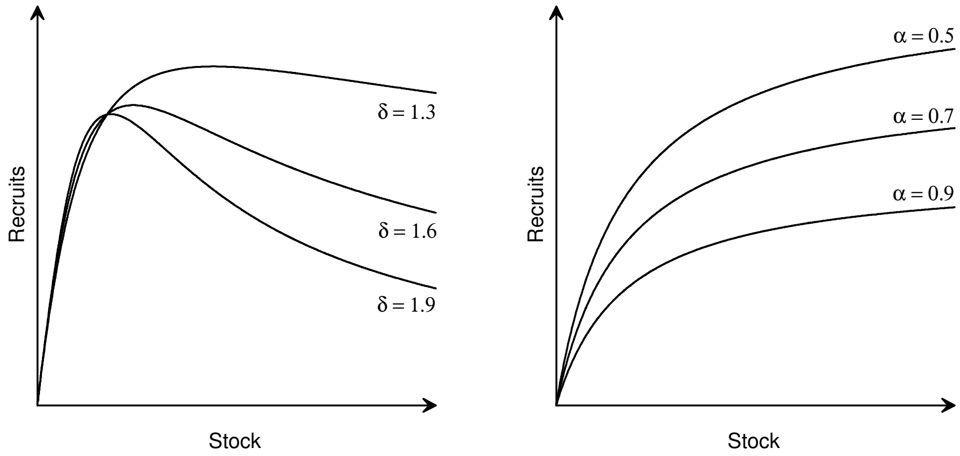

Figura 1. Dos ejemplos arbitrarios del modelo de Shepherd (1982), el cual unificó los modelos clásicos con forma de "campana" y asintótico, propuestos por Ricker (1954; para $\delta > 1$; arriba, izquierda) y Beverton-Holt (1957; para $\delta = 1$; arriba, derecha), respectivamente. Estas aproximaciones asumen que la relación stock-reclutamiento: (i) está gobernada por un único equilibrio (intersección entre la función y línea de remplazamiento o regresión lineal, a través del origen); (ii) responden solamente de forma compensatoria a la mortalidad por pesca, y (iii) alcanzan valores asintóticos (Beverton-Holt) o bajos, cuando el stock adulto tiende a la única e invariante capacidad de carga (Ricker). Estos modelos asumen que los datos observados tienen el mismo peso estadístico (se ignora la evolución temporal) y que los residuos son el resultado de un proceso aleatorio).

Los modelos clásicos tuvieron una amplia aceptación para describir la relación SR e introdujeron un marco general, no-lineal, a la dinámica de poblaciones de peces. No obstante, los mencionados modelos tienen una capacidad limitada para incluir factores determinantes de situaciones específicas y enlazar procesos denso-dependientes, en la población, a aquellos denso-independientes (perturbaciones medioambientales y mortalidad por pesca). Estas carencias de especificidad han sido discutidas en la literatura, entre otros autores, por Clark (1976), Sharp *et al.* (1983), De Angelis (1988), Fogarty (1993), Solari *et al.* (1997), Bas *et al.* (1999).

Estos modelos, también, excluían: (i) características dinámicas, críticas para la comprensión de la mecánica existente detrás de los datos observados (enlace y mecanismos de transición entre equilibrios, comportamiento del sistema, extinción de la pesquería comercial e interacciones medioambientales, entre otros factores) y (ii) la evolución temporal de la población. Estas aproximaciones, también, asumen que la relación stock-reclutamiento: (i) está gobernada por un único equilibrio (intersección entre la función y línea de remplazamiento o regresión lineal, a través del origen); (ii) responden, solamente, en una forma compensatoria a la mortalidad por pesca; (iii) alcanzan valores asintóticos (Beverton-Holt) o bajos, cuando el stock adulto tiende a la única e invariante capacidad de carga (Ricker).

Durante la década de 1970, un marco más avanzado fue presentado por Paulik (1973) que propuso un modelo general para SR formado por la concatenación de funciones de supervivencia. Este modelo podía describir equilibrios múltiples, estables y dinámica compleja y era el resultado de un proceso multiplicativo donde la producción inicial de huevos podía ser modificada por funciones no-lineales, específicas para cada etapa del ciclo de vida y tamaño de la población o cohorte. El principal problema con el mencionado modelo era la interdependencia entre las funciones debido a la naturaleza multiplicativa del mismo.

Crítica.

Los modelos clásicos fueron, ampliamente, aceptados como funciones para describir la relación entre el stock adulto y el reclutamiento e introdujeron, en su momento, un marco general, no-lineal aplicado a la dinámica de poblaciones de peces y otros organismos marinos así como stocks explotados: no obstante, los mencionados modelos tienen una capacidad limitada para incluir factores fundamentales de situaciones específicas y enlazar dinámicas internas (intrínsecas a la población) a factores externos (medioambiente y pesca). Esta carencia de especificidad ha sido discutida, en la literatura, por Clark (1976), De Angelis (1988) y Fogarty (1993), entre otros autores.

Los modelos clásicos asumían que: (i) las poblaciones bajo explotación estaban limitadas, naturalmente, de forma que podían responder compensatoriamente a la mortalidad por pesca (Beverton y Holt, 1957; Ricker, 1975; Cushing, 1977; Rothschild, 1986); (ii) la capacidad de carga era un valor invariante (a pesar que el medioambiente fluctúa contínuamente); (iii) un solo equilibrio operaba, durante toda la extensión de la serie temporal; (iv) los residuos eran el resultado de procesos aleatorios y (v) los datos observados tienen el mismo peso estadístico (se ignora la evolución temporal).

También, los modelos clásicos asumen que las poblaciones explotadas están limitadas de tal forma que pueden responder de una forma compensatoria a la pesca (Beverton y Holt, 1957; Ricker, 1975; Cushing, 1977; Rothschild, 1986), lo cual puede ser una falacia si se consideran las variaciones y múltiples oscilaciones y dependencias entre las variables del sistema dinámico.

Los modelos clásicos excluyen características dinámicas que son críticas para comprender los mecanismos existentes detrás de las observaciones: enlace y transiciones entre distintos estados de equilibrio, comportamiento del sistema, extinción de la pesquería comercial y otros factores de gran importancia.▪

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(ii)
El Nuevo Marco Teórico
(Cap. 2)

En trabajos previos de Solari *et al.* (1997), Bas *et al.* (1999), Castro *et al.* (1999) y Solari *et al.* (2003), se propone el reclutamiento, tanto a la población (influjo de juveniles en la población adulta), al área (migraciones de cohortes/individuos en áreas de pesca) y pesca (dinámica de la pesquería), como un sistema o sumatoria de funciones no-lineales (múltiples órbitas de estabilidad o estados de equilibrio) con características dinámicas que pueden comprender desde el caos (cuando las condiciones externas son extremadamente benignas), pasando por un rango de ciclos (o cuasi-ciclos) convergentes, relativamente estables (cuando el estrés externo aumenta) a un estado sin oscilaciones claras (cuando la mínima población viable es aproximada). Este sistema tiene la capacidad de evolucionar y retornar, persistentemente, en un amplio rango de equilibrios y permite la descripción enlazada de múltiples capacidades de carga así como procesos denso-dependientes (compensación y depensación debido a la densidad de población y mecanismos asociados al canibalismo, competencia intraespecífica, valores críticos de densidad que aumentan la mortalidad natural/enfermedades), denso-independientes (compensación y depensación debido a perturbaciones medioambientales y mortalidad por pesca) y denso-dependencia-inversa (el éxito reproductivo y reclutamiento se reducen debido a densidades de población muy bajas).

Este modelo puede describir un sistema dinámico con capacidad de evolución a través de un amplio rango de estados de estabilidad de los cuales puede alejarse y retornar, persistentemente, y permitir la incorporación de capacidades de carga múltiples así como denso-dependencia (compensación y depensación debido al número de individuos en la población), denso-independencia (compensación y depensación debido a variaciones medioambientales y pesca) y denso-dependencia-inversa (un equilibrio inestable donde el éxito reproductivo y el reclutamiento declinan debido a un número muy bajo de individuos en la población; extinción de la pesquería comercial).

El reclutamiento (*R*), en el nuevo marco, se define (Ecuación 2) como la sumatoria de funciones no-lineales del stock adulto, *S*, y se expresa como

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

donde la entrada $i = 1 \ldots m$ representa el número de estados de equilibrio u órbitas de estabilidad, en el sistema stock-reclutamiento, donde *m* es el equilibrio más alto que la relación alcanza, donde se encuentra el "techo" o máxima capacidad de carga posible (K_{max}). La descripción de los estados de equilibrio es controlada por los coeficientes a_i (pendiente de la curva, en el origen) y b_i y c_i que afectan la mortalidad denso-dependiente. Por ejemplo, el coeficiente a_i cumple una función similar al la velocidad natural de crecimiento de la ecuación logística y los valores de b_i definirán los rangos del stock adulto para los cuales surgen nuevos equilibrios. Estos coeficientes definirán los estados u órbitas de equilibrio y sus valores pueden ser fijos.

Representaciones gráficas de un único y un sistema de múltiples equilibrios, de acuerdo con nuestro marco dinámico, se muestran en las Fig. 2 y 3, respectivamente. Este modelo puede ser aplicado al espacio de fase (N_t, N_{t+1}) para describir tanto el sistema SR como la dinámica de la pesquería (reclutamiento al área y pesca). Un número *m* de fenómenos oscilatorios, en rangos que pueden comprender desde situaciones con oscilación baja a cuasi-ciclos, ciclos límite y caos, así como denso-dependencia-inversa pueden ser descritos por este sistema, el cual puede ser aproximado por mínimos cuadrados o regresiones polinómicas que incorporen tres constantes para cada equilibrio. Más detalles sobre el modelo propuesto son discutidos extensamente en Solari *et al.* (1997).

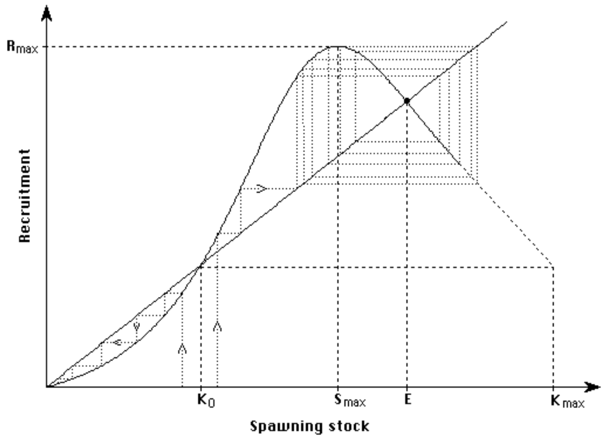

Figura 2. Representación gráfica de un estado de equilibrio arbitrario (Ecuación 2). El análisis de estabilidad se muestra con las líneas discontinuas. Mientras E es un equilibrio, relativamente, estable, la trayectoria puede evolucionar hacia K_{max} o K_0 (el "techo" y "piso" del sistema; eso es, la máxima capacidad de carga y mínima población viable del sistema, respectivamente). El máximo valor de reclutamiento (R_{max}) puede ser alcanzado debido a un máximo en el stock adulto (S_{max}). La oscilación alrededor del equilibrio es causada por la compensación (números aumentan, se tiende a K_{max}) y depensación (números disminuyen, se tiende a K_0) denso-dependiente. Si la trayectoria alcanza un valor por debajo de K_0 (un equilibrio inestable), ésta puede tender hacia el origen o cero (debido a la denso-dependencia-inversa). Las características dinámicas y forma de esta función nos permiten enlazar distintos tipos de equilibrios, en un sistema, a través de un modelo aditivo. Este ejemplo se muestra para comparación con los modelos clásicos.

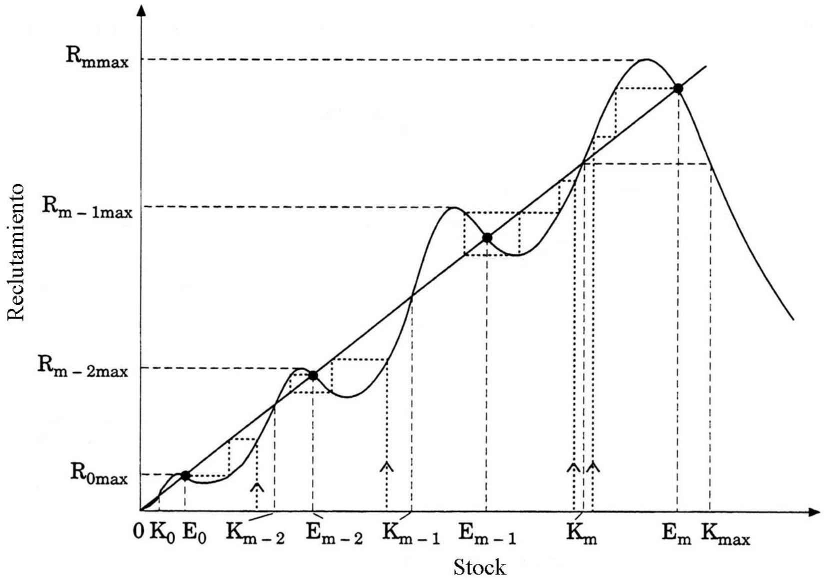

Figura 3. Representación de un sistema dinámico con *m* estados de equilibrio (Ecuación 2), según Solari *et al.* (1997). Este nuevo modelo se usa como base para describir la dinámica del reclutamiento a la población, área y pesca. Esta aproximación permite la incorporación de todos los aspectos de la mecánica de la población y perturbaciones multivariantes en la misma trayectoria/ecuación. K_m, K_{m-1}, K_{m-2} representan las mínimas poblaciones viables para los estados de equilibrio m, m-1 and m-2 y las capacidades de carga para los equilibrios inmediatamente inferiores, respectivamente. E_m, E_{m-1}, E_{m-2}, E_0 representan los equilibrios, alrededor de los cuales, el sistema SR evoluciona en fases de compensación y depensación. K_{max} es la máxima capacidad de carga del sistema y cualquier valor por encima de este "techo" inducirá un cambio depensatorio hacia equilibrios más bajos. K_0 es la mínima población viable y cualquier valor por debajo de este "piso" puede inducir un cambio de la trayectoria hacia el origen o cero (extinción de la pesquería comercial). La persistencia del sistema y estabilidad se muestra con el análisis de estabilidad (líneas discontinuas) para $K_0 < S < K_{max}$ and $R(K_0) < R < R_{max}$ (cotas del sistema). En el modelo se pueden incorporar un número *m* de fenómenos oscilatorios desde caos, ciclos límites, cuasi-ciclos y multii-periódicos hasta denso-dependencia-inversa (efecto Allé).

Este nuevo marco ofrece una serie significativa de ventajas conceptuales sobre los modelos clásicos debido a la multiplicidad de características dinámicas que puede describir y enlazar, en una ecuación, relativamente, simple sin ninguna interdependencia matemática entre las funciones.

El nuevo marco dinámico se justificaba como aproximación *ad hoc* debido a la flexibilidad que permite. También, ofrece varios avances conceptuales sobre los modelos clásicos ya que permite la incorporación de: (i) múltiples equilibrios, independientes uno del otro pero enlazados entre sí (sin interdependencia matemática debido a la naturaleza sumatoria del modelo); (ii) la capacidad del sistema de aceptar tanto equilibrios más altos como más bajos, cuando estos surjan; (iii) las transiciones entre los equilibrios debido a oscilaciones denso-dependientes y denso-independientes y, entre otros factores, (iv) varios máximos y mínimos y dinámica depensatoria pueden ser descritos en la misma relación. Esto, a su vez, permite la auto-similaridad dinámica, simultánea, para distintas escalas espacio-temporales y substocks/poblaciones locales. Todas estas cualidades pueden variar en cada uno de los stocks estudiados y, como veremos posteriormente, puede proveer una perspectiva más realista sobre la estructura y dinámica de las poblaciones.▪

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(iii)
Casos de Estudio que apoyan el Nuevo Marco Teórico
(Cap. 3)

En el Capítulo 2 de la tésis, se propone el nuevo marco teórico basado en un ejemplo sobre la dinámica del stock-reclutamiento en el bacalao del Báltico. En la presente sección, se presentarán otros casos con la intención de validar las nuevas ideas sobre dinámica de poblaciones que proponemos en el trabajo original (*Solari et al., 1997*).

A pesar que los distintos casos de estudio puedan requerir la incorporación/formalización de nuevos conceptos en el marco teórico (eso es, una aproximación ad hoc para cada caso particular), varios de los conceptos generales propuestos y la ecuación básica del modelo pueden ser útiles.

Los casos complementarios que presentaremos son los siguientes: mientras que la dinámica del bacalao del Báltico ocurre en un medioambiente semi-cerrado con flujo de agua limitada desde Kattegat-Skagerrak, las poblaciones del bacalao de Islandia (Cap. 3.2) pueden estar afectadas por condiciones diferentes y mostrar dinámicas distintas causadas por el sistema medioambiental más abierto. Pensamos que el caso del bacalao de Islandia podía servir para proponer nuevas ideas dentro del marco teórico que se ha presentado a la vez que validara el mismo para poblaciones de peces demersales explotados en sistemas marinos relativamente más amplios.

