GLOBAL OCEAN ECOSYSTEM DYNAMICS

GLOBEC Report No.22

SMALL PELAGIC FISHES AND CLIMATE CHANGE PROGRAMME

Report of a GLOBEC / SPACC Meeting on Characterizing and Comparing the Spawning Habitats of Small Pelagic Fish

14-16 January 2004, Concepción, Chile
This report documents the meeting entitled “Small Pelagic Fish Spawning Habitat Dynamics and the Daily Egg Production Method (DEPM)”, held under the auspices of SPACC (Small Pelagic Fishes and Climate Change) Theme 3: Reproductive Habitat Dynamics. The meeting was held in Concepción, Chile, from the 14th to the 16th of January 2004. The meeting was oriented to analyse and compare the biological and oceanographic information obtained in DEPM and other studies around the world to assess of the effect of environmental variability across spawning habitats of small pelagic fish populations. Convenors of the meeting were Leonardo R. Castro (Universidad de Concepción), Pierre Fréon (IRD; IDYLE) and Carl D. van der Lingen (M&CM, RSA). The Meeting was sponsored by the Universidad de Concepción, GLOBEC, IRD, IDYLE, IAI, SCOR, Sub-Secretaría de Pesca CONICYT, Sociedad Chilena de Ciencias del Mar, and Lota Protein Ltd.

This document may be cited as:

JOHN HUNTER

After more than 40 years as a scientist, Dr John R. Hunter (or J. Roe Hunter) retired from the Southwest Fisheries Science Center (SWFSC) of the National Marine Fisheries Service (NMFS), USA in the summer of 2003. Hunter’s doctoral dissertation concerned nest parasitism of sunfishes by minnows. These divergent areas of study prepared him for the diversity of scientific approaches he has used to understand and manage the coastal pelagic species off California. Initially, his research was concentrated on tuna and porpoise interaction in order to define the behavior of tuna near flotsam. Tropical tuna fisheries now take advantage of the aggregation of tuna around artificial floating devices. Later, he became a laboratory scientist defining the progress of fish egg and larva development and particularly that of schooling and feeding behavior of aggregations of larvae preying on patches of motile plankton. Many of his publications concern the details of spawning and the importance of that knowledge in evaluating fish resources.

Hunter’s international recognition as a scholar was furthered by his book with J.H.S. Blaxter on clupeoid biology, published in Advances in Marine Biology 20 years ago under a Rockefeller Foundation Fellowship. This work constituted the unification of field and laboratory studies that have been grist for field, laboratory, and modeling works to this day. He has been an adjunct professor at Scripps Institution of Oceanography (SIO), La Jolla, California, USA and kept close contact with other fishery research centers around the world. Through these international activities, he has played an important role of supervision and planning of research for the US Agency for International Development, US Global Ocean Ecosystem Dynamics (GLOBEC), and International GLOBEC by designing the International Geosphere-Biosphere Programme in relation to Small Pelagics and Climate Change (SPACC) which Hunter founded in 1994, and has been carried on by his colleagues led by Dr Juergen Alheit.

Recently, following the massive recovery of the sardine population and its expansion from small habitats in the Southern California Bight to dominance of the pelagic biota from Mexico to Canada and Alaska, Hunter proposed a multi-institutional program to overcome the parochial geography from Baja California to California, USA and to expand biological and oceanographic measurements through the entire California Current System from British Columbia to Baja California, Mexico, namely the Pacific Coastal Observing System (PaCOS) which likely expands the CalCOFI grid beyond its present scope.

Hunter is best at careful observation. He together with a group of scientists adapted and modernised river and coastline methods for tagging fish that could be used in the open ocean habitat, especially for tuna scanned by satellites. Hunter studied archival tags nearly two decades ago when the existing technology was far behind researchers’ needs. Hunter has been spreading the understanding and application of daily egg production methods for the rapid and precise assessment of the spawning biomass of multiple spawning schooled fishes around the world. He recently applied continuous sampling by the Checkley egg-pump sampler, which in its first use on the West Coast forced the revision of our time honoured opinions about the life and geography of the Pacific sardine. Lastly, Hunter forged airborne Light, Detection and Ranging (LIDAR) technologies to assess schooling surface fishes, which are resistant to normal acoustic surveys. As a result, the upper areas of the ocean are now rapidly observable, and these methods are the methods of choice for slow-schooling fishes and virtually the only methods for rapid-swimming fishes like mackerel. Hunter’s research exemplifies how basic research can be combined with applied research to address management needs. His paper on ultraviolet radiation damage to surface-living anchovy larvae, co-authored with John Taylor and Geoff Moser, has been cited 43 times in the 25 years since its publication. A quarter of these citations relate to invertebrate and fish damage and appear in works published in the last three years, long after his personal involvement.

In his scholarly wake, he has also left us the definitive handbook on fisheries science writing, Writing for Fishery Journals. While Hunter is leaving the field of science administration, we are confident that there will be issues in fishery research that will rise to his standard for giving guidance and consideration.

# TABLE OF CONTENTS

PREFACE ............................................................................................................................................i

TRIBUTE TO Dr JOHN HUNTER ........................................................................................................ii

TABLE OF CONTENTS .........................................................................................................................iii

LIST OF ABBREVIATIONS AND ACRONYMS ..................................................................................vi

ABSTRACT ...............................................................................................................................................viii

ACKNOWLEDGEMENTS .........................................................................................................................ix

COLOUR PLATE LEGENDS ...................................................................................................................x

COLOUR PLATES ....................................................................................................................................xi

INTRODUCTION ......................................................................................................................................1

ABSTRACTS OF PRESENTATIONS ........................................................................................................3

I. SPAWNING HABITATS

1. Spawning of anchovy, mackerel, and sardine in the California and Humboldt Current regions
   *D. Checkley, Jr., P. Ayon, T. Baumgartner and M. Braun* .............................................................3

2. Investigation of interannual dynamics of suitable spawning habitat for anchovy (*Engraulis encrasicolus*) in the southern Benguela using a 3D hydrodynamic model.
   *C. Roy, P. Penven and C.D. van der Lingen* .................................................................................4

3. Predicting spawning habitat location of anchovy and sardine in the southern Benguela using remotely-sensed data
   *L. Drapeau and C.D. van der Lingen* ...........................................................................................6

4. Characterization of the anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) spawning habitats in the Bay of Biscay from the routine application of the annual DEPM surveys in the southeast Bay of Biscay.

5. *Sardinia pilchardus* spawning patterns off Portugal
   *M.M. Angélico and P.B. Oliveira* .................................................................................................13

6. Tentative approaches to describe anchovy and sardine spawning habitats in the Bay of Biscay
   *B. Planque, P. Petitgas and J. Massé* .............................................................................................14

7. Ichthyoplankton variability and fish catches in the Canary Current
   *P. Bécognée, F. Bordes, J.M. Rodríguez and S. Hernández-León* ..............................................17

8. Regime shifts in the Humboldt Current ecosystem
   *J. Alheit and M. Ñiquen* ..................................................................................................................19

   *G. Claramunt, J. Oliva, G. Herrera, R. Escibano, R. Serra and R. Roa* .................................20