También, orientamos nuestro interés sobre poblaciones en el Area 34 de pesca de la FAO (Atlántico Centro Oriental) la cual es una zona interesante para la dinámica tanto de peces como cefalópodos: por un lado, elegimos al atún bonito listado (Cap. 3.3) debido a la naturaleza migratoria del stock y, por otro lado, al pulpo común (Cap. 3.4) debido a que, aún, no existe un marco predictivo para el estudio y explotación de esta última especie. Ambas especies son de un alto valor bioecológico y socio-económico y la explotación de estos recursos pesqueros es crítica para varios países de la menciona área.

También, abordamos una pesquería orientada a túnidos en las "almadrabas" atlánticas españolas de los años 1525-1756 (Cap. 3.5) para investigar si los conceptos que proponemos en nuestro marco podrían ser de uso para una dinámica en ausencia de pesca industrial y sobreexplotación así como un claro cambio climático (la "mini" glaciación de los 1600): esta caso de estudio nos podría indicar un "cuadro" sinóptico de la dinámica pesquera en el pasado y, así, permitirnos comprender en mayor grado como tratar tanto teórica- como prácticamente los stocks modernos bajo alta e intensa mortalidad por pesca (estimaciones de tendencias, respuestas en la población a perturbaciones medioambientales, proposición de rangos de mortalidad por pesca sostenibles, adaptados a los distintos cofactores que gobiernan la dinámica de los stocks, entre otros aspectos).▪

(iv)
Dinámica del bacalao de Islandia: equilibrios enlazados y pesca
(Cap. 3.2)

En este capítulo se estudia la relación stock-reclutamiento (SR) en el bacalao de Islandia: a la luz de los datos de campo, se asume que la relación SR consta de dos (alternativo tres) órbitas de estabilidad debido a (a) la interacción entre compensación y depensación denso-dependientes y (b) transiciones denso-independientes entre las órbitas de estabilidad (o seudo-equilibrios) debido a perturbaciones externas (medioambientales y pesca). La relación propuesta es un sistema de múltiples seudo-equilibrios que se describe como una suma de funciones no-lineales con múltiples líneas de reemplazo y techos ("ceilings") y pisos ("floors"), eso es capacidades de carga variables que permiten dinámica estable, periódica y caótica. La aproximación propuesta tiene la capacidad de describir y enlazar, dentro del marco de un contínuo dinámico limitado por una capacidad de carga máxima y una mínima población viable todos los procesos de población conocidos (eso es, compensaciones y depensaciones denso-dependientes y denso-independientes y denso-dependencia inversa o Efecto Allé) en una ecuación relativamente simple. Las ventajas conceptuales del nuevo marco teórico se discuten en relación a los modelos clásicos de Shepherd (1982) y Paulik (1972). También, se observa que (a) las funciones matemáticas del modelo son independientes una de la otra lo cual permite describir situaciones dinámicas diferentes sin que la descripción de una afecte a la otra, (b) órbitas de estabilidad altas pueden desaparecer del sistema debido a perturbaciones externas a medio o largo plazo, (c) son posibles las descripciones de distintos seudo-equilibrios en distintas escalas espacio-temporales y sub-stocks, (d) la mínima población viable puede permitir tanto un incremento del tipo de la ecuación logística (o modelos derivados), representar un punto sin oscilaciones claras o un equilibrio intestable por debajo del cual comienza a operar la denso-dependencia-inversa o Efecto Allé y (v) bajo niveles extremadamente altos de mortalidad por pesca, el modelo propuesto, aquí, admite persistencia del sistema en órbitas de estabilidad muy bajas mientras que los modelos clásicos proponen inestabilidad y extinción del stock. Finalmente, en el capítulo se sugiere que el efecto combinado de una tendencia negativa, mesoescalar en la temperatura y una alta mortalidad por pesca puede haber contribuído al establecimiento de la órbita de estabilidad relativamente baja durante la década de los años 1990.▪

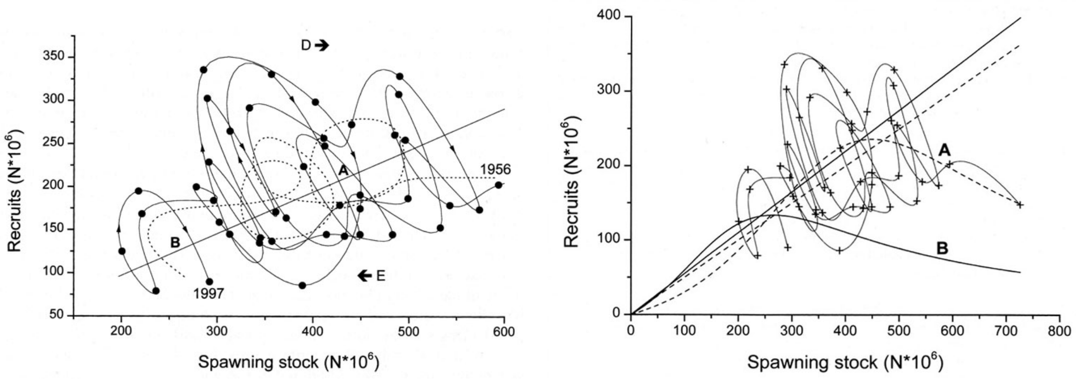

Figura 4 a-b. Ambas figuras muestran la relación stock-reclutamiento en el bacalao de Islandia, interpolada por un "espline" cúbico: en la figura superior izquierda, la trayectoria está suavizada (línea punteada) mientras que en la figura superior derecha se muestran los ajustes de las órbitas de estabilidad A (que puede constar de dos sub-órbitas) y B. D y E representan las transiciones denso-independientes. Las líneas rectas son regresiones través del origen; 1956 y 1997 indican el año del comienzo y el final de la serie.

(v)
Dinámica del atún bonito listado: similaridad en varias escalas
(Cap. 3.3)

En el presente capítulo, se propone un nuevo marco conceptual matemático que puede contribuir a la explicación de la oscilaciones en las descargas y la dinámica del reclutamiento a la pesquería en el listado *Katsuwonus pelamis*. Los autores proponen al reclutamiento a la pesca como un sistema o suma de funciones no-lineales con características dinámicas que pueden comprender el caos (cuando las condiciones externas son extremadamente benignas), un rango o serie de ciclos convergentes, relativamente estables (cuando el estrés externo aumenta) hasta un estado cuasi-estático con oscilaciones no muy claras (cuando el sistema se acerca a la mínima población viable). Estos nuevos conceptos teóricos se asocian a equilibrios múltiples, capacidad de carga variable, denso-dependencia inversa, mínima población viable así como a la mecánica de acoplamientos entre estos mediada por fases de compensación y depensación de naturaleza denso-dependiente y denso-independiente. Se estudian tres series de capturas (Mogán, Canarias y Area 34 de FAO) para las cuales se detectan efectos de memoria y periodicidad y se proponen, para los tres casos, situaciones dinámicas que se constituyen por dos estados dinámicos (órbitas de establidad) acoplados. Así también, se observa una estructura dinámica auto-similar en las tres series. El marco conceptual no-lineal propuesto admite la incorporación y parametrización de diferentes situaciones medioambientales y de pesca en un modelo simple y altamente flexible y permite comprender la dinámica y evolución temporal de las oscilaciones y las tendencias en las descargas y reclutamiento a la pesquería de *K. pelamis* lo cual no era posible, anteriormente, con los modelos clásicos utilizados en la ciencia pesquera. Las características dinámicas del sistema se relacionan a los conceptos de capacidad de carga variable, poblaciones mínimas viables, múltiples órbitas de estabilidad, compensaciones y depensaciones, extinción de la pesca comercial y migración del stock a través de un sistema marino fractal. Se concluye que el marco teórico propuesto por Solari et al. (1997) y subsecuentes estudios pueden permitir la descripción de procesos que gobiernan la migración y el reclutamiento, enlazar dinámica de poblaciones entre distintas escalas espaciales y estimar/extrapolar las tendencias observadas en escalas espaciales menores a zonas más amplias del sistema marino. Finalmente, se simula un sistema auto-similar para discutir otros conceptos ligados a la similaridad en varias escalas.

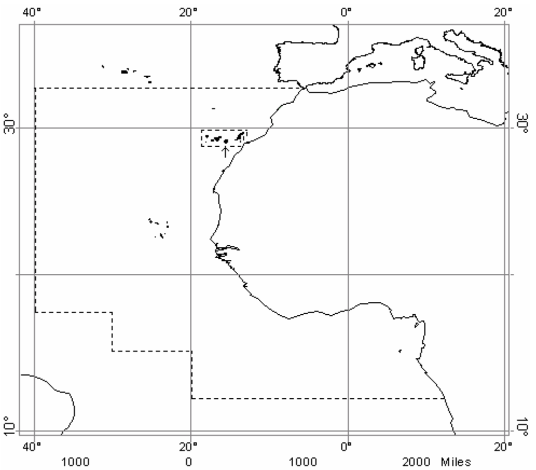

Figura 5. Las tres escalas espaciales de muestreo del atún bonito listado: area 34 de FAO (de Gibraltar al río Congo, Lat. 36°00'N-6°04'36''S, Long. 12°19'48''E-5°36'W); la zona de Canarias (area menor indicada por las línea punteada; Lat. 29°40'N-27°10'N, Long. 13°W-18°20'W) y el Puerto de Mogán (Gran Canaria, Lat. 27°55'N-Long. 15°47'W, punto geográfico indicado por la flecha). Mapa modificado después de FAO (2001).

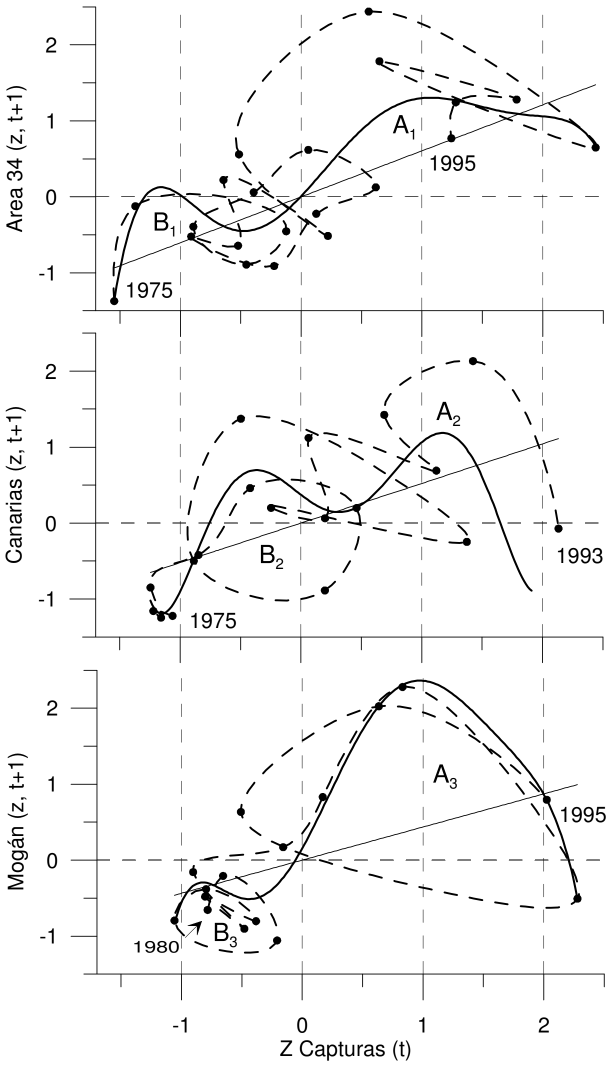

Figura 6 a-c. Espacio de fase de las capturas de *K. pelamis* el año *t* (N_t) y las capturas o reclutamiento a la pesquería el año *t+1* (N_{t+1}), para la zona del Area 34 de FAO (Atlántico Centro Oriental; figura superior) durante los años 1972-95, toda la zona de Canarias (figura intermedia), años 1975-92 y el puerto de Mogán (figura superior), isla de Gran Canaria para los años 1980-95.
Las líneas de remplazamiento están determinadas por regresiones lineales, a través del origen. La situación dinámica propuesta es similar en las tres escalas espacio-temporales. A y B son órbitas de estabilidad (o seudo-equilibrios) bajo y alto, respectivamente: en ambos casos, las trayectorias giran en una órbita de estabilidad la cual es determinada por fases de compensación y depensación denso-dependientes y están acoplados por una fase de compensación denso-independiente. Máximos y mínimos convergen, (órbita inferior), y divergen, en el superior. Cuando A_i alcanza su capacidad de carga, el sistema “salta” al equilibrio inferior, B_i. La similaridad dinámica entre las tres escalas espaciales sugieren que flotas con distinto esfuerzo, mortalidad por pesca y artes muestran tendencias similares lo cual valida la propuesta de capturas como índice de abundancia. También, se validan los conceptos de reclutamiento extendido (reclutamiento a la población se refleja en el influjo de individuos al área y pesca), capacidad de carga variable y contínuo dinámico, así como se propone en Solari et al. (1997). Los números sobre las trayectorias indican los años de comienzo y final de las series; Z indica número de individuos (N) normalizados.

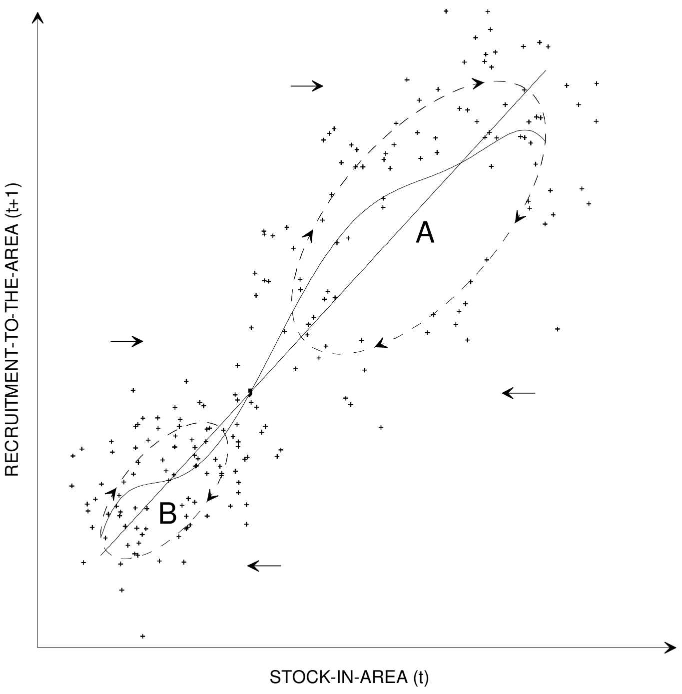

Figura 7. Sistema teórico propuesto para la relación stock-reclutamiento en-área para tres escalas espaciales en el Atlántico Centro Oriental (Puerto de Mogán, zona de Canarias y Area 34 de FAO). La regresión lineal representa la línea de reemplazo y el ajuste polinímico describe la evolutión del contínuo dinámico del sistema. El punto singular representa la transición entre las órbitas de estabilidad. Las fases de compensación y depensación denso-dependientes están indicadas por las flechas sobre las trayectorias de las órbitas de estabilidad (elipses punteadas). Las transiciones denso-independientes (compensación, → y depensación, ←) se indican con las flechas. Los datos representados son arbitrarios y fueron simulados por senoides con ruido.

Para proponer la base teórica sobre la migración, se simula un sistema auto-similar, a través de la iteración de la función $f(x) = x^2+m$. Se Deja que la función pueda adquirir, de forma aleatoria, entre dos inversas (+1 o -1) y que esta iterará hasta obtener un número arbitrario de datos (N=19851). De este modo, los datos resultantes fueron normalizados y se muestran en la Figura 16. Las variables (*R, IM*), el valor inicial del parámetro *m* y el número de iteraciones fueron arbitrarios. También, para mostrar los datos referenciados, dinámicamente, se utilizó una regresión lineal, un polinomio de sexto grado, un “espline” cúbico (para mostrar más detalles de la dinámica local) y elipses bivariadas del 50 y 95% (también, intervalos de confidencia). La serie producida por la iteración fue muestreada tanto de forma aleatoria como secuencial, a un 10, 5, 1 y 0.1% del número total de datos (para recrear distintas escalas espaciales o “ventanas de muestreo”). En todos los casos se observaron tendencias similares. Como en los casos de capturas y reclutamiento al área o al arte en el atún bonito-listado, el sistema simulado describe una dinámica similar en varias ventanas de muestreo. Estos resultados son importantes porque llevan a proponer que parte (o toda) la dinámica del sistema multioscilatorio en el atún bonito-listado se desarrolla en un marco de auto-similaridad que abarca tanto a la población como a las variables externas que afectan a esta.▪

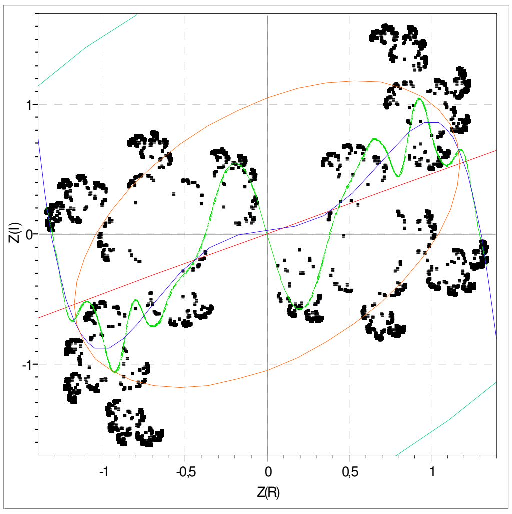

Figura 8. Simulación de un sistema autosimilar de Stock-en-área [Z(R)] y Reclutamiento-al-área [Z(I)]. El muestreo aleatorio y secuencial al 10, 5, 1 y 0.1% del número total de datos (N=19851) mostraron tendencias similares (como en la pesquería del atún bonito-listado para distintas ventanas de muestreo) y pueden representar capturas en escalas espaciales distintas (o distintas “ventanas” de muestreo. Los distintos puntos pueden representar muestreos sobre cohortes o stocks, poblaciones migratorias o localizadas. La iteración, datos, valores de los parámetros y función son arbitrarias.

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(vi)
Dinámica del pulpo común: hacia un nuevo marco teórico
(Cap. 3.4)

Este capítulo trata sobre una primera aproximación hacia la proposición de un marco *ad-hoc*, no-lineal para el estudio de la dinámica y la explotación del pulpo común, *Octopus vulgaris* (Cuvier, 1797), en el Atlántico Centro Oriental (zona de pesca 34 de FAO). Las capturas son utilizadas como un indicador de la abundancia y son asumidas como un reflejo de las tendencias en el reclutamiento a la población, área y arte de pesca. Se estudia la relación Stock-Reclutamiento (SR). Pulsos en la Oscilación del Atlántico Norte (NAO) son considerados como una variable externa o "fuerza externa" que puede determinar, de forma directa o indirecta, la evolución temporal de la población. Las series son analizadas para determinar efectos de memoria, correspondencias y periodicidades. Se propone que (i) la evolución de la población, durante los 40 años que comprende la serie, ha sufrido cuatro órbitas de estabilidad (dos equilibrios de largo periodo y dos de corto periodo) que pueden ser originados por pulsos cuasi-cíclicos en la NAO, un factor que puede gobernar la dinámica de la población; y (ii) la relación SR es un continuo dinámico multi-oscilatorio, enlazado por múltiples órbitas de estabilidad determinadas por una capacidad de carga variable. Este sistema se describe por un nuevo modelo matemático que representa una suma de funciones no-lineales que admite dinámica estable, periódica y caótica. El sistema propuesto tiene la capacidad de evolucionar y retornar, persistentemente, dentro de un amplio rango de órbitas de estabilidad, lo cual permite la incorporación de todos los procesos (denso-dependientes y denso-independientes) observados y variables estresoras/promotoras, en la mecánica de la población, en una misma relación descrita por una ecuación relativamente simple. También, se presenta una actualización de datos para la zona de afloramientos del Sahara Occidental y Mauritania y discuten varios de los conceptos propuestos.

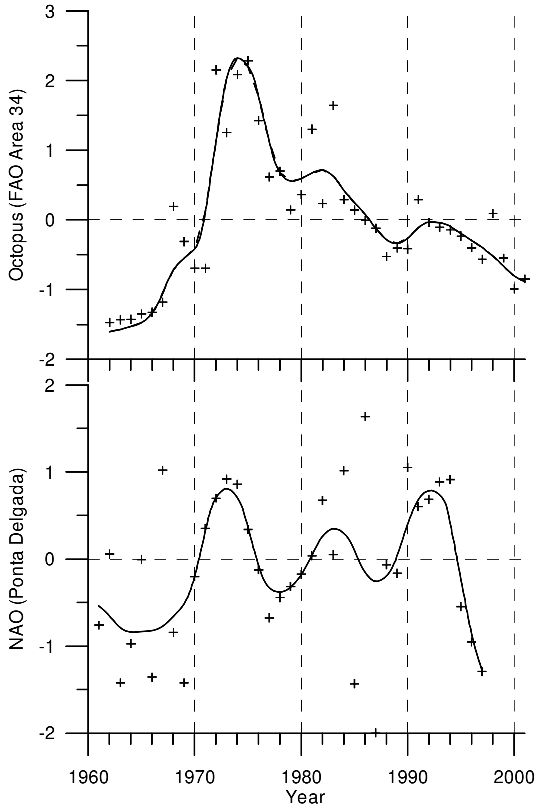

Figura 9. La Oscilación del Atlántico Norte (NAO; Presión atmosférica medida en Punta Delgada, Azores, años 1961-97) y capturas del pulpo común (*Octopus vulgaris*; Área 34 de FAO, años 1962-2001), estandarizados (medias anuales, +) y suavizados (en negrita).

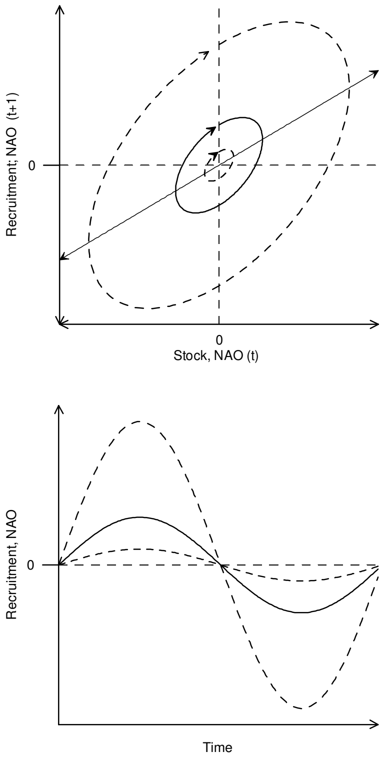

Figura 10. Modelo del efecto de un pulso de la Oscilación del Atlántico Norte (NAO, línea continua) sobre las tendencias del reclutamiento a la población y/o pesca, en el pulpo común (*Octopus vulgaris*), en el Área 34 de FAO: una perturbación similar puede inducir un equilibrio relativamente alto (línea discontinua exterior) o uno bajo (línea discontinua interior) dependiendo de (a) el nivel de números y capacidad de carga, durantes los (3 a 5) años inmediatamente anteriores y (b) la pendiente y duración de la misma, en la perturbación externa. El espacio de fase del ejemplo se ilustra, arriba a la izquierda, y la serie temporal, a la derecha.

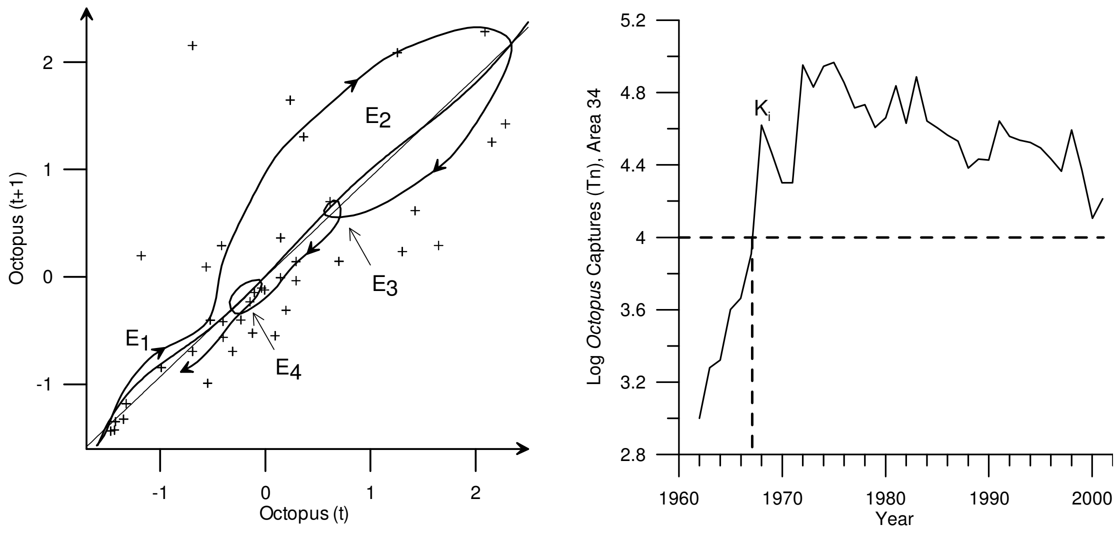

Figure 11. Arriba, izquierda: el sistema stock-reclutamiento (SR) o plano N_t, N_{t+1} del pulpo común (*Octopus vulgaris*), en el Área 34 de FAO (años 1962-2001). La trayectoria dinámica se muestra con los datos en bruto (+) y la serie suavizada (en negrita). La dinámica global y local están indicadas por los equilibrios E_1-E_2 and E_3-E_4, respectivamente. Las flechas sobre la trayectoria indican compensación (➤) y depensación (❮). El efecto de memoria es altamente significativo (exponente de Hurst ≥1). Las oscilaciones en el sistema SR pueden ser causadas, de forma directa o indirecta, por pulsos en la Oscilación del Atlántico Norte (NAO), variable externa que podría gobernar la capacidad de carga variable. Arriba, derecha: la serie fue log transformada para determinar el incremento de la actividad pesquera, durante la década de los 1960, y el año aproximado (1967) cuando la sistema de pesca comenzó a oscilar (eso es, cuando las capturas comienzan a reflejar las oscilaciones en la abundancia, indicado por los líneas punteadas). El primer pico refleja la primera capacidad de carga variable (K_i) del sistema durante los años de la serie despues del cual la pesquería (y población) oscila debido a los efectos combinados del medioambiente y la mortalidad por pesca.

El trabajo sobre capturas de *Octopus* (FAO) y la NAO fue realizado con datos hasta el año 2001. El subsiguiente material, en el sumario del capítulo (3.4), se realizó (Agosto 2007) con una actualización de datos del Instituto Español de Oceanografía (series de capturas y esfuerzo, de la zona del afloramiento del Sahara Occidental, hasta el año 1999) y del Instituto Mauritano de Pesca (IMROP) sobre la zona de Mauritania (índice de abundancia, hasta el año 2005). En ambos casos, veremos validadas las propuestas del modelo multi-oscilatorio propuesto por Solari et al. (1997) así como el uso de capturas como índice de abundancia, la dependencia del reclutamiento a la población, área y pesca con la Temperatura Superficial del Mar (en parte, efecto de la NAO) y sub-modelos propuestos para ambos casos. ▪

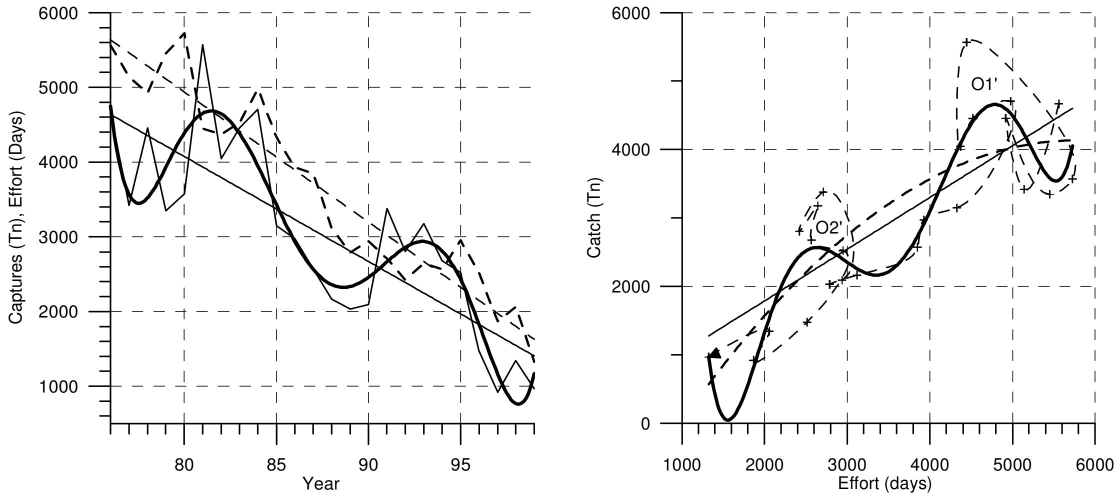

Figura 12 a-b. Arriba, izquierda (a), capturas (Tn; línea contínua en negrita) y esfuerzo (días; línea punteada) de la pesca española de pulpo común en la zona de afloramiento del Sahara Occidental para los años 1976-1999 (IEO, 2007). Arriba, derecha (b), relación captura-esfuerzo ajustada por una regresión simple, una aproximación clásica de segundo orden (línea punteada) y un ajuste polinómico que aproxima nuestro modelo dinámico. O1' y O2' son órbitas de estabilidad. Capturas reflejan esfuerzo y abundancia y viceversa y la relación es autosimilar: la flota española muestra tendencias y oscilaciones aunque disminuya el esfuerzo y área de pesca en el tiempo (retirada de la flota en 1999).

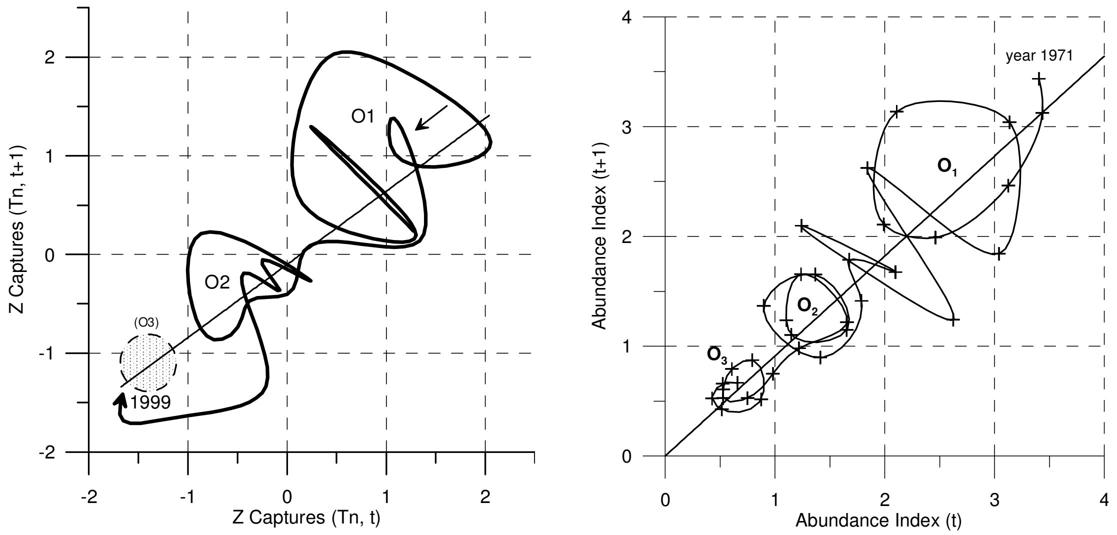

Figura 13 a-b. Arriba, izquierda: (a), el espacio de fase (considerado como aproximación al sistema stock-reclutamiento) para el pulpo común en la zona de afloramiento del Sahara Occidental para los años 1976-1999 (IEO, 2007). O1 y O2 son órbitas de estabilidad. O3 (área punteada) fue el rango estimado de oscilación, según nuestros criterios teóricos. La flecha indica un ejemplo de dinámica local. Arriba, derecha: (b) el espacio de fase de la abundancia del pulpo común en aguas de Mauritania (años 1971-2005). O_1-0_3 indican las órbitas de estabilidad (también, estados de equilibrio) que se proponen en el marco multi-oscilatorio propuesto por Solari et al. (1997). La recta es una regresión lineal a través del origen (línea de remplazamiento) que determina los valores de equilibrio lineales para todo el sistema. El ajuste no-lineal es de tipo LOWESS y consiste en la concatenación de varios ajustes locales de un punto con sus homólogos más inmediatos (“vecinos”). Los datos presentados validan claramente el modelo propuesto donde la población se asume como un sistema de múltiples órbitas de estabilidad (divergentes cuando el sistema se acerca a K_{max} y convergentes cuando la población/stock se acerca a la mínima población viable) gobernadas por una capacidad de carga variable. Año de comienzo de la serie es 1971.