<table>
<thead>
<tr>
<th>Number</th>
<th>Title</th>
<th>Authors</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>11</td>
<td>Topographic control of the larval Clupeiform distribution in the coastal upwelling area off Concepción, central Chile</td>
<td>M. Sobarzo, B. Yannicelli, L.R. Castro, M. Landaeta and W. Schneider</td>
<td>26</td>
</tr>
<tr>
<td>12</td>
<td>The oceanic spawning of Chilean jack mackerel: daily egg production, spawning biomass, and habitat conditions</td>
<td>L.A. Cubillos, S. Núñez, J. Páramo and A. Sepúlveda</td>
<td>28</td>
</tr>
<tr>
<td>13</td>
<td>Synthesis of early life-history dynamics and spawning habitat characterization of small pelagic fishes in south-eastern Australia: past and current research</td>
<td>F.J. Neira</td>
<td>32</td>
</tr>
<tr>
<td>14</td>
<td>Spawning of small pelagic species in New Zealand waters</td>
<td>P. Taylor</td>
<td>35</td>
</tr>
<tr>
<td>15</td>
<td>An overview of the application of the daily egg production method (DEPM) to Mediterranean anchovy stocks</td>
<td>S. Somarakis, I. Palomera, A. Garcia, L. Quintanilla and C. Koutsikopoulos</td>
<td>37</td>
</tr>
<tr>
<td>II</td>
<td>REPRODUCTION AND EGG DEVELOPMENT</td>
<td></td>
<td></td>
</tr>
<tr>
<td>16</td>
<td>Is the daily spawning fraction dependent on female size?</td>
<td>G. Claramunt, R. Roa, P. Pizarro and R. Serra</td>
<td>41</td>
</tr>
<tr>
<td>17</td>
<td>Effect of major atresia on the egg production of Pacific sardine (Sardinops caeruleus) of Bahía Magdalena in the 1999-2000 season</td>
<td>J. René Torres-Villegas, L. Perezgómez and G. García-Melgar</td>
<td>44</td>
</tr>
<tr>
<td>18</td>
<td>Cytological validation of follicle and ooplasm characteristics for estimating Pacific sardine (Sardinops caeruleus) batch fecundity</td>
<td>R.I. Ochoa-Báez, G. García and L. Perezgómez</td>
<td>46</td>
</tr>
<tr>
<td>19</td>
<td>Variation in adult reproductive parameters of Engraulis mordax anchovy from the Gulf of California</td>
<td>C.E. Cotero Altamirano</td>
<td>49</td>
</tr>
<tr>
<td>20</td>
<td>Temperature-dependent development rate of eggs of the southern anchoveta Engraulis ringens</td>
<td>S.A. Soto, G. Claramunt and R. Escribano</td>
<td>51</td>
</tr>
<tr>
<td>21</td>
<td>Temperature-dependent egg-development models for Strangomera bentincki and Engraulis ringens in the area off central-south Chile</td>
<td>A. Sepúlveda, L. Cubillos, I.M. Canales, D. Bucarey and A. Rojas</td>
<td>54</td>
</tr>
<tr>
<td>22</td>
<td>A temperature-dependent model of yolk sac larval development and the effects of the addition of yolk sac larvae data on the estimations of $P_0$ in the DEPM</td>
<td>K. Riquelme, A. Llanos, L. Cubillos and L.R. Castro</td>
<td>55</td>
</tr>
<tr>
<td>III</td>
<td>REPRODUCTIVE STRATEGIES AND VERTICAL DISTRIBUTION</td>
<td></td>
<td></td>
</tr>
<tr>
<td>23</td>
<td>Buoyancy, vertical distribution, and models of vertical distribution of sardine and anchovy eggs in the Bay of Biscay</td>
<td>G. Boyra, S. Coombs, L. Rueda, M. Santos and A. Uriarte</td>
<td>57</td>
</tr>
<tr>
<td>24</td>
<td>Fine-scale spatial variation of pelagic fish eggs in relation to ontogenetic variation over the Western Agulhas Bank, South Africa</td>
<td>M. Dopolo, C.D. van der Lingen, L. Drapeau and C. Moloney</td>
<td>59</td>
</tr>
<tr>
<td>25</td>
<td>Vertical distribution of eggs of anchovy (Engraulis capensis) and sardine (Sardinops sagax) in the northern Benguela</td>
<td>E.K. Stenevik, S. Sundby and A. Kreiner</td>
<td>62</td>
</tr>
</tbody>
</table>
26. Variation in daily egg production, spawning area, and instantaneous mortality rate; necessary parameters for the biomass estimation of northern anchovy (Engraulis mordax) in the Gulf of California
Y.A. Green-Ruiz, N.C.H. Lo and L.M. Jacob-Cervantes..................................................64

27. Euphausiid predation on anchoveta (Engraulis ringens) eggs and its incidence on the natural egg mortality estimations in the spawning zone of northern Chile
M.C. Krautz, L.R. Castro and M. González .................................................................65

28. Growth and mortality of jack mackerel Trachurus symmetricus larvae in the southern east Pacific
M. Reyes, A. Sepúlveda and L.R. Castro........................................................................68

29. Inter-population differences in early life history traits of the anchoveta Engraulis ringens along Chile: any relationship with the spawning habitat characteristics?
L.R. Castro, A. Llanos, J.L. Blanco, M. Landaeta, M.C. Krautz, R. Escribano and E. Tarifeño..........................................................70

30. Spatial spawning strategy of jack mackerel (Trachurus symmetricus murphyi) off the central-south region of Chile
M. A. Barbieri, J. Cordova, F. Gerlotto and M. Espejo................................................73

IV. METHODS

31. CUFES-aided ichthyoplankton surveys to assess Pacific sardine egg production and the spatial distributions of pelagic fish off California
N.C.H. Lo..................................................................................................................75

32. Comparing the abundance of pelagic fish eggs estimated using the CalVET net and the CUFES
C.D. van der Lingen and D.M. Checkley, Jr..................................................................78

33. Catching capabilities of CUFES vs PAIROVET and implications for its use in egg surveys
M. Santos, A. Uriarte and L. Ibaibarriaga .....................................................................81

34. Consecutive in-season DEPM biomass estimates: is the method consistent? The case of Bay of Biscay anchovy in 1989 and 1990
L. Motos, J. Santiago and A. Uriarte .............................................................................84

35. Assessing the Bay of Biscay anchovy population by DEPM: a review 1989-2001
L. Motos, A. Uriarte, P. Prouzet, M. Santos, P. Alvarez and Y. Sagarminaga.............88

36. Application of generalized additive models to the daily egg production method for the Bay of Biscay anchovy (Engraulis encrasicolus L.)

37. Applying new statistical tools to improve DEPM-based estimates of spawning biomass of Ibero Atlantic sardine (Sardina pilchardus, Walb.)

RECOMMENDATIONS FROM THE DISCUSSION SESSIONS.............................................96

LIST OF PARTICIPANTS ...............................................................................................104
# List of Abbreviations and Acronyms