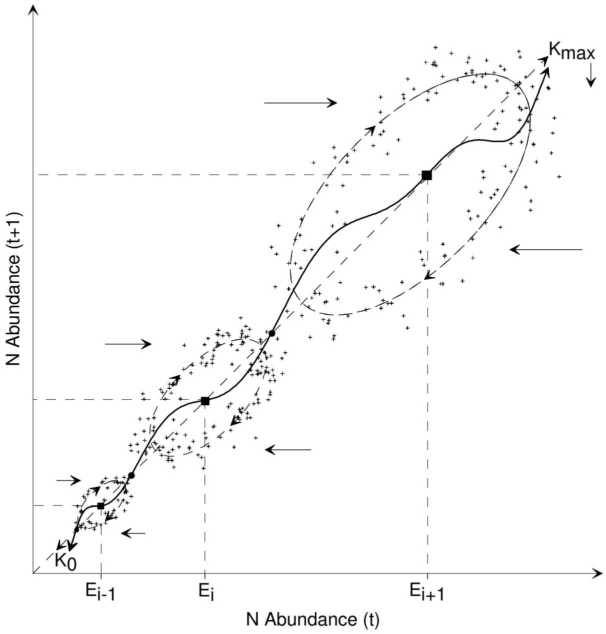

Figure 14. Representación gráfica del sistema multi-oscilatorio (contínuo dinámico gobernado por una capacidad de carga variable) propuesto para el sistema Stoc-Reclutamiento y dinámica de stocks explotados en el Area 34 de FAO (Atlántico Centro Oriental y zona de Canarias). E_i (■) representan los equilibrios para cada una de las órbitas de estabilidad. K_{max} es la máxima capacidad de carga (techo) del sistema (valor crítico por encima del cual el sistema evoluciona hacia órbitas de estabilidad más bajas) y K_0 es la mínima población viable (valor por debajo del cual las oscilaciones pueden cesar o el sistema tender a cero a través de la denso-dependencia inversa o Efecto Allé). La línea de remplazamiento da los valores de equilibrio globales (regresión lineal) mientras que el ajuste no-lineal (en negrita) incorpora 3 constantes por cada equilibrio. Este sistema puede describir, simultáneamente, dinámica cíclica, periódica y caótica además de Efecto Allé. La denso dependencia (diferencia entre máximos y mínimos) incrementa cuando el sistema evoluciona a K_{max}, pasa por un rango de órbitas convergentes, relativamente estables, cuando el estrés externo aumenta para alcanzar un estado sin oscilaciones cuando evoluciona hacia K_0 (colapso de la pesca comercial). Las oscilaciones son mediadas por los efectos combinados (multivariantes) de la dinámica intrínseca a la población (interacción entre fases de compensación y depensación denso-dependiente), la transición entre las mismas por el medioambiente (mecanismos denso-independientes) y la mortalidad por pesca pasada y presente. Variables externas como la Anomalía de la Temperatura Superficial del Mar y componente Sur de la Oscilación del Atlántico Norte se han demostrado ser "mejores descriptores" y pueden gobernar el sistema dinámico de formas directas y/o indirectas. El sistema presenta autosimilaridad dinámica en varias escalas espacio-temporales.

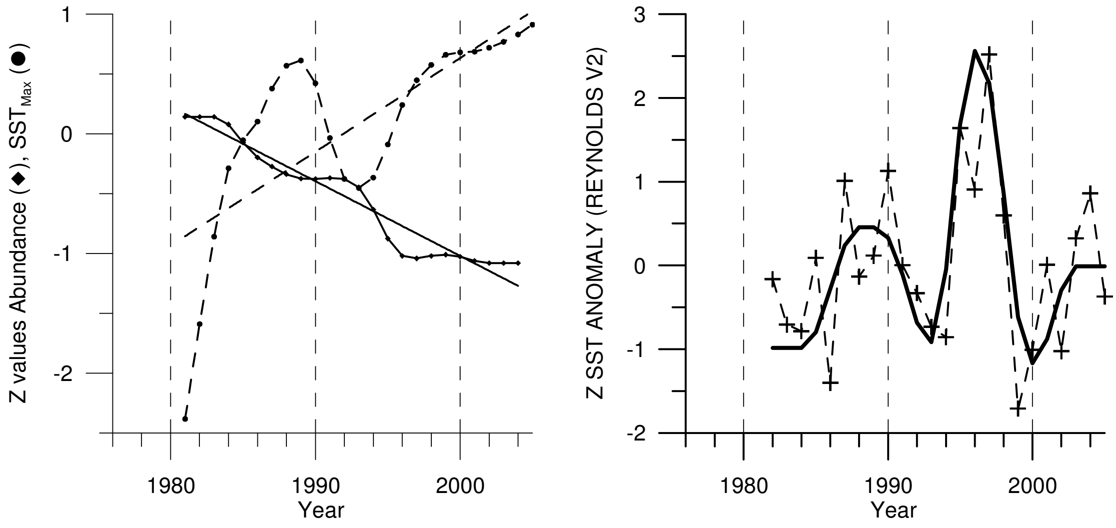

Figure 15 a-b. Arriba, izquierda (a), serie de máximos de Temperatura Superficial del Mar (SST; según Reynolds y Smith, 1994) para el área Long. 17.5-19.5° W – Lat 19.5-21.5° N (usada comp proxy) e Indice de Abundancia (IA; según FAO, 2006). La abundancia del pulpo común está altamente correlacionada con las tendencias en los máximos (p<.01, **) y medias (p<.05, *) de SST y puede modelarse una como inversa de la otra con diferentes parámetros de amplitud y tendencias. Arriba, derecha: tendencias (datos en bruto y suavizados) en la Anomalía de la SST (SSTA, según IGOSS, 2007) aparece como uno de los mejores descriptores para las tendencias del pulpo común en el Area 34 de FAO. Los valores están estandarizados.

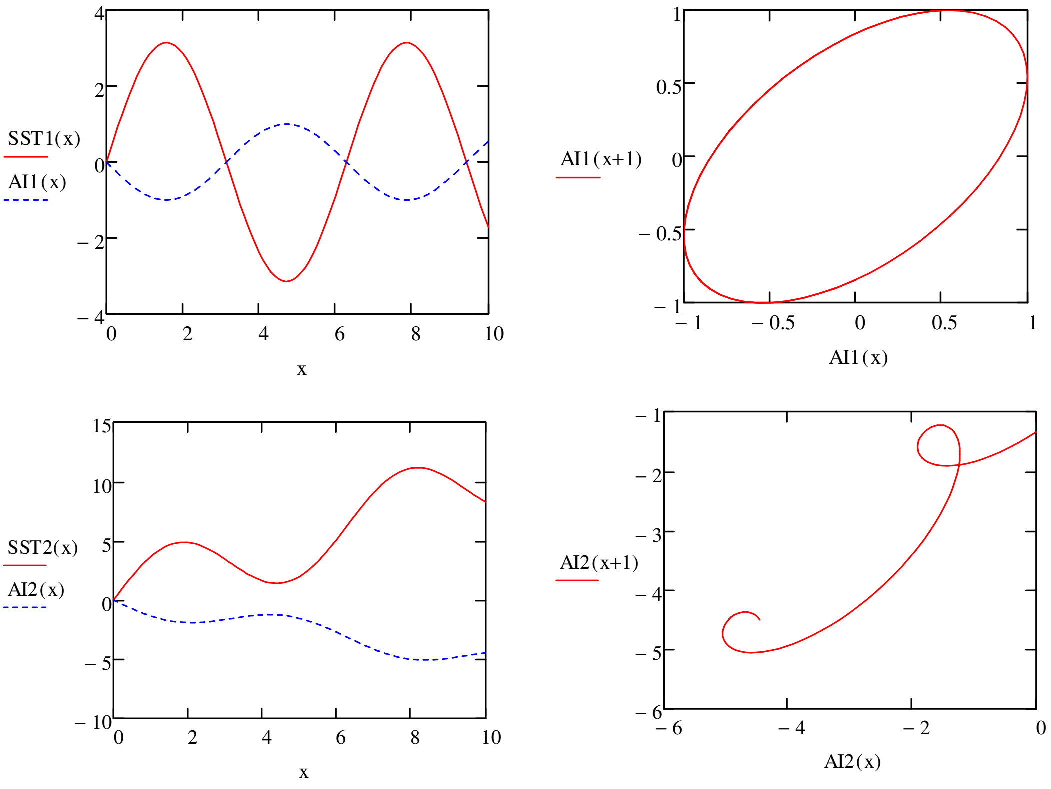

Figure 16 a-d. Modelados propuestos para la relación entre la abundancia del pulpo común (AI) en aguas de Mauritania (años 1971-2005) y las serie de máximos de Temperatura Superficial del Mar (SST) para el cuadrante de Long. 17.5-19.5º W – Lat 19.5-21.5º N. Por un lado, presentamos la relación como una senoide y su inversa con diferente amplitud (figura superior izquierda; SST1(x), AI1$_{x+1}$), y el espacio de fase de la abundancia (también, reclutamiento al área y pesca) que representa un ciclo límite, [AI1(x), AI1$_{x+1}$]: en este caso, no se consideran las tendencias lineales. Por otro lado, presentamos una segunda relación más compleja en la cual se consideran las tendencias lineales (figura inferior izquierda; SST2(x) and AI2(x)) y la evolución del correspondiente espacio de fase de la abundancia/reclutamiento (figura inferior derecha; AI2(x), AI2$_{x+1}$). X es el tiempo (10 generaciones o años).

(vii)
Dinámica de la pesca en Almadrabas españolas años 1525-1756
(Cap. 3.5)

Este capítulo trata sobre la dinámica de una pesquería orientada a los túnidos (particularmente el atún rojo) en las "Almadrabas" atlánticas españolas, durante los años 1525-1756, en base a una compilación de datos realizada por el monje Martín Sarmiento, en 1757. Las series de las almadrabas de "Conil" y "Zahara" que sumaban el 95% de las capturas, durante los 231 años de datos, son analizadas a la luz del nuevo marco teórico propuesto por Solari et al. (1997) en el cual en reclutamiento a la población, área y pesca se considera como un contínuo dinámico (con dinámica local), gobernado por una capacidad de carga variable. Capturas y temperatura annual sobre el hemisferio Norte son consideradas como "proxis" de abundancia y cambio climático, respectivamente y ambas son relacionadas. Se muestra de dependencia sobre valores precedentes, retardos, correspondencias, períodos y órbitas de estabilidad entre las variables (log transformadas) usando autocorrelación, correlación cruzada, análisis espectral y de "wavelets" así como ajustes lineales y no-lineales. El exponente de Hurst es utilizado como una medida objetiva de la naturaleza determinista de las tendencias. Una relación o sistema multi-oscilatorio fuerte esta propuesto para la relación entre capturas y temperatura. Se sugiere que el sistema pesquero puede estar controlado tanto por tendencias en los máximos (cuando los valores se encuentran por encima de la media) y los mínimos (cuando los valores se encuentran por debajo de la media) de temperatura (durante la "mini" glaciación de mediados de los 1600 que implicó un colapso de la pesquería inducido por el medioambiente). Una representación teórica es propuesta para la pesquería. Finalmente, se sugiere que los datos contemporáneos (s. XX) para el atún rojo y la Anomalía de la Temperatura Superficial del Mar (SSTA) muestran una relación similar, en una escala temporal más reducida.▪

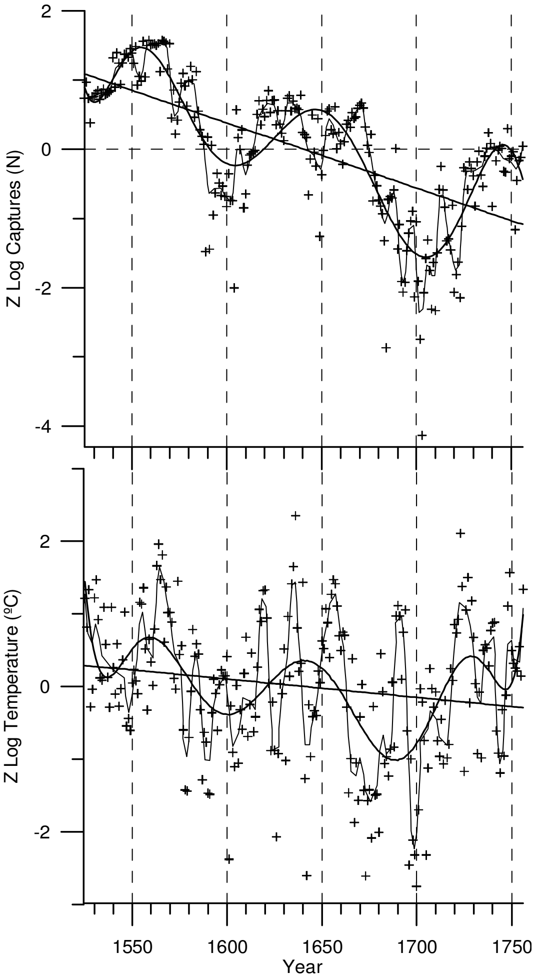

Figura 17. Las series (log transformadas y estandarizadas, Z número de individuos, N) de la pesquería de almadrabas españolas ("Conil" y "Zahara") entre los años 1525-1756) y la temperatura anual del aire (hemisferio Norte; según Mann et al., 1998; NOAA, 2007).

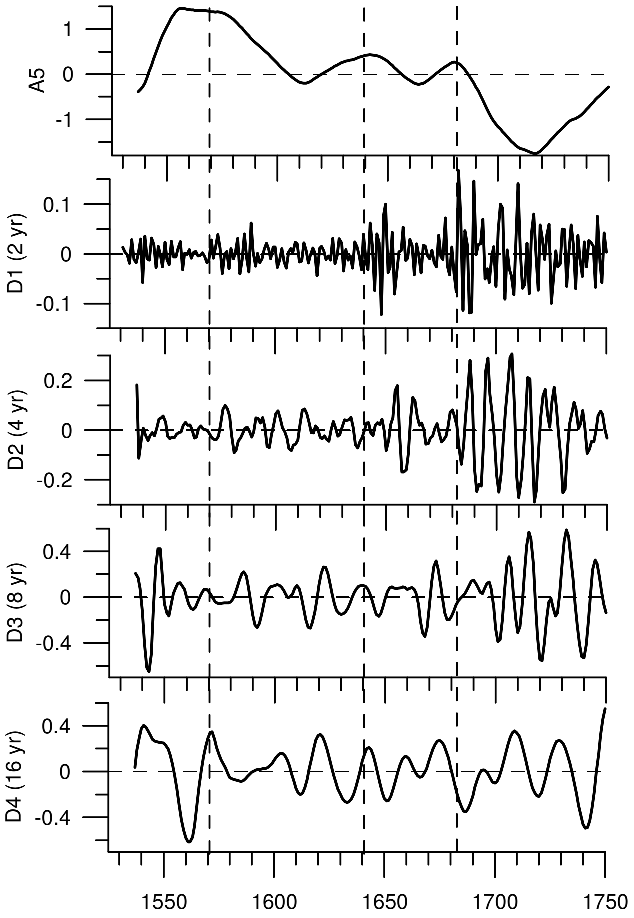

Figura 18. El análisis de "wavelets" sobre las series de capturas de la pesquería de almadrabas españolas (años 1525-1756). A5 muestra las tendencias sin ruido en la serie donde se observan las periodicidades a medio y largo plazo en las capturas. Mientras que existen oscilaciones de corto plazo, la tendencia general es negativa. D2 a D4 muestran los procesos de 2, 4, 8 y 16 años y se observan tres "zonas" discretas (indicadas por las lineas punteadas) con comienzo en los años 1570, 1640 y 1687. La dinámica del sistema pesquero puede haber estado gobernada por un cambio climático (una "mini" glaciación) con comienzo aproximado en el año 1640 y el máximo período de estrés medioambiental durante los años 1687-1705. La evolución temporal de los procesos ruidosos (D1) muestran diferencias claras entre los períodos marcados y el ruido aumenta durante las etapas de máximo estrés medioambiental. También, los procesos denso-dependientes (asumidos como el reclutamiento a la población y pesca; D2 y D3) muestran una clara divergencia (máximos y mínimos divergen) cuando comienza la glaciación. También, las oscilaciones de aproximadamente 16 años (más estables) pueden ser consecuencia de los ciclos de actividad solar (11 a 13 años) más los 3 a 4 años de retardo que existe en el reclutamiento en túnidos.

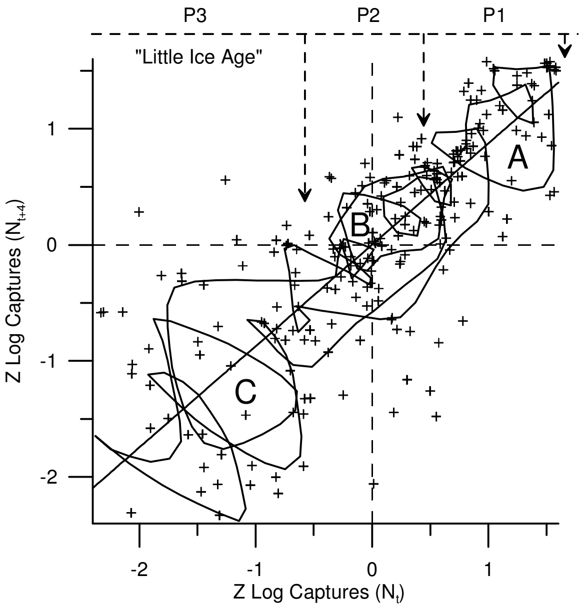

Figura 19. El espacio de fase (Z Log Capturas N_t, N_{t+4}) sobre las serie de capturas de la pesquería de almadrabas españolas (años 1525-1756). Los datos fueron ajustados por una regresión lineal a través del origen y un espline cúbico. Dos valores extremos fueron excluídos para facilitar la visión de la figura. El atractor consta de órbitas complejas de estabilidad (A-C) multi-oscilatorias: la órbita A (y parte de B) es gobernada por las tendencias en los máximos de temperatura (períodos P1 y P2) mientras que la C está gobernada por la glaciación (período P3) y es más ruidosa. Las fuentes del ruido pueden ser varias (errores de muestreo o falta de mano de obra bajo temperaturas bajas). No obstante, la amplitud entre máximos y mínimos durante la glaciación nos puede indicar cambios significativos en la denso-dependencia bajo condiciones medioambientales extremas (número de individuos reclutados a la población disminuye significativamente lo cual puede causar picos relativos de reclutamiento en años posteriores). La dinámica es autosimilar en varias escalas temporales.

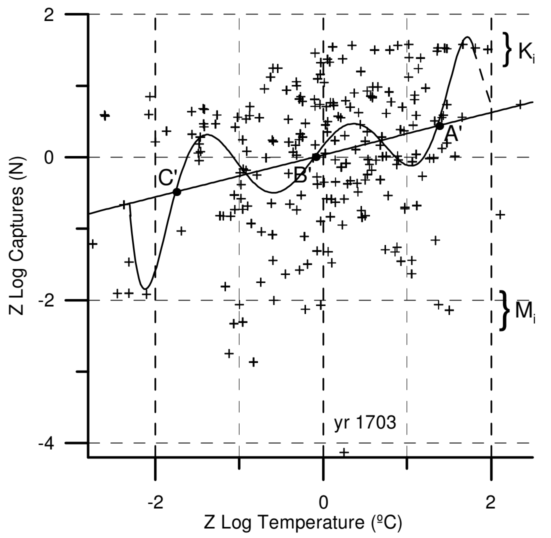

Figura 20. La relación entre la temperatura (según Mann et al. 1998; NOAA, 2007) y las capturas en la almadrabas atlánticas españolas (años 1525-1756, según López-Capont, 1997). Las series fueron log transformadas, estandarizadas, Z, y se consideró el retardo de 4 años (tiempo de reclutamiento para algunos túnidos). A'-C' indican tres siatuaciones multi-oscilatorias y K$_i$ la capacidad de carga de la pesquería. El valor extremo (año 1703) puede mostrar el effecto relativo de una guerra (invasión de Gibraltar por tropas británicas) sobre la pesquería, si se compara el valor con respecto al rango de mínimos (M$_i$) en las series. Los datos fueron ajustados por una regresión a través del origen y un polinomio. Los seudo-equilibrios son indicados por los puntos singulares para cada zona de estabilidad. El sistema pesquero puede ser controlado por las tendencias en los máximos de temperatura (para el rango por encima de la media) y por los mínimos y "mini" glaciación (para el rango de temperatura por debajo de la media).

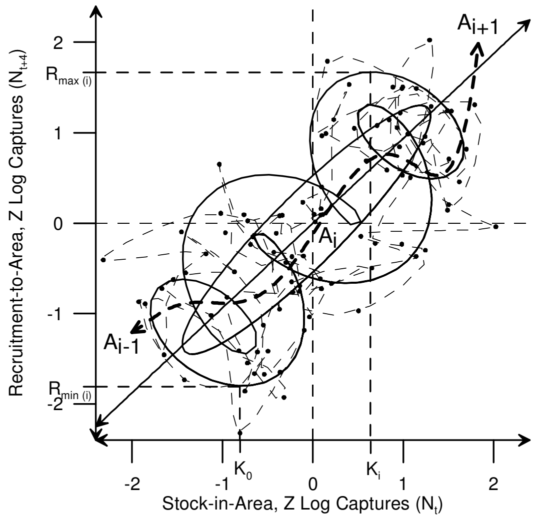

Figura 21. La representación de un atractor teórico (stock-reclutamiento en-área) propuesto para la serie de 231 años de la pesca en las principales almadrabas atlánticas españolas (años 1525-1756). Las trayectorias superimpuestas representan el ciclo de largo plazo en el atractor (elipse o ciclo límite), la intermedia que muestra las oscilaciones de corto y medio plazo y la línea punteada (interpolación de los valores con cierto grado de ruido blanco). El ruido, en este contexto, es considerado como la diferencia entre el valor teórico y el punto más cercano de la trayectoria intermedia. La línea de ajuste no-lineal representa el contínuo dinámico que evoluciona desde el seudo-equilibrio A$_i$ hacia la capacidad de carga (K$_i$) y la órbita de estabilidad superior (A$_{i+1}$) o a la mínima población viable (K$_0$) y la órbita inferior (A$_{i-1}$). El sistema es auto similar en diferentes escalas (espacio-temporales y de números). R es el reclutamiento a la población, área y/o pesca.

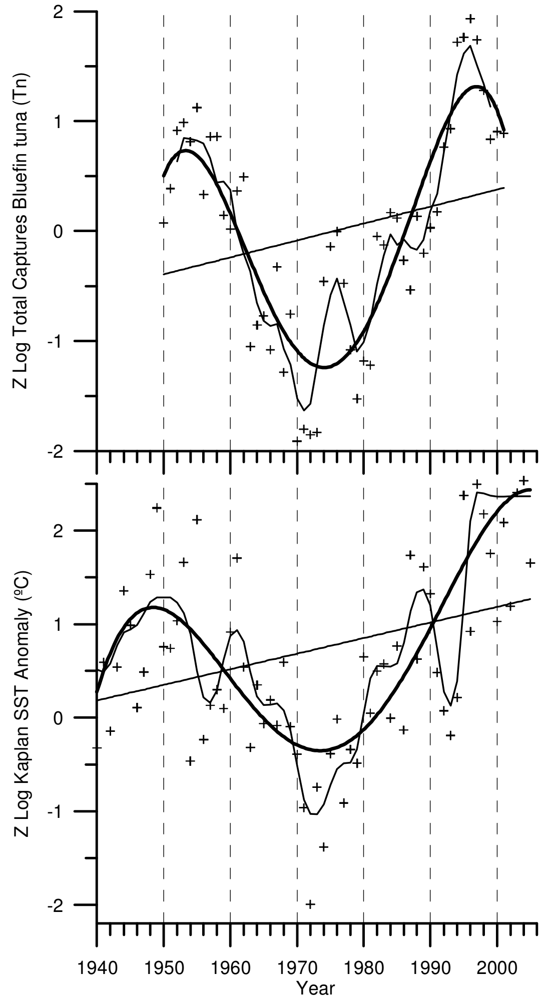

Figura 22. Capturas contemporáneas (Tn) en el Atlántico Norroriental y el Mediterráneo (1950-2002, según FishStat/FAO, 2003) y la Anomalía de la Temperatura Superficial del Mar (SSTA, según Kaplan, 1998; IRI/LDEO, 2007). La correlación cruzada entre las series con un retardo de 4 años es altamente significativa (p<.01). Los datos en bruto (+) están suavizados y ajustados por un poliniomio y una regresión simple.

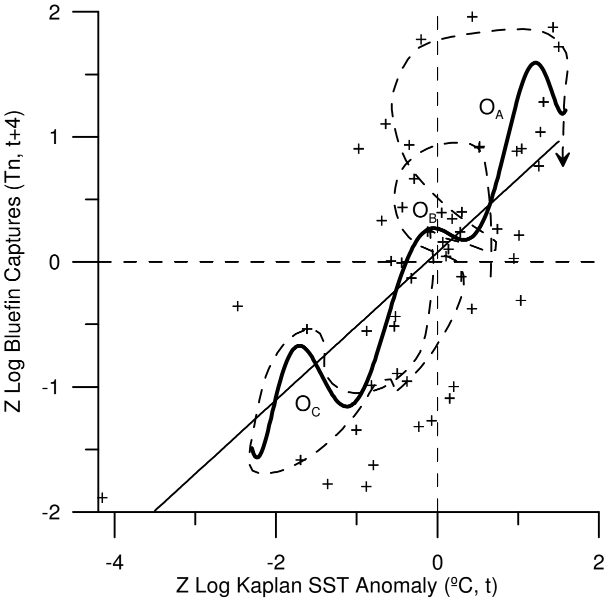

Figura 23. El sistema multi-oscilatorio propuesto para las series contemporáneas de capturas (según FishStat/FAO, 2003) de atún rojo en el Atlántico Noroccidental y Mediterráneo combinados para los años 1950-2002 y la Anomalía de la Temperatura Superficial del Mar (SSTA; según Kaplan, 1998; IRI/LDEO, 2007). Series log transformadas y estadarizadas. O_i son las órbitas de estabilidad. Los ajustes son lineal (recta), espline cúbico (punteado) y polinómico (negrita).

(viii)
Discusión general sobre los casos de estudio (Cap. 3.6)

El marco teórico propuesto ofrece varias ventajas conceptuales y prácticas sobre los modelos clásicos, y puede ser considerado como un primer paso hacia una nueva teoría para el estudio y la explotación de stocks de peces y cefalópodos. Es posible realizar un análisis más realista con una mayor "resolución" para la búsqueda de los mecanismos que gobiernan la dinámica de los stocks explotados. Entre otros aspectos, cabe señalar los siguientes:

(i) la persistencia ecológica del sistema SR. Es decir, la capacidad del stock para soportar tanto perturbaciones medioambientales como una tasa de mortalidad por pesca alta y rehabilitarse desde equilibrios bajos;

(ii) la determinación de los efectos combinados tanto medioambientales como de mortalidad por pesca que pueden conducir, en etapas depensatorias, a colapsos del stock, el establecimiento del sistema SR alrededor de equilibrios extremadamente bajos y la extinción de la pesquería comercial;

(iii) la predicción de las tendencias (años entre paréntesis) tanto a corto (4-8) como medio (9-18) plazo para el ajuste de niveles de explotación sostenibles, selectividad de tallas y otros parámetros de la pesca;

(iv) la explicación de la alta variabilidad en los datos y la determinación de cómo correspondencias multivariantes, efectos de memoria, retardos, oscilaciones periódicas, ruido y sensibilidad a condiciones externas (pulsos medioambientales) pueden afectar el sistema SR;

(v) el control preventivo de la población, a través del estudio del efecto de la mortalidad por pesca diferencial sobre el sistema SR, durante etapas de compensación y depensación, denso-dependientes y denso-independientes;

(vi) el retro-cálculo y determinación de colapsos pasados o establecimiento del sistema SR alrededor de equilibrios extremadamente bajos (cerca de la mínima población viable) como función de situaciones medioambientales extremas (ej. pequeña glaciación europea ocurrida entre 1640 y 1715), cuando no existía pesca industrial y otras situaciones de cambio climático a medio y largo plazo;

(vii) la existencia de auto-similaridad dinámica, en varias escalas espacio-temporales y posibilidad de extrapolación de las tendencias dinámicas, entre las mismas;

(viii) la determinación multidimensional del sistema SR como función del tiempo y espacio (latitud y longitud), y como las variables externas acotan y determinan la evolución temporal de la estructura 3D/4D que representa a la población.

Se propone un marco dinámico que puede ser útil para contribuir a la comprensión y la gestión de los stocks y a proponer preguntas más realistas y adecuadas para el estudio dinámica compleja de poblaciones que pueden estar gobernadas por mecanismos causales multivariantes.

Otros conceptos inherentes al marco dinámico propuesto, tales como (i) la ecuación matemática que lo describe, (ii) la línea de remplazamiento, (iii) las órbitas de estabilidad, (iv) la capacidad de carga variable o "techos", (v) la máxima capacidad de carga del sistema, (vi) las mínimas poblaciones viables ("pisos"), entre otros aspectos, están discutidos, extensivamente en publicaciones anteriores (Solari *et al.*, 1997; Bas *et al.* 1999; Castro *et al.*, 1999; Solari *et al.*, 2003).

También, hasta la fecha, hemos indagado, someramente, en las tendencias de 137 stocks explotados (peces marinos), en todo el mundo, 120 casos de los cuales, nuestros conceptos dinámicos pueden ser aplicables.

Solari et al. (1997) fue motivo de la reunión (workshop) "Internacional "New non-linear model for stock-recruitment and management of fish stocks", auspiciada por el Programa FAIR (Dirección General XIV –Pesquerías- de la Unión Europea; referencia: MAC/12/97), la Consejería de Agricultura, Ganadería y Pesca del Gobierno de Canarias y la Universidad de Las Palmas de Gran Canaria (ULPGC). Esta reunión fue celebrada en Las Palmas de Gran Canaria (Facultad de Ciencias del Mar de la ULPGC) entre los días 31 de marzo y 3 de abril de 1998.

A continuación, se discuten varios de los conceptos que derivan del nuevo marco teórico propuesto:

Las ecuaciones propuestas.

Una modelo aditivo que describe la población o proceso como una suma de funciones no-lineales es extremadamente flexible, simple y robusto y puede describir dinámicas complejas. También, las órbitas de estabilidad se enlazan unas con otras con la particularidad que cada una de las funciones es matemáticamente independiente de la otra permitiendo la descripción de un amplio rango de situaciones dinámicas (caos, ciclos, cuasi-ciclos, situaciones sin oscilaciones o multiperiódicas) dentro del marco de un sistema el cual puede ser aproximado por varios métodos matemático-estadísticos sin establecer un método determinado que, en ocasiones, puede no ser de conveniencia para biólogos y gestores de pesca con distintos niveles de orientación técnico-matemática. También, pueden existir situaciones en las cuales los valores sean cero (por ejemplo, "reclutamiento cero" o "extinción local" en un área determinada por efecto de una gran perturbación medioambiental o antropogénica sin que el modelo colapse.

El espacio de fase.

En principio, el "espacio de fase" que refleja la relación entre dos variables puede ser una herramienta analítica básica de nuestro marco teórico: en él, veremos las distintas características dinámicas del sistema que estudiamos y nos permitirá, combinado al uso de herramientas estadísticas paramétricas (y no-paramétricas para algunos casos de series cortas o situaciones complejas como las determinadas por los residuos autocorrelados), observar la relación estudiada de una forma sinóptica y, a la vez, ver los detalles (dinámicas locales, por ejemplo) que sean de interés. También, el espacio de fase nos permitirá observar cuales son los retardos, dependencias, períodos, ruido y otras características que caracterizan al sistema.

Capacidad de carga variable (K_i).

Este es un concepto central en nuestro marco conceptual y que fue formalizado por primera vez, en la literatura científica, en Solari et al. (1997). En los modelos clásicos, la capacidad de carga es única mientras que en nuestro modelo la capacidad de carga es variable. Cada estado de equilibrio tiene su capacidad de carga y esta es un umbral o valor crítico de stock: valores por encima del umbral implicarán una evolución del stock-reclutamiento hacia niveles o estados de equilibrio superiores. Asímismo, la capacidad de carga de un equilibrio determinado es el piso o valor mínimo del equilibrio siguiente. Este concepto dinámico de capacidad de carga variable es nuevo, puede ayudarnos a explicar como un sistema de stock-reclutamiento permite la transición hacia equilibrios más bajos y nos permite observar posibles variaciones en utilización de recursos según las escalas espacio-temporales relevantes y como estas afectan el reclutamiento a la pesca. Por ejemplo, una variación significativa en la abundancia de alimento en una localidad espacial determinada (Mogán, por ejemplo) no tiene necesariamente que implicar un cambio global en la dinámica de la población (resto del archipiélago Canario, por ejemplo). De ahí podemos deducir que los distintos estados de equilibrio pueden tener un amplio margen de tolerancia y el sistema stock-reclutamiento ser persistente a pesar de existir cambios o perturbaciones externas locales y evolucionar entre distintos estados de equilibrio. En general, la capacidad de carga es un factor determinante en la dinámica de las poblaciones: el crecimiento, la mortalidad natural y, particularmente el nivel de reclutamiento estarán afectados por la capacidad de carga correspondiente a cada equilibrio. Si las condiciones externas mejoran, el sistema stock-reclutamiento llegará al umbral K_i y habrá una evolución a un estado de equilibrio superior. Por el contrario, si el estrés externo aumenta, el sistema stock-reclutamiento evolucionará hacia un estado de equilibrio inferior con una capacidad de carga inferior. De esta forma, el sistema puede evolucionar en ambos sentidos de forma dinámica. También, la máxima capacidad de carga permitida por el sistema (K_{max}) permite la transición hacia equilibrios más bajos.

Múltiples seudo-equilibrios (E_i) y órbitas de estabilidad (O_i).