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>AVHRR</td>
<td>Advanced Very High Resolution Radiometer</td>
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<tr>
<td>AZTI</td>
<td>Technological Institute for Fisheries and Food, País Vasque, Spain</td>
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<tr>
<td>IMARPE</td>
<td>Instituto del Mar del Perú, Perú</td>
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<td>CalCOFI</td>
<td>California Cooperative Oceanic Fisheries Investigations</td>
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<td>CalVET</td>
<td>California Cooperative Oceanic Fisheries Investigation (CalCOFI) Vertical Egg Tow</td>
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<tr>
<td>CICESE</td>
<td>Centro de Investigación Científica y Educación Superior de Ensenada, México</td>
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<tr>
<td>CICIMAR</td>
<td>Centro Interdisciplinario de Ciencias Marinas, México</td>
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<tr>
<td>CONICYT</td>
<td>Comisión Nacional de Ciencia y Tecnología, Chile</td>
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<tr>
<td>COPAS</td>
<td>Centro de Oceanografía del Pacífico Sur Oriental, Chile</td>
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<tr>
<td>CSIC</td>
<td>Consejo Superior de Investigaciones Científicas, Spain</td>
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<tr>
<td>CUFES</td>
<td>Continuous Underway Fish Egg Sampler</td>
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<td>DEPM</td>
<td>Daily Egg Production Method</td>
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<td>DSF</td>
<td>Daily Specific Fecundity</td>
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<td>EAI</td>
<td>Egg Abundance Index</td>
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<td>ECOS</td>
<td>The Environmental Council of the States</td>
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<td>ELISA</td>
<td>Enzyme Linked ImmunoSorbent Assay</td>
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<tr>
<td>ESDU</td>
<td>Elementary Sample Distance Units</td>
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<tr>
<td>GAM</td>
<td>Generalized Additive Model</td>
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<td>GLOBEC</td>
<td>Global Ocean Ecosystem Dynamics</td>
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<td>GRI</td>
<td>Gonadic Relative Index</td>
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<td>GSI</td>
<td>Gonodosomatic Index</td>
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<tr>
<td>IDYLE</td>
<td>Interaction and Spatial Dynamics of Renewable Resources in Upwelling Ecosystems</td>
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<tr>
<td>IEO</td>
<td>Instituto Español de Oceanografía, Spain</td>
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<tr>
<td>IFOP</td>
<td>Instituto de Fomento Pesquero, Chile</td>
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<tr>
<td>IFREMER</td>
<td>Institut Français de Recherche pour l’Exploitation de la Mer, France</td>
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<tr>
<td>INPESCA</td>
<td>Instituto de Investigación Pesquera, Chile</td>
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<tr>
<td>INRH</td>
<td>Institut National de Recherche Halieutique, Morocco</td>
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<td>IOC</td>
<td>International Oceanographic Commission</td>
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<tr>
<td>IRD</td>
<td>Institut de Recherche pour le Développement, France</td>
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<tr>
<td>LOPEL</td>
<td>Laboratorio de Oceanografía Pesquera y Ecología Larval, Chile</td>
</tr>
<tr>
<td>MCM</td>
<td>Marine and Coastal Management, South Africa</td>
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<td>NOAA</td>
<td>National Oceanographic and Atmospheric Administration, USA</td>
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<td>NMFS</td>
<td>National Marine Fisheries Service, USA</td>
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<td>OSI</td>
<td>Occupied Surface Indices</td>
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<td>PaCOS</td>
<td>Pacific Coastal Observing System</td>
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<td>PUCV</td>
<td>Pontificia Universidad Católica de Valparaiso, Chile</td>
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<td>ROMS</td>
<td>Regional Oceanic Modeling System</td>
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<td>SCHCM</td>
<td>Sociedad Chilena de Ciencias del Mar, Chile</td>
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<td>SCOR</td>
<td>Scientific Committee on Oceanic Research</td>
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<tr>
<td>SeaWiFS</td>
<td>Sea-viewing Wide Field-of-view Sensor</td>
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<tr>
<td>SIO</td>
<td>Scripps Institution of Oceanography, USA</td>
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<td>SPACC</td>
<td>Small Pelagics and Climate Change</td>
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<tr>
<td>SSB</td>
<td>Spawning Stock Biomass</td>
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<td>Acronym</td>
<td>Full Form</td>
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<tr>
<td>SST</td>
<td>Sea Surface Temperature</td>
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<tr>
<td>SWFSC</td>
<td>Southwest Fisheries Science Center</td>
</tr>
<tr>
<td>UCT</td>
<td>University of Cape Town, South Africa</td>
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<tr>
<td>UDEC</td>
<td>Universidad de Concepción, Chile</td>
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<tr>
<td>UNAP</td>
<td>Universidad Arturo Prat, Chile</td>
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<tr>
<td>UNESCO</td>
<td>United Nations Education, Scientific and Cultural Organization</td>
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<tr>
<td>SPACC</td>
<td>Small Pelagic Fishes and Climate Change</td>
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<tr>
<td>SUBPESCA</td>
<td>Sub-Secretaría de Pesca, Chile</td>
</tr>
<tr>
<td>VPA</td>
<td>Virtual Population Analysis</td>
</tr>
<tr>
<td>WGHMSA</td>
<td>ICES Working Group on the Assessment of Mackerel, Horse Mackerel, Sardine, and Anchovy</td>
</tr>
</tbody>
</table>
ABSTRACT

A SPACC (Small Pelagic Fishes and Climate Change) Theme 3: Reproductive Habitat Dynamics meeting was held in Concepción, Chile, 14th - 16th January 2004. The meeting was oriented to analyze and compare the biological and oceanographic information obtained in DEPM and other studies around the world to assess the effect of environmental variability across spawning habitats of small pelagic fish populations. The meeting was attended by over 75 participants from 15 countries that showed 39 presentations from major systems such as Benguela, Humboldt, Canary, and California Current systems, the Bay of Biscay, South Eastern Australia and New Zealand, and the Mediterranean Sea.

The meeting was organized around three major topics:

- Early life history of fishes and their spawning habitat quality and dynamics,
- Reproductive biology of small pelagic fishes in relation to their spawning habitat,
- New methodological approaches to the study of spawning habitat and the DEPM.

The meeting lasted for three days, the first two of which were dedicated to oral presentations and the last to a parallel discussion session. The oral presentations were organized into four themes: Spawning Habitats, Reproduction and Egg Development, Reproductive Strategies and Methods. The discussion sessions of the third day focused on a) Habitat Characterization, Reproductive Strategies, and Development and Early Life History and b) The DEPM, Reproductive Parameters, Sampling Methods, and New Approaches for Data Analyses. A final discussion and summary session was held on the afternoon of the third day, from which a series of preliminary recommendations were drawn, some of which were reported on the GLOBEC International Newsletter 10(1), April 2004.

This report contains extended abstracts, including figures and tables from each presentation, color plates, summaries of the 2 discussion sessions and a list of participants with their addresses and institutional affiliations.
ACKNOWLEDGEMENTS

The convenors and editors of this Report thank the organizers and graduate and undergraduate students from LOPEL who assisted in the preparation of the meeting: L. Huckstadt, M.C. Krautz, B. Yannicelli, C. Chandía, M.I. Muñoz, P. Inostroza, S. Vasquez, K. Riquelme, R. León, A. Llanos, M. Landaeta and C. Bustos. Miss Dawn Ashby from GLOBEC (IPO) kindly helped in the edition and publishing of this report. Financial support was provided by IRD, IDYLE, SCOR, IAI, Sociedad Chilena de Ciencias del Mar, GLOBEC, Lota Protein Ltd. and Universidad de Concepción. CONICYT (Chile) and SubSecretaria de Pesca (Chile) also sponsored the Meeting.
COLOUR PLATE LEGENDS

Plate 1: A snapshot (18 November 1991) of the simulated suitable spawning area for anchovy. Areas suitable for spawning are highlighted in white. See contribution by Roy et al., “Investigation of interannual dynamics of suitable spawning habitat for anchovy (Engraulis encrasicolus) in the southern Benguela using a 3D hydrodynamical model”, for details see page 4.

Plate 2: Overlays of predicted (from a multivariate model that used single parameter quotient curves applied to satellite-derived observations of SST, ocean colour and wind speed, and water depth) and observed (from CalVET net samples) spawning habitats of anchovy in the southern Benguela in November 2000. See contribution by Drapeau and van der Lingen, “Predicting spawning habitat location of anchovy and sardine in the southern Benguela using remotely-sensed data”, for details see page 6.

Plate 3: Average relative abundance of eggs spawned from 1999 to 2002 for anchovy (left) and for sardine (right). See contribution by Sagarminaga et al., “Characterization of the anchovy (Engraulis encrasicolus) and sardine (Sardina pilchardus) spawning habitats in the Bay of Biscay from the routine application of the annual DEPM surveys in the southeast Bay of Biscay”, for details see page 9.