Otro de los aspectos fundamentales de nuestro marco conceptual es que los equilibrios pueden comprender caos, ciclos, cuasi-ciclos y estados sin oscilaciones o multi-periódicos, acoplados en un continuum dinámico y descritos por una ecuación simple. Según los modelos clásicos, la falta de relaciones causales entre stock y reclutamiento ha implicado una discusión sobre si el reclutamiento es un proceso determinista (Kot et al. 1988, Fogarty 1993). En nuestra opinión, los modelos clásicos no han podido detectar la mecánica del stock-reclutamiento porque asumen que los valores residuales (una vez los datos se ajustan a los modelos) son producto del azar. De esa forma, los modelos clásicos son incapaces de describir la evolución dinámica que muestran los datos de stock-reclutamiento. En nuestra opinión, el reclutamiento a la pesca puede ser un fenómeno determinista aunque de altamente complejo. Nuestro modelo propone un continuum dinámico en el cual podemos describir situaciones de caos cuando las condiciones externas son extremadamente buenas, una serie de ciclos o cuasi ciclos convergentes que pueden ser producto de un aumento en las perturbaciones negativas (por ejemplo, el efecto combinado del empobrecimiento medioambiental y la alta mortalidad por pesca) hasta una situación sin oscilaciones denso-dependientes cuando el stock-reclutamiento se acerca a la mínima población viable y la pesquería comercial se extingue. En este sistema altamente flexible, el stock-reclutamiento puede evolucionar desde y hacia un amplio rango de estados de equilibrio lo que permite que el proceso sea persistente. Rothschild (1992) sugirió que las poblaciones reducidas por pesca que compensan con reducciones en factores vitales pueden transitar entre dinámicas estables, periódicas y caóticas. También, en la literatura se han observado una serie de ejemplos que se atribuyen a fenómenos oscilatorios aunque sin formalizar un marco conceptual en forma matemática como el que presentamos en nuestro estudio: Garcia (1998) y Sharp et al. (1983) sugirieron que las series de sardina de Hokaido estaban caracterizadas por órbitas (loops) y propusieron un sistema que consistía en dos atractores extraños, acoplados, que operaban en dos niveles distintos de stock y reclutas. Conrad (1986), Schaffer (1986) y Kot et al. (1988) sugirieron que los mecanismos caóticos podrían servir para mantener la adaptabilidad de la población. También, Powers (1989) sugirió el caos para un sistema de 2 especies y Berg y Getz (1988) que el stock-reclutamiento en una población de sardinas se movía a través de una trajectoria o atractor. Conan (1994) observó que las descargas de cangrejos y langostas en la costa Atlántica de Canadá podrían seguir dos órbitas de estabilidad y Tyutyunov et al. (1993) demostró ciclos de diferente período y caos en la dinámica de población de perca en 10 lagos. También, Caddy (1998) observó otros casos, en areas semi-cerradas, donde la dinámica stock-reclutamiento podría ser ligada a fenómenos oscilatorios: (i) una periodicidad de 9-18 años en los stocks de vieiras (Caddy 1979); (ii) una periodicidad de 12 años –independiente del esfuerzo pesquero- en las descargas de merluza en la isla de Mallorca (Astudillo and Caddy, 1986) y una oscilación de 12-13 años en las capturas de la sardina del Adriático. Así también, el sistema propuesto puede incluir todos los modelos clásicos. Por ejemplo, aproximaciones al modelo de Ricker (1954) y el logístico pueden obtenerse cuando los valores de ai y/o bi son altos lo cual puede suceder cuando el medioambiente es extremadamente benigno.

Mínima población viable (K_0) y dinámica depensatoria.

Cuando el stock-reclutamiento evoluciona a fases depensatorias, el efecto combinado de alta mortalidad por pesca y el estrés medioambiental pueden implicar un cambio hacia estados de equilibrio bajos o hacia la mínima población viable. En nuestro marco conceptual, el sistema stock-reclutamiento evoluciona a un estado sin oscilaciones denso-dependientes mientras se acerca a K_0. Esto implica que la pesquería comercial se puede extinguir hasta que el stock-reclutamiento se rehabilite a estados de equilibrio bajos con ligeras oscilaciones denso-dependientes cuando las variables externas permitan la compensación denso-independiente. Así también, cuando el sistema de stock-reclutamiento evoluciona hacia K_0, existe la posibilidad que el reclutamiento tienda a cero debido a que la mínima población viable es un equilibrio inestable y a que el éxito reproductivo de la población puede disminuir gradualmente cuando el número de individuos alcance un umbral mínimo. Si este tipo de mortalidad depensatoria se detecta, el simple hecho de dejar de pescar puede ser insuficiente para que el sistema stock-reclutamiento se rehabilite. Según nuestro criterio, es importante que un marco conceptual admita estas características dinámicas. Los modelos clásicos no admiten la mínima población viable ni la dinámica depensatoria debido a que asumen que el stock-reclutamiento siempre compensará a la mortalidad por pesca. No obstante, la literatura indica que existen casos donde se ha detectado dinámica depensatoria. Myers et al. (1995) detectó dinámica depensatoria para tres stocks de peces y Solari et al. (1997) para el stock-reclutamiento en el bacalao del Báltico.

Continuo dinámico.

El sistema SR sigue una trayectoria determinada por procesos intrínsecos (debido a la denso-dependencia) y externos (debido a la denso-independencia; medioambiente y pesca) a la población. De esta forma, asumimos que todos estos procesos pueden estar enlazados a un continuo dinámico que está mediado por: (i) un rango de órbitas de estabilidad que evolucionan (a través de compensaciones) y retornan (a través de depensaciones), entre la mínima población viable del sistema (K_0) y la máxima capacidad de carga admitida por el mismo (K_{max}), y (ii) una capacidad de carga variable que cambiará, constantemente, y gobernará las tendencias y evolución de la población. Las transiciones hacia diferentes órbitas de estabilidad pueden ocurrir cuando se alcanzan valores críticos tales como $K0_i$ y K_i.

La idea sobre continuo dinámico nos permite aproximarnos al sistema SR como un atractor global, con distintas características locales, y determinar las interacciones en la trayectoria multi-oscilatoria bajo el efecto combinado del reclutamiento y las influencias medioambientales y antropogénicas. García (2004, Serge.Garcia@fao.org, comunicación personal) ha sugerido que: (i) cambios graduales en las respuestas del stock pueden suceder debido a cambios continuos en el clima; es decir, los fenómenos multi-oscilatorios o múltiples respuestas del stock a los múltiples estados del medioambiente; y (ii) el sistema multi-oscilatorio podría constar de un único estado con cambios continuos en el nivel de escalas de números, donde ningún nivel sería estable debido al constante cambio de la capacidad de carga.

La idea de continuo dinámico es interesante tanto para plantear preguntas sobre los mecanismos causales de la trayectoria como para determinarlos y comprender la evolución temporal del sistema.

Sharp *et al.* (1988, 1997, 1998, 2002) sugieren que el estado actual de las pesquerías mundiales puede ser atribuido a la negación de la importancia de la dinámica de los sistemas.

Dinámica global y local.

Por un lado, dinámica global (trayectoria que determina la cota exterior del atractor) puede surgir como consecuencia de las transiciones denso-independientes entre distintas órbitas de estabilidad y ser el resultado de pulsos medioambientales de medio y largo plazo y una capacidad de carga oscilatoria que permite al sistema SR evolucionar y retornas entre estados de equilibrio altos y bajos.

Por otro lado, dinámica local (órbitas de estabilidad menores) pueden ser el resultado de dos posibles causas: (i) pulsos externos de menor amplitud o de amplitud similar a otros pulsos que generan mayores oscilaciones pero que, por motivos de denso-dependencia, cuando el sistema de halla en equilibrios bajos, no puede responder, cuantitativamente, como equilibrios más altos (cada nivel de números tiene su propia capacidad de respuesta y cotas denso-dependientes), o (ii) estos equilibrios locales pueden ser el resultado del efecto de la tendencia positiva de un pulso externo pero que aumento temporal de la mortalidad por pesca impide que la población pueda desarrollar una respuesta adecuada en un lapso de tiempo mayor (recuperar una órbita de mayor amplitud).

Esta es la primera vez, en los estudios que hasta el momento hemos realizado, que detectamos una dinámica global y una local y que se asocian a los distintos pulsos en la NAO, SST, SSTA, presión en Azores (componente Sur de la NAO), entre otros descriptores. Si un sistema SR es suficientemente sensible a pulsos externos que determinen dinámicas locales, esta característica del sistema podría contribuir a la estabilidad y persistencia ecológica del mismo.

Residuos: señal, ruido y variabilidad/dispersión.

Mientras que los modelos clásicos asumen que los residuos son el resultado de un proceso aleatorio o ruido, en el marco teórico que aquí se propone estos valores son, en alto grado, señales que incorporan una parte marginal de ruido debido a procesos de advección/difusión, en el sistema marino, y errores de muestreo. Esta inferencia está basada en los resultados de las correlaciones y efectos de memoria. En general, los modelos clásicos pueden explicar entre el 20-40% de la variabilidad en los datos y es una temeridad asumir que entre el 60-80% de la variabilidad es causada por procesos aleatorios que no se pueden identificar. También, se asume que los datos son independientes uno del otro, eso que, que no existe el efecto de memoria – lo cual es incierto. Las variables ecológicas muestran un fuerte grado de autocorrelación y, cuando la evolución temporal de los datos es considerada, el concepto de ruido se marginaliza debido a los fuertes efectos de memoria que se detectan.

En el presente marco, los residuos que muestran un suavizado equivalente a una media móvil con ventana 5 se consideran ruido.

Algunos de los aspectos que pueden requerir estudios más profundos son aquellos relacionados con (i) la advección/difusión como factor de persistencia y (ii) si éste varía en relación a los distintos pulsos externos (una variable puede generar más ruido que otra, en las tendencias, en la evolución temporal de la población).

También, en esta nueva situación se asume que el ruido es variable y que puede aumentar cuando el sistema SR evoluciona hacia equilibrios altos o K_{max}. Esto puede ser explicado por la divergencia entre máximos y mínimos y denso-dependencia, en equilibrios, relativamente, altos.

Efectos diferenciales de la mortalidad por pesca.

Los efectos de la mortalidad por pesca son diferenciales, según el presente marco dinámico: (i) durante etapas de compensación denso-independiente, aumentos en la mortalidad por pesca pueden no afectar significativamente a la tendencia global (siempre que el sistema SR no se encuentre en equilibrios extremadamente bajos, cercanos a K_0). Esto implica que el esfuerzo pesquero puede aumentar durante estas etapas sin que ello tenga consecuencias negativas importantes para la población; (ii) no obstante, cuando la trayectoria alcanza valores de K_i (los "techos" de los equilibrios) y comienza una etapa de depensación denso-independiente, la mortalidad por pesca invariante o aumentos en la misma pueden contribuir al aumento de la pendiente negativa (o velocidad de decremento en la población) de la tendencia, propiciando una transición brusca hacia equilibrios más bajos. Este es un mecanismo que observamos en la pesquería de varias especies donde (a) a través de modelos VPA se determina la cuota de pesca a partir de datos del año anterior, y (b) si el mencionado año fue un pico y la trayectoria comenzó en una fase combinada de depensación denso-dependiente y denso-independiente, también, se aumenta la mortalidad por pesca (cuando tendría que disminuirse). Las consecuencias de tal error es una pendiente depensatoria que puede llevar el sistema SR a equilibrios extremadamente bajos; (iii) también, durante etapas de compensación denso-dependientes, la mortalidad por pesca puede mantenerse, relativamente, constante o aumentarse ligeramente siempre que el marco utilizado –como el que aquí se propone- pueda predecir las tendencias a corto plazo y los picos dentro de la órbita actual, así como permita disminuir la presión pesquera el año que comience la etapa depensatoria; (iv) así también, durante etapas de depensación denso-dependiente, los efectos del esfuerzo pesquero invariante (o en aumento) pueden ser negativos y contribuir a cambiar (reducir) las escalas de números en el sistema. En etapas de depensación, particularmente aquellas donde operan simultáneamente la denso-dependiente y denso-independiente, la mortalidad por pesca debería reducirse. Aunque no existan datos fiables de esfuerzo, se puede trabajar con simulaciones que reflejen distintas pendientes para determinar los porcentajes (o valores de velocidad de decremento en la población) de presión pesquera sobre la pendiente original.

Cada órbita de estabilidad puede soportar un determinado nivel de mortalidad por pesca, diferenciado por las distintas fases de la oscilación, y el efecto actual o retardado de las variables externas que determinan la capacidad de carga particular (K_i) para cada órbita.

Explotación de sistemas con múltiples equilibrios.

Según el marco propuesto, los sistemas con múltiples órbitas de estabilidad pueden retener sus cualidades dinámicas auque existan cambios en la mortalidad por pesca. Por un lado, el reclutamiento a la pesca puede aumentar hasta que una oscilación llega a su capacidad de carga (Ki), después de lo cual, la trayectoria entrará en una fase de depensación que resultará en un nuevo ciclo u órbita similar, o evolucionará a un equilibrio inferior. También, si las variables externas son benignas para el reclutamiento, la órbita podrá evolucionar hacia un equilibrio superior cuando el valor K_i sea alcanzado.

Si la mortalidad por pesca se incrementa durante etapas depensatorias, la trayectoria SR alcanzará, rápidamente, un equilibrio inferior o mantendrá la tendencia depensatoria, durante varios años, si el medioambiente implica perturbaciones negativas para el reclutamiento.

La explotación de sistemas con múltiples equilibrios ha de adaptarse a las distintas situaciones dinámicas, de manera que el efecto de la pesca no induzca que el sistema se establezca en situaciones alrededor de K_0. Esto implica que la predicción de las tendencias tanto del reclutamiento como de las variables externas que afectan el sistema son críticas para explotar el sistema de forma sostenible.

La estrategia de explotación para sistemas con oscilaciones múltiples debería estudiarse, detenidamente, para la proposición de un marco de pesca sostenible basado en los efectos diferenciales de la mortalidad por pesca.

Extinción de la pesquería comercial.

Se pueden considerar varios aspectos interesantes para analizar, en profundidad, acerca de la posible extinción o colapso de la pesquería comercial. Varios mecanismos pueden operar por sí solos o combinados entre sí: (i) la sobrepesca económica puede implicar que la mortalidad por pesca, en algunos casos, pueda alcanzar valores asintóticos cuando la pesquería se acerca al denominado “valor neto cero” (eso es, los beneficios de la pesquería se reducen a cero, seguido de una reducción estabilizadora en el esfuerzo pesquero) como sugirió Clark (1976); (ii) la sobrepesca de reclutamiento puede ocurrir debido a una depensación, en la relación esfuerzo vs. capturas, debido a una mortalidad por pesca que afecte el potencial de reclutamiento (sobrepesca biológica), como sugirieron Pitcher and Parrish (1993). Esto puede ocurrir cuando se establece el sistema SR alrededor de equilibrios extremadamente bajos (cerca de K_0), sin oscilaciones claras, debido a perturbaciones medioambientales erráticas o al efecto combinado de situaciones medioambientales extremas y mortalidad por pesca, durante depensaciones con altas pendientes. La denso-dependencia-inversa (o “Efecto Allé”), que sucede cuando el sistema SR se encuentra en escalas de números alrededor de K_0, implica que el reclutamiento puede tender a cero y la pesquería extinguirse cuando la trayectoria se encuentre por debajo del mencionado valor crítico.

Incorporación de variables externas.

Así, proponemos, también, la incorporación de perturbaciones externas con una ecuación modificada del nuevo modelo dinámico la cual puede ser usada para el análisis y simulación del sistema SR en el atún listado. De esta forma, el stock adulto, en el comienzo de cualquier año, en particular, S_{t+1}, es descrito por la ecuación

$$S_{t+1} = \sigma \cdot S_t + R\left(S_{t-\tau}\right) \qquad (3)$$

donde σ es el coeficiente de supervivencia que afecta al stock adulto, S_t, y el reclutamiento (*R*) es una función del stock adulto τ años antes (τ = 1 en el atún listado debido a su tiempo de generación y maduración). Así, el reclutamiento es determinado por

$$R\left(S_{t+1}\right) \cong \sum_{i=1}^{m} \frac{a_i \cdot P_t \cdot (S_{t-\tau})}{(S_{t-\tau} - b_i)^2 + c_i} \qquad (4)$$

donde a_i, b_i, c_i son aquellos parámetros definidos para la Ecuación 5:2 y τ es un retardo fijo de 3 años.

P_t es un término de perturbación que puede incorporar valores de variables externas, estandarizadas y suavizadas (V_1 … V_n) o índices de las mismas, lo cual se expresa como

$$P_t = \sum_{t=1}^{n} V_{t-T} \qquad (5)$$

donde T es el retardo para el cual la correlación cruzada entre el reclutamiento y la variable externa es máximo.

También, existen varios aspectos de relevancia para el término de perturbación: (i) cada variable externa debería multiplicarse por un factor alfa (α) que dependerá de la misma como descriptor de la trayectoria SR (esto puede determinarse con regresiones múltiples); (ii) los retardos entre el reclutamiento y las distintas variables pueden cambiar, contribuyendo a la naturaleza multi-oscilatoria del sistema y a las distintas características de las diferentes órbitas, sub-stocks localizados o diferentes áreas, y (iii) el impacto de las distintas variables sobre diferentes tallas puede ser diferencial. Todos estos factores han de ser investigados en futuros estudios.