Plate 5: Spatial distribution of eggs abundance (eggs/0.05m$^2$) of anchovy and common sardine in the central zone and southern sector of the study area in central Chile. See contribution by Cubillos et al., “Spawning, daily egg production and spawning biomass of common sardine, Strangomera bentincki, and anchoveta, Engraulis ringens, off central south Chile in 2002”, for details see page 23.

Plate 6: Distribution of blue mackerel eggs along southeastern Australia during October 2003. Mean SST images from sampling periods were provided by CSIRO Marine Research, Hobart. See contribution by Neira et al., "Synthesis of early life-history dynamics and spawning habitat characterization of small pelagic fishes in south-eastern Australia: past and current research", for details see page 32.

Plate 7: Yolk sac length/ total length ($R_1$), at temperatures between 18 and 10°C. It is observed that the development time from hatching (age) is temperature dependent. See contribution by Riquelme et al., “A temperature-dependent model of yolk sac larval development and the effects of the addition of yolk sac larvae data on the estimations of $P_0$ in the DEPM”, for details see page 55.

Plate 8: Distribution maps of anchovy Engraulis encrasicolus, sardine Sardinops sagax and round herring Etrumeus whiteheadi, eggs by stage category. See contribution by Dopolo et al., “Fine scale spatial variation of pelagic fish eggs in relation to ontogenetic variation over the Western Agulhas Bank, South Africa”, for details see page 59.

Plate 9: Spatial distribution of Pacific sardine, anchovy and jack mackerel and sea surface temperature off California in 1998, 1999 and 2003 surveys. See contributions by Barbieri et al., “Spatial spawning strategy of jack mackerel (Trachurus symmetricus murphyi) off the central-south region of Chile”, for details see page 73.

Plate 10: Spatial models of a) Spawning fraction, b) female weight, c) egg production and d) SSB estimates. The colors represent the fitted values, with dark blue means the lower values and red is the larger value. Circles represent the observations, with circle size proportional to the observed values. On panel d), the circles represent acoustic energy from the Portuguese survey (data from the Spanish survey was not available for this work). See contribution by Bernal et al., “Applying new statistical tools to improve DEPM-based estimates of spawning biomass of Ibero Atlantic sardine (Sardina pilchardus, Walb.)”, for details see page 94.
Average length:
- 11.582 - 12.787
- 12.787 - 14.298
- 14.298 - 15.382
- 15.382 - 16.269
- 16.269 - 16.967

~22°C
- ~15°C

Eggs per 100 m³:
- 0
- 1 - 10
- 10 - 50
- 50 - 100
- 100 - 300
- 300 - 700

Central zone
- Anchovy eggs
- Sardine eggs

Southern zone
- Anchovy eggs
- Sardine eggs

Plate 4

Plate 5

Plate 6

~22°C

Eggs per 100 m³:
- 0
- 1 - 10
- 10 - 50
- 50 - 100
- 100 - 300
- 300 - 700

~15°C
Plate 9

Sardine spawning fraction distribution in 2002

Sardine female mean weight distribution in 2002

Fitted DEPM SSB vs acoustic EDSU in March 2002

Plate 10

Sardine egg production January/March 2002

Sardine egg production January/March 2002

0304 CalCOFI/EPM Cruise
April 4-30, 2003

R/V Roger Revelle
0304 CalCOFI/EPM Cruise
April 4-30, 2003

R/V Roger Revelle
0304 CalCOFI/EPM Cruise
April 4-30, 2003

Plate 10

Sardine spawning fraction distribution in 2002

Sardine female mean weight distribution in 2002

Fitted DEPM SSB vs acoustic EDSU in March 2002

Plate 10

Sardine spawning fraction distribution in 2002

Sardine female mean weight distribution in 2002

Fitted DEPM SSB vs acoustic EDSU in March 2002
INTRODUCTION

In order to understand the linkages between fish population dynamics and ocean climate variability, SPACC has developed a program that considers four major scientific themes: Long term changes in ecosystems and retrospective analysis; Comparative population dynamics; Reproductive habitat dynamics, and Economic implications of climate change. Within the third theme, a series of initiatives specifically concerning spawning habitat quality and dynamics have been developed to date: the first was the “Workshop on the use of the Continuous Underway Fish Egg Sampler (CUFES) for mapping spawning habitats of pelagic fishes” held in San Sebastián (9-11 February 2000; see Checkley et al., 2000), a second initiative was the GLOBEC-SPACC/IDYLE/ENVIFISH Workshop “Spatial approaches to the dynamics of coastal pelagic resources and their environment in upwelling Areas” held in Cape Town (6-8 September 2001; see van der Lingen et al., 2002), and recently two joint initiatives “GLOBEC/SPACC Workshop on Characterizing and Comparing the Spawning Habitats of Small Pelagic Fish” and “GLOBEC/SPACC Meeting on Small Pelagic Fish Spawning Habitat Dynamics and the Daily Egg Production Method (DEPM)”, both of which were held in Concepción between the 12th and 16th January 2004.

The objectives of the last meeting in Concepción were to analyze and compare the biological and oceanographic information obtained by utilizing the daily egg production method (DEPM) and other studies around the world to assess of the effect of environmental variability on spawning habitats of small pelagic fish populations. The DEPM has been utilized by most nations that have significant fisheries for small pelagic fish (Clupeiforms) and has been regularly utilized for several years in many areas around the world. The DEPM involves the collection a large number of environmental and biological parameters pertinent to small pelagic fish populations. Additionally, and in concordance with the natural development of the method, a number of technical and statistical tools as well as new approaches to analyze the data have started to emerge that are improving our understanding of the dynamics of Clupeiform populations. Accordingly, a comparative analysis of data provided by the DEPM from different systems and species was considered important within the SPACC context, to provide valuable information on the mechanisms by which environmental changes could modulate the reproductive biology and survival of early life history stages of small pelagic fish around the world.

The meeting was organized around three major topics that included (i) the relationship between the early life history of small pelagic fish and their spawning habitat quality and dynamics, (ii) the reproductive biology of small pelagic fish in relation to their spawning habitat, and (iii) new methodological approaches and spatial analyses applicable to the DEPM. The Meeting was attended by 76 participants from 15 countries, and was divided into two days of presentations and one day of parallel discussion sessions.

A total of 39 oral presentations were made at the Meeting, these being grouped into four sessions:

- **Spawning Habitat**: presentations described methods for characterizing spawning habitat and included a summary of results from the Workshop on Characterizing and Comparing the Spawning Habitats of Small Pelagic Fish (see van der Lingen et al., 2005); the potential use of such characterizations to model the dynamics of spawning habitat via 3D hydrodynamic models and to predict spawning habitat from satellite-derived information; and provided descriptions of spawning habitats of small pelagic fish from a variety of systems.

- **Reproduction and Egg Development**: presentations described reproductive parameters such as spawning fraction, gonad atresia, and batch fecundity, and variations in these, as well as presenting temperature-dependent egg development models for a variety of small pelagic fish.
• **Reproductive Strategies:** presentations described observations and models of horizontal and vertical distribution patterns of anchovy and sardine eggs; inter-population variability in early life history traits of anchovy along latitudinal gradients; egg mortality via euphausiid predation estimated using immunological techniques, and field studies on larval growth and mortality of anchovy and jack mackerel. Additionally, as part of a larger reproductive strategy, a presentation described the aggregative/dispersive behavior of jack mackerel during spawning.

• **Methods:** presentations described the use of the continuous, underway fish egg sampler (CUFES) in assessing distribution patterns of pelagic fish eggs and compared estimates of egg abundance from this sampler with other ichthyoplankton samplers; reviewed the use of the DEPM in estimating pelagic fish biomass; and described the application of new statistical tools such as generalized additive models (GAMs) to improve DEPM-based estimates.