Aproximaciones (ajustes) para sistemas multi-oscilatorios.

En general, el ajuste de datos de sistemas multi-oscilatorios requieren métodos no-lineales y estimaciones de parámetros basados en aplicaciones de ordenador. También, puede ser necesario trabajar con los datos en bruto y distintos tipos de transformaciones como las logarítmicas y la raíz cuadrada así como las series suavizadas con distintos métodos.

El marco que proponemos puede ser aproximado por mínimos cuadrados, regresiones lineales y lineales robustas (que ignoran el efecto relativo de valores extremos) las cuales indican la línea de sustitución o valores de equilibrio generales del sistema y no-lineales (esplines cúbicos, medias móviles con distintas “ventanas”, lowess y técnicas de suavizado). Por ejemplo, las distintas óbritas de estabilidad pueden ser aproximadas con esplines cúbicos, elipses bivariadas y suavizados de ventana 5 mientras que el contínuo dinámico puede ser aproximado por polinomios, mínimos cuadrados, lowess y otros tipos de métodos no-lineales. El factor crítico es el modelo teórico de población sin el cual las estadísticas, en sí, pueden ser herramientas menos útiles.

Crítica.

Algunos de los aspectos que deseamos mencionar, en una autocrítica sobre el presente estudio, son los siguientes:

(i) Del modelo original (Solari *et al.,* 1997), se ha cambiado el concepto original de “equilibrio” por el de “cuasi-equilibrio” u “órbita de estabilidad”. Esto es así por dos motivos: (a) por un lado, la capacidad de carga del sistema (vista como as K_i y/o K_{max}) es variable y variará, constantemente, por lo que debemos adoptar un concepto que no refiera a equilibrios invariantes y (b) porque algunos autores entienden, desde la perspectiva de los modelos clásicos, que los equilibrios siempre son invariantes (lo cual puede ser una falacia); el concepto de equilibrio, en sí, es una herramienta que nos ayuda a describir una situación dinámica (que, siempre, cambia), en torno a unas determinadas condiciones, una situación típica o media de las cotas de una órbita de estabilidad.

(ii) También, se usan las series de captura como indicadoras de abundancia. Algunos autores puede argumentar que, si se incrementa el esfuerzo pesquero, se sobrevalorarían los incrementos de biomasa y se infravalorarían las disminuciones de la misma, nosotros demostramos en Solari *et al.* (2003) que, en poblaciones del atún listado (*Katsuwonus pelamis*) existe una auto-similaridad dinámica, en las tendencias del reclutamiento a la pesca, en tres escalas espaciales distintas donde operan flotas distintas con diferentes métodos de pesca y esfuerzo pesquero; García (2004, Serge.Garcia@fao.org, comunicación personal) sugirió que si los datos de esfuerzo fueran incorporados, las correlaciones podrían explicar la mayor parte de la variación en los datos.

(iii) La dinámica global puede estar, también, enlazada con ciclos económicos y de mercado (cotización del combustible, evolución del precio de los productos de la pesca, relaciones entre las monedas, inflación, precio del dinero, entre otros factores macro-económicos).

(iv) También, algunos autores pueden argumentar que las dependencias (correlaciones cruzadas) entre algunas variables (por ej. aquellas que muestren tendencias similares) podrían estar "infladas". Sin embargo, en algunos casos, se puede excluir un sesgo significativo ya que las variables pueden responder a procesos. También, existe el caso de variables que pueden responder a mecanismos causales comunes (por ej. el índice de afloramiento y la SST) lo cual es común en el efecto del medioambiente sobre procesos de población.▪

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(ix)
Conclusiones y trabajo futuro
(Cap. 4)

El trabajo contenido en esta tésis incluye una parte teórica (proposición de un nuevo modelo no-lineal para dinámica de poblaciones y explotación pesquera) y la validación, en varios casos de estudio, de los conceptos teóricos propuestos. El trabajo, inicialmente planteado como un nuevo modelo en dinámica de poblaciones con un ejemplo sobre el bacalao del Báltico se desarrolló a una nueva teoría con un número significativo de nuevos conceptos y nomenclatura de los cuales se realiza un breve sumario.

Contribución teórica.

(i) Un nuevo modelo dinámico, no-lineal para el estudio y explotación de recursos pesqueros: en este marco conceptual, se propone a la población y pesquería como un sistema o contínuo dinámico gobernado por una capacidad de carga variable. Este sistema puede constar de múltiples órbitas de estabilidad (con dinámicas locales), cada una con un seudo-equilibrio, una mínima población viable y una capacidad de carga particular.

(ii) El modelo propuesto puede describir un amplio rango de fenómenos oscilatorios enlazados que pueden comprender desde situaciones con oscilación baja o nula a cuasi-ciclos, ciclos límite, multiperiódicas y caos, así como denso-dependencia-inversa o Efecto Allé. El sistema está acotado por una máxima capacidad de carga (valor por encima del cual la población evoluciona hacia órbitas de estabilidad inferiores) y mínima población viable (valor alrededor del cual las oscilaciones o amplitud entre máximos y mínimos son mínimas o puede tender a la extinción local/valores perdidos o cero). Ningún modelo general anterior tenía la capacidad de incorporar todos los mecanismos conocidos de la dinámica de poblaciones.

(iii) Se formaliza, por primera vez en la literatura científica, el concepto de capacidad de carga variable.

(iv) Se propone el concepto de similaridad dinámica en varias escalas espacio-temporales y se explica este fenómeno como un resultado de la respuesta de procesos en la población a efectos combinados de variables externas que operan mesoescalarmente (NAO, SST, SSTA, afloramientos, ciclos de actividad solar, entre otros).

(v) Se presenta el espacio de fase como herramienta analítica de los sistemas estudiados.

(vi) Se hacen nuevas proposiciones sobre: (a) dinámica global y local; (b) residuos: señal, ruido y variabilidad/dispersión en los datos; (c) efectos diferenciales de la mortalidad por pesca; (d) explotación de sistemas con múltiples equilibrios; (e) extinción de la pesquería comercial; (f) naturaleza cíclica del esfuerzo pesquero y las relaciones captura y esfuerzo; (g) incorporación (multivariante) de variables externas al análisis de poblaciones y (h) aproximaciones (ajustes) para sistemas multi-oscilatorios y sistemas dinámicos y residuos autocorrelados.

(iv) Se da una explicación más realista y compleja a la la variabilidad en los datos y a como correspondencias multivariantes, efectos de memoria, retardos, oscilaciones periódicas, ruido y sensibilidad a condiciones externas (pulsos medioambientales) pueden afectar a la población y la pesca.

(vii) Se argumenta sobre el uso de capturas como "proxy" de abundancia.

(viii) Se propone la persistencia o plasticidad del stock de soportar tantos perturbaciones externas combinadas a una alta tasa de mortalidad por pesca y rehabilitarse a óbritas de estabilidad bajas (tendencia del sistema a estabilizarse) o superiores (a través de mecanismos denso-independendientes).

(ix) También, se propone que los efectos combinados de la mortalidad por pesca durante etapas depensatorias denso-dependientes y denso-independientes pueden conducir la trayectoria de la población a órbitas de estabilidad bajas (y eventualmente a la extinción local o de la pesquería comercial).

(x) Se proponen las bases teóricas para la predicción a corto y medio plazo de mecanismos que gobiernan la evolución temporal de la población para determinación del ajuste de niveles de mortalidad por pesca sostenibles, durante depensaciones.

Contribución analítica: validación y nueva inferencia.

En la búsqueda para validar el nuevo marco conceptual, se ha elegido incluir los estudios sobre las dinámicas de (a) los bacalaos del Báltico e Islandia, (b) el atún bonito listado y el pulpo común, en el Area 34 de FAO y (c) el análisis de una serie histórica de pesca de túnidos (particularmente el atún rojo), en las almadrabas atlántica españolas entre los años 1525-1756.

Hasta la fecha, se han validado los siguientes nuevos aspectos:

(i) Que la dinámica de los mencionados stocks (casos de bacalao del Báltico e Islandia, atún bonito listado en el Atlántico Centro Oriental, pulpo en las zonas de afloramiento en Marruecos/Sahara Occidental y Mauritania) evoluciona, temporalmente, dentro de un sistema que consta de múltiples órbitas de estabilidad, cada uno de los cuales muestra características propias (mínima población viable y capacidad de carga variable), está acotado y es producto de la interacción entre fases de compensación y depensación denso-dependientes (debidas a las características bioecológicas y uso de recursos, en la población) y fases de compensación y depensación denso-independientes (debidas a factores medioambientales), además de la mortalidad por pesca que puede afectar factores internos a la población (reproducción, denso-dependencia, reclutamiento y distribución, entre otros factores). Este sistema de equilibrios es representado por una suma de funciones no-lineales, puede describir características dinámicas que van desde el caos (cuando se aproxima a la cota superior del sistema, bajo condiciones medioambientales extremadamente benignas), pasando por una serie de ciclos o cuasi-ciclos convergentes (la amplitud entre máximos y mínimos disminuye), relativamente estables (cuando el estrés externo aumenta) hasta un estado con oscilaciones relativamente débiles (cuando el sistema se aproxima a su cota mínima). Se ha podido enlazar, por primera vez, los conceptos dinámicos propuestos en el nuevo marco conceptual y se ha hecho posible explicar las transiciones que pueden ocurrir en los sistemas estudiados. También, en los casos que hemos podido actualizar los datos desde la publicación del modelo original, en 1997, se ha podido confirmar (Agosto del 2007) las estimaciones que hicimos en la década de los 90 en base a datos de capturas, esta vez, con datos de esfuerzos y abundancias.

(ii) Que existe una similaridad dinámica, en varias escalas espacio-temporales. Esto permite conocer las tendencias, a corto y medio plazo (debido a "memorias", retardos y dependencias entre las variables), en áreas de interés pesquero de distintas dimensiones (por ejemplo, un punto geográfico en el área de Canarias, todo el Archipiélago Canario y el Atlántico Centro-Oriental), conociendo las tendencias de las variables, en cualquiera de las restantes escalas.

(iii) Que este nuevo marco conceptual puede aplicarse para estudiar y modelizar las dinámicas de los stocks de interés pesquero (especies de peces demersales, pelágicos pequeños y grandes, así como cefalópodos) y derivar estrategias de explotación sostenible adaptadas a cada caso.

De ésta tesis, se excluyen resultados similares sobre la sardina europea, la merluza y varias especies del Atlántico Sur así como los resultados preliminares de 120 de 137 stocks de peces y cefalópodos basados en datos de FAO.

Trabajo futuro.

El trabajo futuro más inmediato estará ligado a proyectos internacionales y colaboraciones con el Instituto Español de Oceanografía, en parte, basados en el nuevo marco teórico propuesto:

(i) Parametrización multivariante de la capacidad de carga variable en los núcleos de stock del pulpo común en las zonas de afloramiento del Noroeste africano (casos de Senegal, Mauritania y Marruecos), así como el Golfo de Cádiz.

(ii) Marco multi-específico de estructura de comunidades basado en datos georeferenciados de asociaciones ("clusters") de cefalópodos, peces y bentos con los objetivos de prevenir la "erosión de la biodiversidad".

(iii) Desarrollo de una aplicación informática (trabajo en progreso) en C#SHARP orientado a análisis y modelado de datos para estudio, explotación y gestión de la pesca tanto para personal científico como para gestores sin orientación matemática.

(iv) Desarrollo de una metodología de explotación del pulpo común, en las zonas de afloramiento del Noroeste de Africa, asumiendo sistemas multi-oscilatorios, efectos diferenciales de la mortalidad por pesca y área de reserva para el reclutamiento. Este trabajo está orientado a la sostenibilidad de la pesca, particularmente, cuando los sistemas se encuentren en órbitas de estabilidad bajas.

De esta forma, consideraremos un posterior desarrollo de nuestro marco teórico en el cual describiremos a la comunidad con el siguiente sistema de ecuaciones

$$C_{1(t+1)} \cong \begin{bmatrix} f_1(E_{1(t-T)}) \\ f_2(E_{2(t-T)}) \\ f_3(E_{3(t-T)}) \\ \vdots \\ f_n(E_{n(t-T)}) \end{bmatrix}$$

donde $C_1(t)$ es la "comunidad 1 en tiempo t", la cual la representamos como un sistema de ecuaciones donde

(a) la abundancia de cada una de las especies *(E)* es descrita por las funciones $f_1 \dots f_n$, en tiempo t-T (considera retardos específicos);

(b) las funciones pueden ser lineales y no-lineales y dentro de estas últimas podemos usar aquellas de los modelos clásicos para la dinámica de poblaciones (logística, Beverton-Holt, Ricker, Schaffer, etc.) así como el modelo más complejo que hemos desarrollado nosotros (en Solari et al. 1997, Bas et al., 1999, Solari et al. 2003 y otros trabajos);

(c) las funciones se relacionan unas con otras en base al concepto de *"mejor descriptor"* o *"especie indicadora"* (la especie más representativa de la comunidad es la primera de la matriz y el concepto de "representatividad" depende de abundancia y correlación con las otras especies que se hallan en el entorno inmediato); esto nos sirve, también, para determinar especies indicadoras, evaluar el estado relativo de la comunidad y proponer estrategias de conservación, entre otros factores;

(d) el sistema de ecuaciones se puede reproducir para la descripcion de las comunidades en distintas cotas de profundidad (o longitud) y latitud, determinar cotas de distribución biogeográfica y, en un futuro, cuando las series sean más completas estimar la evolución de las comunidades con respecto a cambios (climáticos) a medio plazo (decenas de años).

Con eas bases teóricas, podemos hacer una representación "global" de las distintas comunidades (o "comunidad global", $C_{G(t)}$) que se expresa por un sistema de eduaciones como el siguiente (en este caso sería para 4 comunidades):

$$C_{G(t+1)} \cong \begin{bmatrix} \begin{bmatrix} f_1(E_{1(t-T)}) \\ f_2(E_{2(t-T)}) \\ f_3(E_{3(t-T)}) \\ \vdots \\ f_n(E_{n(t-T)}) \end{bmatrix} & \begin{bmatrix} f_7(E_{1(t-T)}) \\ f_8(E_{2(t-T)}) \\ f_9(E_{3(t-T)}) \\ \vdots \\ f_{n2}(E_{n(t-T)}) \end{bmatrix} \\ \begin{bmatrix} f_4(E_{1(t-T)}) \\ f_5(E_{2(t-T)}) \\ f_6(E_{3(t-T)}) \\ \vdots \\ f_{n1}(E_{n(t-T)}) \end{bmatrix} & \begin{bmatrix} f_{10}(E_{1(t-T)}) \\ f_{11}(E_{2(t-T)}) \\ f_{12}(E_{3(t-T)}) \\ \vdots \\ f_{n3}(E_{n(t-T)}) \end{bmatrix} \end{bmatrix}$$

De esta forma, tendríamos las herramientas teóricas para describir las comunidades/poblaciones o "clusters" de peces y bentos (visto como reclutamiento a la población y/o área y pesca) y las variables externas que se consideren relevantes.▪

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(x)
Capturas como “proxy” de abundancia (Apéndice I)

En esta sección, mostramos dos ejemplos arbitrarios que tratan sobre la dinámica de una población oscilatoria sometida a cuatro regímenes de mortalidad por pesca (dos lineales y dos no-lineales).

La lectura detallada de esta argumentación es crítica para la comprensión del estudio debido a que: (i) los modelos clásicos que se utilizan tradicionalmente para analizar datos sobre poblaciones explotadas dan lugar a una sobrevaloración de la importancia relativa del esfuerzo pesquero; y (ii) es importante entender como pueden responder sistemas dinámicos multi-oscilatorios (“ondas”) al efecto o perturbación de variables externas (medioambiente y pesca) que también tienen naturaleza oscilatoria (otras ondas).

El objetivo de este ejercicio es mostrar que las capturas sobre una población natural que, en general, fluctúa de forma sinusoidal o, para referirnos a los conceptos dinámicos que propone nuestro marco conceptual, un sistema de múltiples equilibrios o multi-oscilatorio pueden ser usadas (i) como descriptor de la abundancia; (ii) para inferir la dinámica y estimar tendencias a corto y medio plazo, en el reclutamiento a la pesca y (iii) para gestionar la pesquería, aunque los datos sobre el esfuerzo no sean fiables o no existan/estén accesibles.

Asumimos que la tendencias en (i) números, en la población (compensaciones y depensaciones denso-dependientes y denso-independientes) y (ii) el reclutamiento (influjo de juveniles a la población adulta) pueden oscilar debido a pulsos medioambientales o a una combinación de éstos con la mortalidad por pesca; (iii) las relaciones entre mortalidad por pesca y esfuerzo pueden ser lineales (positivas y negativas) y no-lineales (de segundo grado); y (iv) un retardo de 1 (año) entre generaciones inmediatas (eso es, en tiempo t_{n-1}, t_n and t_{n+1}) sin solapamiento: esto implica que el espacio de fase o plano N_t, N_{t+1} (o N_t, N_{t+1+3}, si el retardo es 3) puede reflejar las tendencias en la relación o sistema stock-reclutamiento (SR).