After the two days of presentations, parallel discussion sessions that focused on (i) Habitat characterization, reproductive strategies, development, and early life history, and (ii) DEPM applications and methodological advances, were held during the morning of Friday 16th January. In the afternoon rapporteurs from each session provided summaries of those discussions. This report contains extended abstracts of presentations made at the meeting, in addition to the summaries of the final discussion sessions.

**References**


SPAWNING OF ANCHOVY, MACKEREL AND SARDINE IN THE CALIFORNIA AND HUMBOLDT CURRENT REGIONS

Dave Checkley, Jr.\textsuperscript{1}, Patricia Ayon\textsuperscript{2}, Timothy Baumgartner\textsuperscript{3} and Mauricio Braun\textsuperscript{4}

\textsuperscript{1}Scripps Institute of Oceanography, University of California, 9500 Gillman Drive, La Jolla, CA 92093-0218, USA (d.checkley@ucsd.edu).

\textsuperscript{2}Instituto del Mar del Peru, Esuina Gamarrar y General Valle, Chucuito, Callao, Peru (payon@imarpe.gob.pe).

\textsuperscript{3}CICESE, Apdo Postal 2372, Ensenada, Baja California, Mexico (tbaumgar@cicese.mx).

\textsuperscript{4}Institute de Fomento Pesquero, PO Box 8-V, Valparaiso, Chile (mbraun.irop.cl).

Fluctuations in the abundance of small, pelagic fish, including anchovy, mackerel, and sardine, are common in the Pacific Ocean off both North and South America. To achieve a better understanding of the causes of these fluctuations and enable optimal management and policy decisions, spawning of these fish has been studied. Fish eggs and their environment were sampled with the Continuous Underway Fish Egg Sampler (CUFES; Checkley \textit{et al.}, 1997) off California, Mexico, Peru, and Chile between 1996 and 2003. Species include anchovy (\textit{Engraulis mordax}), sardine (\textit{Sardinops sagax}), and jack mackerel (\textit{Trachurus symmetricus}) off California, USA, and Baja California, Mexico, and anchovy (\textit{Engraulis ringens}) and sardine (\textit{S. sagax}) off Peru and Chile. The coverage of samples discussed here varied in time and space by country: USA 1996-2003 (15 cruises), Mexico 2000-2001 (6 cruises), Peru 1999-2002 (5 cruises) and Chile 1999-2002 (5 cruises). Eggs were sampled with CUFES and, in most cases, concurrent measurements were made of temperature and salinity. The data were organized in a common structure to allow for analysis within and between cruises. Our focus here is on the use of temperature-salinity plots and their relation to spatial pattern (cf. Checkley \textit{et al.}, 2000).

For each of the four regions, either two or three main water types were sampled. These appear to include the California Current, coastal upwelling, and North Pacific Central Water (California and Mexico), Peru Coastal Water, Subtropical Surface Water and Tropical Surface Water (Peru), and Subantarctic Water and Subtropical Surface Water (Chile). These water types showed complimentary distributions in both aerial maps and on TS plots. There was no common pattern of spawning in TS space by species over all regions. Rather, species in each region appear to adapt to the range of water types available at the time of spawning but remain, on average, separate both spatially and in TS space within a region at any time. For example, spring spawning of anchovy and sardine off California, and available water types, was more variable in 2000 than 2001 (Checkley, 2005).

We conclude that (a) temperature and salinity are useful variables to characterize the spawning environment of small, pelagic fish; (b) it is useful to consider the oceanography of the spawning environment, including water types; and (c) that anchovy, sardine, and mackerel spawning habitats vary over time and space, with populations adapting to the available conditions. Further analyses with both TS plots and quotient analyses should better resolve commonalities within and differences between these genera, species, and populations.

References


INVESTIGATION OF INTERANNUAL DYNAMICS OF SUITABLE SPAWNING HABITAT FOR ANCHOVY (ENGRAULIS ENCRASICOLUS) IN THE SOUTHERN BENGUELA USING A 3D HYDRODYNAMIC MODEL

Claude Roy¹, Pierric Penven¹ and Carl D. van der Lingen²

¹Centre IRD de Bretagne, 29280 Plouzané, France.
²Marine and Coastal Management, Pvt Bag X2 Rogge Bay 8012, South Africa.

Environmental characterization of the spawning habitat of anchovy in the southern Benguela through single parameter quotient analysis has identified ranges of environmental variables within which this species “prefers” to spawn (Twatwa et al., 2004). The objective of this work is to test the potential of using simulations from an hydrodynamic model as a surrogate for direct measurements of the physical environment to explore the interannual variability of the potential anchovy spawning habitat. Once validated, it is thought that this approach could provide a methodology to diagnose the impact of future climate change on anchovy spawning habitat.

A ten year simulation (1991 to 2000) of the physical environment of the southern Benguela has been produced using an hydrodynamic model based on the ROMS numerical code. The model is forced at the surface with realistic weekly wind. Details of the configuration are given by Penven et al. (2001) and Blanke et al. (2002). The simulation provides modeled fields of temperature, salinity and currents in 3D with a spatial resolution ranging from 9 km inshore to 18 km offshore and with a temporal resolution of two days. The quotient analysis gives the ranges of temperature, salinity, current speed and water depth within which anchovy select to spawn, using observations made during annual cruises conducted in November (the peak anchovy spawning period). At each time step of the simulation, the Boolean combination of temperature, salinity and current speed ranges given by the quotient analysis is compared to surface values of those parameters given by the model over the whole domain, and areas meeting the criteria ranges are identified. Incorporation of the depth range identified by the quotient analysis provides a means of defining the area that is suitable for anchovy spawning. The resulting output is a ten year simulation with a two day time-step of the location and size of suitable anchovy spawning habitat in the southern Benguela. Plate 1 (page xi) presents a snapshot of suitable spawning habitat that corresponds to 18 November 1991.

A validation of the simulated suitable spawning habitat is performed by comparing the number of anchovy eggs collected during November surveys from 1991 to 1998 with the suitable spawning areas calculated by the model (Fig. 1). A positive correlation is found for area A (the west coast) and for the major anchovy spawning ground that corresponds to the combination of areas B+C+D (the

![Figure 1. The relationship between the simulated suitable spawning surface and observed anchovy egg number during the November surveys from 1991 to 1998.](image-url)
southwest coast, and western and central Agulhas Bank, respectively). In those areas, an increase in the simulated suitable spawning area corresponds to an increase in the observed abundance of anchovy eggs. An unexplained negative correlation is found on the eastern Agulhas Bank.

Using a simple combination of environmental parameters deduced from data collected during November surveys, the hydrodynamic model is able to partly reproduce the observed interannual variability in the distribution of anchovy spawning. This result gives us some confidence in the ability of such tools to investigate the impact of climate changes on spawning habitats. Future work will include a new configuration of the model with a southward and eastward extension of the oceanic boundary of the south-east corner of the domain. This will allow a better representation of the Agulhas retroflexion and of the influence of the Agulhas current on the Agulhas bank. Further development will include a realistic forcing at the oceanic boundaries in order to integrate the impact of remote events such as ENSO.

References


PREDICTING SPAWNING HABITAT LOCATION OF ANCHOVY AND SARDINE IN THE SOUTHERN BENGUELA USING REMOTELY-SENSED DATA

Laurant Drapeau\textsuperscript{1} and Carl D. van der Lingen\textsuperscript{2}

\textsuperscript{1}IDYLE, IRD, Cape Town, South Africa.
\textsuperscript{2}Marine and Coastal Management, Pvt. Bag X2 Rogge Bay 8012, South Africa.

A multivariate model developed to predict the probability of finding eggs of either anchovy (\textit{Engraulis encrasicolus}) or sardine (\textit{Sardinops sagax}) in the southern Benguela from four remotely-sensed environmental variables (Twatwa \textit{et al.}, 2004) was tested by comparing predicted spawning habitat with observed spawning habitat in 2000 and 2001. These years were not used in construction of the predictive model and therefore provide an independent test to assess model validity. The multivariate model was based on quotient curves of anchovy/sardine egg abundance and four environmental parameters, namely water depth, wind speed, SST and ocean colour (Fig. 1). These quotient curves were considered as references for defining ranges of each environmental parameter that were suitable for spawning, with a quotient value above 1 considered to indicate selection.

Predicted spawning habitat was derived from 3-day “moving average” (to account for daily cloud cover) satellite images of SST (AVHRR), ocean colour (SeaWiFS), satellite-derived daily measurements of wind speed (Quickscat), and from measured water depth (ETOPO 2). These temporal composite data were then combined to provide a spatial composite of the surveyed area using a Dirichlet tessellation algorithm based on the survey track. Such spatio-temporal composite images are considered to provide the most realistic illustration of actual environmental conditions observed during the survey. The environmental parameter ranges identified from the quotient analysis as suitable spawning habitat were then applied individually to the spatial-temporal composites to provide spatially explicit visualisations of suitable spawning habitat over the duration of the survey.

![Figure 1. Results of single parameter quotient analyses for egg abundance and environmental parameters for anchovy (diamonds and solid lines) and sardine (circles and dashed lines) in the southern Benguela, for (a) water depth, (b) wind speed, (c) SST and (d) phytoplankton biomass. Frequency distributions of the environmental variables are shown as histograms, and the horizontal line indicates a quotient value of 1. After Twatwa \textit{et al.} (2004).](image-url)
A Bayesian approach was then used to predict the probability of suitable spawning habitat by combining the maps derived from individual parameters, weighted according to their perceived importance in controlling selection of spawning habitat (Twatwa et al., 2004). Predicted spawning habitat was then compared with observed spawning habitat, as indexed by egg abundance and distribution data collected from CalVET net samples taken during the surveys. The CalVET net is considered to provide a better representation of abundance and distribution patterns of anchovy eggs than of sardine eggs, due to the highly patchy distribution of sardine eggs. This problem appears to be resolved by sampling for sardine eggs using the CUFES (van der Lingen and Huggett, 2003).

Maps showing the overlap between predicted and observed spawning habitat for anchovy and sardine are shown in Plate 2 (page xi), and show better mesoscale correspondence between predicted and observed spawning habitat for anchovy than for sardine. High anchovy egg concentrations were generally found in areas predicted as being suitable (i.e. probability >0.5) for spawning in both years, and areas of a low suitability (e.g. inshore regions of the west coast in both years and inshore on the south coast in 2001) tended to have low observed anchovy egg densities. Relatively high densities of sardine eggs were occasionally observed in areas predicted as having a low suitability for spawning, such as on the south coast between 20-23°E in 2000, and between 22-24°E in 2001. However, regions on the west coast with a high-predicted suitability for sardine spawning were associated with high egg densities, particularly in 2001.

The percentage match and mismatch between predicted and observed spawning habitat for each parameter individually, and all four parameters combined, are given in Table 1. These indicate a higher match than mismatch between predicted and observed spawning habitat for anchovy and sardine, both for individual parameters and when they were combined, which provides some validation of the model. Additionally, percentage match levels were generally higher for anchovy than for sardine. When the parameters are considered individually, sardine showed a higher percentage match for SST than did anchovy, most likely arising from their broader quotient curve for this parameter, but not for the other parameters.

Table 1. Percentage match (% +) and mismatch (% -) between predicted and observed spawning habitats of anchovy and sardine in the southern Benguela for 2000 and 2001. The table shows the percentage of eggs that were observed in areas having a predicted spawning suitability >0.5 (i.e. a match), and the percentage of eggs that were observed in areas having a predicted spawning suitability <0.5 (i.e. a mismatch), for each of the four parameters individually and from the combined analysis. Values >50% are shown in bold and italic.

<table>
<thead>
<tr>
<th>Year</th>
<th>Species</th>
<th>SST</th>
<th>Bathymetry</th>
<th>Chlorophyll a</th>
<th>Wind speed</th>
<th>Combined parameters</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>%+</td>
<td>%+</td>
<td>%+</td>
<td>%+</td>
<td>%+</td>
</tr>
<tr>
<td>2000</td>
<td>Anchovy</td>
<td>54</td>
<td>46</td>
<td>49</td>
<td>51</td>
<td>78</td>
</tr>
<tr>
<td></td>
<td>Sardine</td>
<td>82</td>
<td>18</td>
<td>64</td>
<td>36</td>
<td>53</td>
</tr>
<tr>
<td>2001</td>
<td>Anchovy</td>
<td>56</td>
<td>44</td>
<td>58</td>
<td>42</td>
<td>68</td>
</tr>
<tr>
<td></td>
<td>Sardine</td>
<td>82</td>
<td>18</td>
<td>16</td>
<td>83</td>
<td>25</td>
</tr>
</tbody>
</table>

The higher percentage match between the predicted and observed spawning habitat of anchovy compared to sardine suggests that using the predictive model to demarcate potential anchovy spawning habitat when egg abundance data are not available would provide meaningful information. This could be useful in monitoring spatio-temporal variability in potential spawning habitat throughout the entire anchovy-spawning season. The relatively low percentage match for sardine is surprising, given that this species appears to be less specific in their selection of spawning habitat than are anchovy (Twatwa et al., 2004). However, this difference may be due to less-efficient sampling of sardine eggs than anchovy eggs by the CalVET net, and comparisons between predicted sardine spawning habitat and observed spawning habitat from CUFES samples will be conducted.
Relating the variability in potential spawning habitat to subsequent recruitment success will contribute to an evaluation of the hypothesis that climate-induced changes in the spatio-temporal extent of suitable spawning habitat of small pelagic fishes cause observed productivity changes. Additionally, comparisons between predicted and observed egg distributions would permit tuning of the model through changing input parameter weightings. Future research will focus on temporal shifts and extent quantification of predicted spawning habitat in order to relate these changes to observed productivity changes as well as integration of others relevant environmental parameters as ocean currents and salinity, which can be obtained from modelling approaches.

References

CHARACTERIZATION OF THE ANCHOVY \textit{(Engraulis encrasicolus)} AND SARDINE \textit{(Sardinia pilchardus)} SPAWNING HABITATS IN THE BAY OF BISCAY FROM THE ROUTINE APPLICATION OF THE ANNUAL DEPM SURVEYS IN THE SOUTHEAST BAY OF BISCAY


AZTI, Food and Fish Technological Institute, Marine Research Unit, Herrera Kaia Portualdea z/g, 20110 Pasaia (Gipuzkoa), Basque Country, Spain (ysagarminaga@pas.azti.es).

The purpose of this paper is to analyse the spatial distribution of anchovy \textit{(Engraulis encrasicolus)} and sardine \textit{(Sardinia pilchardus)} spring spawning and its relationship with the environmental parameters and processes affecting the Bay of Biscay in that period.

Egg abundances and environmental data acquired during DEPM surveys, held in May from 1999 to 2002, have been used. These surveys \cite{Santos et al., 2003} focus on anchovy and are carried out during its peak spawning period in the Bay of Biscay, a bit late than the peak period for sardine which occurs in March and April.

In order to standardize observation from different years with different population biomass values, a relative egg abundance parameter (RA) was calculated as follows:

\[ RA_{i,y} = \frac{N_{i,y}}{\sum_i N_{i,y}} \]

where \( N_{i,y} \) = Number of eggs, \( i \) = station, and \( y \) = year.

The spatial distribution of relative egg abundances (RA) was mapped for all years and the mean surface was calculated to identify the most common spawning areas for both species.