También, el objetivo es la estimación de tendencias (no de números absolutos) y los valores se representan estandarizados (con media = 0) de forma que, mientras las escalas de números pueden cambiar, las tendencias dinámicas pueden ser comparadas, fácilmente.

Así, describimos a la población adulta, en el comienzo de cualquier año, como

$$S_{t+1} = \sigma \cdot S_t + R\left(S_{t-\tau}\right) \qquad (1)$$

donde σ es el coeficiente de supervivencia que afecta el stock, S_t, y el reclutamiento *(R)* es una función del stock adulto τ años antes (el retardo para el atún listado puede variar entre 1 y 3 si trabajamos con el reclutamiento al área/pesca o a la población adulta, respectivamente).

También, la supervivencia del stock adulto se expresa como

$$\sigma \cdot S_t = S_t - H(S_t) - M_t \qquad (2)$$

donde $H(S_t)$ y M_t son la mortalidad por pesca y la natural, respectivamente. También, en los ejemplos que damos, abajo, se asume, por simplicidad que el reclutamiento y la mortalidad natural son constantes.

Ejemplo 1.

Una población oscilatoria (2 equilibrios) está sujeta a dos regímenes lineales de mortalidad por pesca. Describimos la función de la población inicial (S_0) como una senoide que es un ciclo de dos generaciones. Los stocks resultantes $(S_1 \ldots S_2)$ serán determinados por el régimen de mortalidad por pesca $F_n(x)$ sobre la población inicial donde n representa el numero de cada régimen (1, 2). El régimen más alto, $F_2(x)$, duplica al más bajo, $F_1(x)$.

Ejemplo 2:

Una población oscilatoria (2 equilibrios) está sujeta a dos regímenes no-lineales (de segundo grado) de mortalidad por pesca. Procedemos, de forma análoga, al ejemplo anterior con los regímenes de mortalidad por pesca $F_3(x)$ *and* $F_4(x)$ (el más alto duplica al más bajo).

Ambos ejemplos son representados, gráficamente, en las Figuras 6 a-d y 7 a-d en las cuales mostramos los siguientes resultados:

La Figura 6a muestra la evolución temporal de las tendencias en la población inicial $S0(x)$, bajo dos regímenes de mortalidad por pesca que aumentan, linealmente, $F1(x)$ y $F2(x)$ y el stock resultante (descriptores de abundancia), $S1(x)$ y $S2(x)$. A pesar que la mortalidad por pesca aumenta linealmente y se duplica de un régimen al otro, se observa lo siguiente:

(i) tanto las compensaciones como depensaciones que conforman las oscilaciones son persistentes;

(ii) puede haber oscilaciones locales dentro de las tendencias negativas o depensaciones y

(iii) una población inicial puede estar sujeta a una explotación con regímenes con pendientes positivas (incrementan la mortalidad por unidad de tiempo) y retener una dinámica similar. Sólo la escala de números cambia.

La Figura 6b muestra el espacio de fase de las tendencias para la población original, no explotada, *[S0(x), S0(x+1)]* y aquellas para los stocks resultantes *[S1(x), S1(x+1)]* y *[S2(x), S2(x+1)]* de los regímenes de mortalidad por pesca *F1(x)* y *F2(x)*. Esta figura refleja un sistema SR que evoluciona durante dos ciclos y como entra en una depensación, cambia las pendientes de las fases de compensación y depensación y la escala de números, pero retiene cualidades dinámicas similares.

La Figura 6c muestra las relaciones lineales (positiva y negativa) entre la mortalidad por pesca *(x)* y el esfuerzo *E1(x)* y *E2(x)*.

La Figura 6d muestra la evolución temporal de la Captura por Unidad de Esfuerzo *(CPUE)* como función de una relación negativa, *CPUE1(x)*, y una positiva, *CPUE2(x)*, entre la mortalidad por pesca y el esfuerzo. Aunque la naturaleza de la relación sea positiva o negativa, la relación entre captura y esfuerzo resultará en una trayectoria compensatoria-depensatoria (ciclo o quasi-ciclo), mediada por las oscilaciones de la población inicial.

La Figura 6e muestra el espacio de fase de la Captura por Unidad de Esfuerzo *(CPUE)* como función de una relación lineal negativa, *[CPUE1(x), CPUE1(x+1)]*, y una positiva, *[CPUE2(x), CPUE2(x+1)]* entre la mortalidad por pesca y el esfuerzo. Las tendencias son la inversa una de la otra y muestran una dinámica similar.

La Figura 7a muestra la evolución temporal de las tendencias para la población inicial, *S0(x)*, bajo dos regímenes de mortalidad por pesca, *F3(x)* y *F4(x)* y los stocks resultantes, *S3(x)* y *S4(x)*, respectivamente. Análogamente al caso presentado en la figura 6a, a pesar que la mortalidad por pesca es no-lineal y se duplica de un régimen al otro, las cualidades dinámicas del sistema SR persisten.

La Figura 7b muestra el espacio de fase de las tendencias para la población original, no explotada, *[S0(x), S0(x+1)]* y aquellas para los stocks resultantes *[S3(x), S3(x+1)]* y *[S4(x), S4(x+1)]* de los regímenes de mortalidad por pesca *F3(x)* y *F4(x)*. Análogamente al caso presentado en la figura 6b, se refleja como el sistema SR que evoluciona, durante dos ciclos, entra en una depensación, cambia las pendientes de las fases de compensación y depensación y la escala de números pero retiene cualidades dinámicas similares.

La figura 7c muestra las relaciones no-lineales entre la mortalidad por pesca *(x)* y el esfuerzo *E3(x)* y *E4(x)*.

La figura 7d muestra la evolución temporal de la Captura por Unidad de Esfuerzo, *CPUE3(x)* y *CPUE4(x)*, como función de dos relaciones no-lineales entre la mortalidad por pesca y el esfuerzo.

La figura 7e muestra el espacio de fase de la Captura por Unidad de Esfuerzo, *[CPUE3(x), CPUE3(x+1); CPUE4(x), CPUE4(x+1)]*, como función de dos relaciones no-lineales entre la mortalidad por pesca y el esfuerzo.

Discusión.

Los ejemplos que se muestran pueden ser análogos a la explotación pesquera de una población que oscila, aunque por simplicidad se elige que la población inicial evolucione durante dos ciclos límite. No obstante, las poblaciones naturales mostrarán oscilaciones multi-periódicas, adaptadas tanto a las variables externas como al efecto combinado de éstas y la mortalidad por pesca. También, se asume el reclutamiento y la mortalidad natural como constantes, mientras que, en casos reales, ambas oscilarán. No obstante, oscilaciones de estas variables (u otras) pueden no afectar la dinámica básica del sistema ya que seguirán existiendo los efectos de memoria y las dependencias con variables externas ambas de las cuales podrán estar, fuertemente, correlacionadas consigo mismas (efecto memoria alejado de un proceso aleatorio o ruido blanco) y entre ellas (dependencias entre las variables).

También, cabe señalar que, la dinámica de un sistema que es, básicamente, mediada por una onda, mantendrá características dinámicas similares, para un amplio rango de perturbaciones. En principio, por la inferencia en el estudio de los datos y nuestras simulaciones, podemos asumir que, para un sistema SR multioscilatorio, cualquier variable o conjunto de variables que lo afecte, podrá contribuir a cambiar las pendientes, velocidades de incremento/decremento, escalas de números y amplitud entre máximos y mínimos, mientras que la estructura dinámica original será persistente.

Los casos que se muestran clarifican ideas sobre el uso de las capturas como descriptor de la abundancia para una población oscilatoria bajo varios regímenes distintos de mortalidad por pesca (positivo, negativo, lineal y no-lineal). La dinámica de la población reflejará las fases de compensación y depensación, independientemente de la mortalidad por pesca o esfuerzo que se apliquen, dentro de un amplio rango. Este comportamiento del sistema, en el mundo natural, puede ser mediado por una matriz de variables, internas y externas a la población, donde la mortalidad por pesca es sólo un cofactor.

Las poblaciones naturales oscilarán debido a los efectos combinados de las variables externas y la mortalidad por pesca y los colapsos pueden producirse debido al efecto combinado de perturbaciones medioambientales negativas (aquellas que afectan el reclutamiento, negativamente) y alta e intensa mortalidad por pesca, durante etapas de depensación denso-dependientes y denso-independientes. Una situación de esta naturaleza podría inducir una depensación, en el sistema SR, que implicaría la transición de órbitas de estabilidad, relativamente, altas a otras con oscilaciones muy reducidas, en torno a la mínima población viable del sistema.

Asimismo, el uso de las capturas como descriptor de la abundancia puede ser obvio para poblaciones con tiempo de generación corto a medio (retardos de 1 a 3 años entre el reclutamiento a la población/área y pesca, respectivamente).

Los razonamientos basados, en los modelos clásicos, atribuyen al esfuerzo pesquero una importancia relativa alta y no tienen la resolución para determinar estos mecanismos dinámicos, debido a que consideran ruido gran parte de la señal y asumen que las observaciones tienen el mismo peso estadístico, que la capacidad de carga es única e invariante y que sólo opera un equilibrio.▪

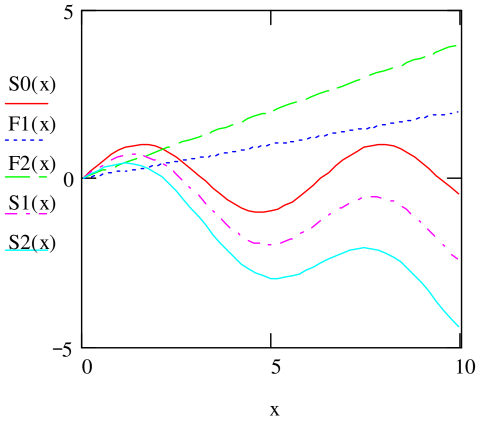

Figura 6a. Evolución temporal de las tendencias en la población inicial, S0(x), bajo dos regímenes de mortalidad por pesca que aumentan linealmente, F1(x) y F2(x), y los stocks resultantes, S1(x) y S2(x).

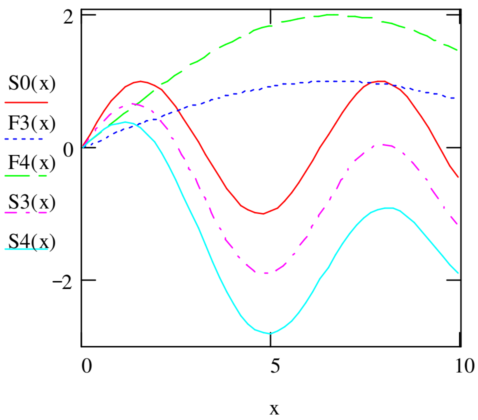

Figura 7a. Evolución temporal de las tendencias en la población inicial, S0(x), bajo dos regímenes de mortalidad por pesca que aumentan no-linealmente, F3(x) y F4(x), y los stocks resultantes, S3(x) y S4(x).

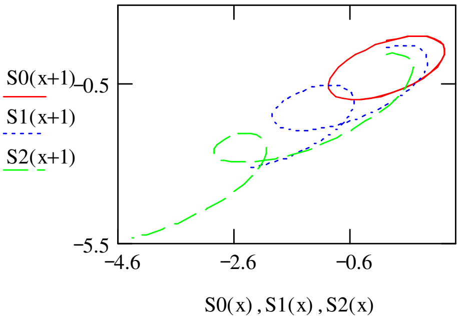

Figura 6b. Espacio de fases de las tendencias en la población inicial, [S0(x), S0(x+1)], y aquellas de la población explotada, [S1(x), S1(x+1)] y [S2(x), S2(x+1)], bajo regímenes lineales de explotación F1(x) y F2(x), respectivamente.

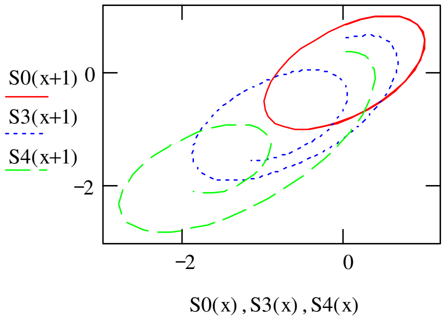

Figura 7b. Espacio de fases de las tendencias en la población inicial, [S0(x), S0(x+1)], y aquellas de la población explotada, [S3(x), S3(x+1)] y [S4(x), S4(x+1)], bajo regímenes no-lineales de explotación F3(x) y F4(x), respectivamente.

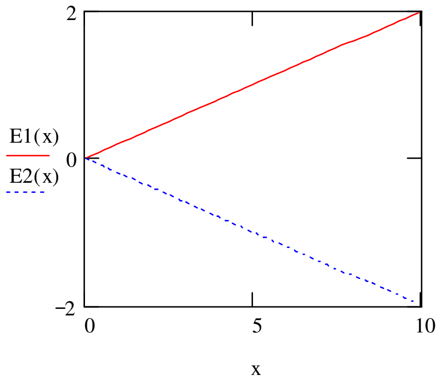

Figura 6c. Relación lineal (positiva y negativa) entre la mortalidad por pesca (x) y los esfuerzos E1(x) y E2(x).

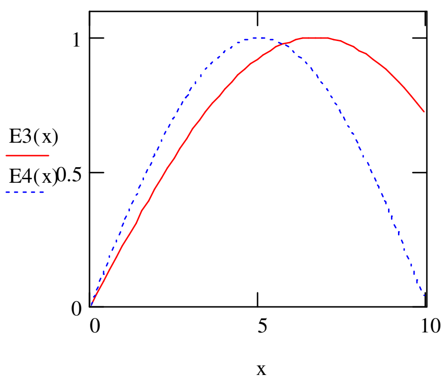

Figura 7c. Relaciones no-lineales entre la mortalidad por pesca (x) y los esfuerzos E3 (x) y E4 (x).

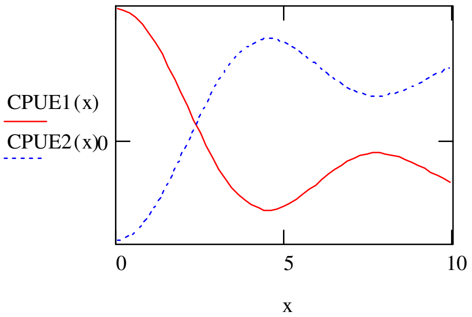

Figura 6d. La evolución temporal de la Captura por Unidad de Esfuerzo (CPUE) como función de una relación negativa, CPUE1(x) y otra positiva, CPUE2(x) entre la mortalidad por pesca y el esfuerzo.

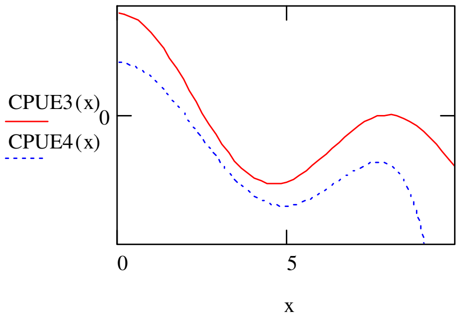

Figura 7d. La evolución temporal de la Captura por Unidad de Esfuerzo, CPUE3(x) y CPUE4(x) como función de dos relaciones no-lineales entre la mortalidad por pesca y el esfuerzo.

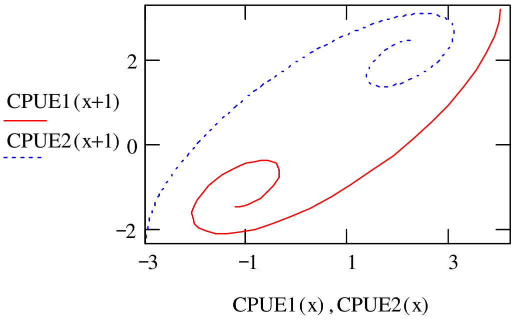

Fig. 6e. Espacio de fase de la Captura por Unidad de Esfuerzo, [CPUE1(x), CPUE1(x+1)] y [CPUE2(x), CPUE2(x+1)], como funciones positiva y negativa entre la mortalidad por pesca y el esfuerzo.

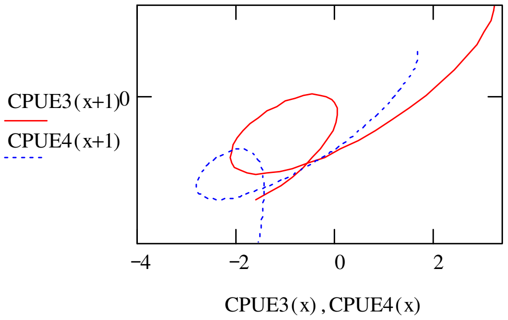

Figura 7e. Espacio de fase de la Captura por Unidad de Esfuerzo, [CPUE3(x), CPUE3(x+1); CPUE4(x), CPUE4(x+1)], como funciones de dos relaciones no-lineales entre la mortalidad por pesca y el esfuerzo.