For anchovy, two main spawning grounds are found in the proximity of Gironde and Adour rivers over the French shelf (areas 1 and 2 in Plate 3, page xi). There is also a noticeable ground in the mid-outer Armorican shelf (area 3 in Plate 3).

For sardine, in the southern Bay of Biscay, two main spawning grounds are found over the Cantabrian shelf and close to the Adour outfall (areas 4 and 5 in Plate 3). On the northern part of the Bay, one linear shaped area is found just over the shelf edge and another one over the mid-inner Armorican shelf between the Gironde and Loire river estuaries (areas 6 and 7 in Plate 3).

On average (Plate 3) a spatial segregation of the main spawning grounds of anchovy and sardine exists. However this segregation is not observed in areas of low relative abundances, in which spawning of both species coexist. Even more, on the Aquitanian shelf (area 8 in Plate 3) both species spawn jointly with relatively high abundances (+1 sd). It is also important to note, that this average pattern is not revealed consistently over the different years, in which the variability of the spatial distribution of the spawning areas are quite important (Mean Coefficient of variation of RA for anchovy=121%, Mean Coefficient of variation of RA for sardine=95%).
Presence/absence and abundance ratios for both species were analysed. Firstly, we calculated the percentage of the RA of anchovy for each station through all years:

$$\text{Anc}_{st} (\%) = \frac{\text{RA}_{\text{anchovy}}}{\text{RA}_{\text{anchovy}} + \text{RA}_{\text{sardine}}}$$

Survey stations were classified according to the Ancst values obtained. Table 1 (2nd column) shows the percentage of stations found in each of the classes. The results obtained show that there are nearly as many stations in which both species do not appear together (48%) as stations in which they coexist (52%).

Then, we calculated a percentage of the number of times anchovy eggs were found over the number of times either anchovy or sardine eggs were found in each station.

$$t_i = \frac{\sum t_i, y, \text{anchovy}}{\sum t_i, y, \text{anchovy} + t_i, y, \text{sardine}}$$

Where:

$$t_i = \begin{cases} 1 & \text{if } \text{RA}_{i, y} > 0 \\ 0 & \text{otherwise} \end{cases}$$

As above, survey stations were classified according to the %t values obtained. Table 1 (3rd column) shows the percentage of stations found in each of the classes. The segregation statistics (28.2%) remained constant over the studied period. For sardine, these segregated areas are located in area 4, and in the northern part of areas 6 and 7 (cf. Plate 3). For anchovy, the constant segregation areas are found out of the shelf break and in the northern Bay of Biscay over the mid shelf between areas 6 and 7 (these last mainly occupied by sardine).

These observations for the period between 1999-2001 outline the main spawning areas. However, as revealed in previous DEPM surveys, other areas occasionally showed important spawning activity. That is the case for the southern offshore grounds over the Cantabrian sea, where from 1999 to 2002 no significant spawning has been detected.

Regarding the relationship of the spawning distribution with the environmental parameters we have analysed the distribution of RA through the range of values of sea surface temperature, sea surface salinity, and sub-surface chlorophyll-a concentration values found during the survey (Fig. 1).

Table 1. Percentages of anchovy relative abundance and presence per stations out of total anchovy and sardine positive stations.

<table>
<thead>
<tr>
<th>Classes by % of anchovy presence</th>
<th>%RAᵢ,ᵧ</th>
<th>%tᵢ</th>
</tr>
</thead>
<tbody>
<tr>
<td>Segregation</td>
<td>48</td>
<td>28.2</td>
</tr>
<tr>
<td>All anchovy</td>
<td>31.8</td>
<td>21.8</td>
</tr>
<tr>
<td>All sardine</td>
<td>16.2</td>
<td>6.4</td>
</tr>
<tr>
<td>Co-existence</td>
<td>52</td>
<td>71.8</td>
</tr>
<tr>
<td>50-100% anchovy</td>
<td>23.4</td>
<td>24.0</td>
</tr>
<tr>
<td>50% each spp.</td>
<td>0.0</td>
<td>35.8</td>
</tr>
<tr>
<td>0-50% anchovy</td>
<td>28.6</td>
<td>12.0</td>
</tr>
<tr>
<td>Number of stations with presence of any spp.</td>
<td>1512</td>
<td>631</td>
</tr>
</tbody>
</table>
The distribution of the sum of the relative abundances by the sea surface temperature, is a unimodal bell-shaped curve with a mode at around 15°C for sardine and 17°C for anchovy.

For sea surface salinity the distribution of spawned eggs is a bimodal curve for sardine with the modes situated in desalted waters near the river plumes (<34.5 psu) and in offshore waters (around 35.25 psu). Anchovy prefers desalted waters and shows a primary mode below 34.5 psu and a secondary one at around 34.75 psu.

Regarding the relationship between relative egg abundances and the sub-surface chlorophyll-a concentration, sardine shows a unimodal distribution with a peak at chlorophyll-a concentration values within the range between 1-2 mg/m$^3$. Anchovy has a more even distribution with a less marked peak in more productive waters (2-4 mg/m$^3$).

From these results we can put forward that sardine spawning is associated with areas of lower sea surface temperature values with ongoing primary production, which in the Bay of Biscay correspond to deep offshore areas in which late vernal blooms take place and in cooler coastal areas like the Cantabrian sea or the Loire river outfall.

Anchovy spawning occurs in areas of higher sea surface temperature values and more desalted waters than those occupied by sardine, with high primary production. These zones mostly correspond to the areas over the Aquitanian and Armorican shelves influenced by the Gironde and Adour river plumes.

Sardine may be more strongly influenced by sea surface temperature than anchovy because it is in an edge of its spawning period and this could have a limiting effect. Nevertheless anchovy, which is at the peak spawning period, benefits from the optimal temperature conditions and its distribution may be more strongly affected by the distribution of the main primary production areas. Anyway, the temperature has an important role in defining the kick off of the spawning period which starts when the steep increase of sea surface temperatures begins during spring in the area of study (Motos et al., 1996).

Apart from these factors, the population stock biomass and the population age structure have an influence on the distribution of spawners in the area. In this sense, some studies dealing with adults distribution have indicated that older sardines exploit more offshore areas whereas younger ones spawn in coastal areas. In the same way older anchovies seem to start spawning earlier in lower temperatures in offshore areas and younger ones spawn later in the season in warmer waters close to the coast (Petitgas et al., 2003; Uriarte et al., 1996). On-going work is underway in this area of research.
Acknowledgements
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References


SARDINIA PILCHARDUS SPAWNING PATTERNS OFF PORTUGAL

Maria Manuel Angélico and Paulo B. Oliveira
Instituto de Investigação Agrária e das Pescas-IPIMAR, Lisboa, Portugal
(angelico@ipimar.pt).

The Continuous Underway Fish Egg Sampler (CUFES) has been in use off Portugal since 2000. A comprehensive data set, resulting from 8 surveys, undertaken during the spawning period of Sardina pilchardus is now available. Data include, plankton volume, egg abundance, temperature, salinity and chlorophyll concentration. This information, together with remotely sensed, sea surface temperature, primary production, winds and hydroacoustic observations, are being analysed in order to characterize the spawning habitat of the species in the Iberian system.

Distribution maps of biotic and abiotic factors show interesting patterns that suggest an association of the sardine spawning areas with regions of fresh water influence. These lower salinity areas present temperatures above or below the surrounding waters according to season of the year and river runoff intensity. Primary production, reflected in the concentration of chlorophyll pigments, is also high in these zones. High concentrations of zooplankton, including ichthyoplankton, appear also to be associated with other hydrographic structures such as frontal zones and mesoscale eddies. The onset of such recurrent circulation features, associated with the poleward flow and local topography, are being analysed with the aim of understanding its relationship with egg and larvae distributions and their role in the (un)successful recruitment to the local populations.
TENTATIVE APPROACHES TO DESCRIBE ANCHOVY AND SARDINE SPAWNING HABITATS IN THE BAY OF BISCAY

Benjamin Planque, Pierre Petitgas and Jacques Massé
IFREMER, Laboratoire Ecologie Halieutique, Rue de l’île d’Yeu, BP21105, 44311 Nantes Cedex 3, France (benjamin.planque@ifremer.fr).

Overall summary
Using egg and environmental data collected during spring 2000-2003 and a suite of numerical methods, we evaluate the potential for simple hydrological variables to model spawning habitat (namely, sea surface and bottom temperature, sea surface and bottom salinity, stratification, mixed layer depth and bottom depth). We observe that (1) analyses of individual years of data provide contradictory results, (2) high abundance of sardine and anchovy eggs are found throughout the full range of the environmental variables measured, (3) when data from all years are combined the optimal habitats are broad but consistent with existing literature and (4) that predictive models based on one or several environmental parameters only explain very small fractions of total variance (or deviance) in the egg distributions.

Using results from hydrodynamical modelling, we attempt to relate egg distribution to particular spring hydrological dynamics rather than to punctual hydrological observations. As in the previous analysis, we observe that analyses of individual years of data provide contradictory results.

We conclude that, in the Bay of Biscay, modelling of spawning habitat from observed hydrological parameters in specific years is not advisable whilst modelling from observations aggregated over several years may prove more successful.

We also conclude that, on their own, hydrological records may not be sufficient to describe spawning habitat. We suggest that other factors need to be included to model spawning habitat, these can include information relative to other trophic levels, adult population abundance, size and age structure, interspecific interactions, diffusion of fish from their habitat, and interannual inertia in population habitat selection patterns.

Data summary
Data over the French part of the Bay of Biscay continental shelf has been collected during spring for the period 2000-2003. The cruises follow a standard sampling plan designed for the assessment of small pelagic fish stocks by acoustic and pelagic trawling. In addition meteorological data (temperature, wind, humidity,….) and hydrological data (subsurface temperature, salinity and fluorescence) are collected en route, as well as during hydrological stations during which vertical CTD casts are performed (temperature, salinity, fluorescence). Fish eggs are continuously collected using a CUFES fitted with a 500 micron mesh net. The egg samples correspond to 20 minutes sampling (approximately 10 m$^3$ of filtered water along 3 nautical miles). Over the 4 years 2866 egg samples were collected. For each sample, the following information is available:

- Sample number
- Latitude
- Longitude
- Date/time
- Bottom depth
- Wind speed and direction
• Subsurface temperature, salinity and fluorescence
• Bottom temperature, salinity and fluorescence
• Stratification (potential energy deficit)
• Mixed-layer depth (using a 2-layered model)
• Hydrological group (these are defined from hydrodynamical modeling. Each group is characterized by specific changes in vertical hydrology during the spring season).

Results
The quotient plot analyses reveal for individual years, the range of temperature/salinity within which most sardine and anchovy eggs are found. However, the conclusions which can be derived from individual years appear sometimes inconsistent or contradictory. For example, in 2000, sardine eggs are found in warmer waters (13-14°C) than anchovy eggs (12-13°C), whilst in 2001 the reverse pattern is observed (Fig. 1).

When data from all years are pooled, the results from the quotient analyses for temperature and salinity are consistent with already published data, with temperature range of 14.5-18.5°C for anchovy and 12.5-16.0°C for sardine, and salinity range of <30-33.5 for anchovy and 30.25-31.5 and >35.25 for sardine.

Using results from hydrodynamical modeling, we attempt to relate egg distribution to particular spring hydrological dynamics rather than to punctual hydrological observations. As in the previous analysis, we observe that analyses of individual years of data provide contradictory results.

![Figure 1](image-url)

**Figure 1.** Top: the range of positive quotient ((i.e. greater abundance of eggs than average) for sardine and anchovy eggs with regard to temperature and salinity values. Note the great variability of quotient analysis results from year to year. Bottom: quotient curve analyses for sardine and anchovy and for surface temperature and salinity, for all years of sampling 2000-2003 (pooled data).
Discussion and conclusions
The results presented above clearly indicate that using quotient curve analysis on individual years does not provide a clear picture of the possible role of physical parameters on sardine and anchovy egg distribution in the Bay of Biscay. On the other hand, grouping data for several years seems to provide outputs that are consistent with existing literature (see e.g. Arbault and Lacroix, 1977). This may be seen as the result of the quotient curve analysis being more adequate to describe potential spawning habitat (SH) that to describe realised SH (potential SH consists of hydrological condition that are potentially suitable for spawning, whereas realised SH is the actual spatial distribution of fish eggs at a given time in a given year). Another important result concerns the potential role of bathymetry and vertical water stratification in structuring SH for sardine and anchovy (not shown here).

The results from Petitgas et al. (2002) also indicate that physical measurements on their own may not provide an optimal representation of water mass characteristics for spawning. In the Bay of Biscay, a large fraction of the information concerning ecosystem structure at low trophic levels (phyto- and zooplankton) is lacking from hydrological proxies.

Finally, we can note that the spawning adult population of anchovy is not evenly distributed in all spawning areas. Fish spawning outside river plume water are generally of larger size (greater age) than those inside the river plumes. Therefore, effects of the physical environment on spawning may go beyond direct effects on spatial distribution of SH, and interact with biological traits of the adult population (Plate 4, page xii).

References


The clupeids and engraulids (Sardina pilchardus, Sardinella aurita and Engraulis encrasicolus) are important commercial species in the Canary Islands waters, mainly because of their use as live bait in tuna fishing. Knowledge of spawning periods and recruitment is thus essential for the management of the fisheries around the archipelago. However, those studies are scarce or lacking in the region and conforms an important gap in the oceanographic studies around the archipelago. The Canary Islands are located on the eastern flank of the North Atlantic subtropical gyre and are in the path of the Canary Current. Hernández-León et al. (2001) described a sharp eddy system downstream of the Canary Islands influencing bacteria, phytoplankton and zooplankton distribution. Moreover, Rodríguez et al. (2001) also showed that Gran Canaria Island and the eddy system acts as a retention area of fish larvae due to two stagnation areas created by the hydrodynamic conditions around the island. The modelled larval drift resulted in enough retention time to allow most of the ichthyoplankton to remain near the island, mainly north and south of the island coinciding with the areas where the main current is reduced due to stagnation.
The distribution and abundance of fish larvae and particularly of three important commercial clupeoid species in the Canary Islands waters was studied along the eastern and southern shelf of Gran Canaria Island (Canary Islands) from July 2000 to June 2001. Oblique bongo hauls were carried out fortnightly during daytime but coinciding with days of full and new moon, except during February in which the area was sampled every 2-5 days.

A total of 3603 fish larvae were found and analysed during the annual cycle. The ichthyoplanktonic community was composed by 17.3% of clupeoid larvae distributed in 92.9% of Sardinella aurita, 4.7% of Engraulis encrasicolus and 2.4% of Sardina pilchardus. Sardinella aurita larvae appeared during the whole year with two periods of maximum abundance (Fig. 1a), June to September and December to February. During the full moon their abundance was on average 38.5% (± 6.8%) of their numbers during the new moon, showing a clear lunar periodicity. Engraulis encrasicolus larvae appeared from November to March but also coinciding with the new moon, and Sardina pilchardus larvae only appeared during two short periods (Fig. 1b), both coinciding with filaments shed from the African coastal upwelling which reached the island. Sardina pilchardus was not reproducing around the islands and appeared as juveniles in the catch of fishermen 2 to 4 months later. Therefore, the contact of filaments of upwelling with the islands suggests important social and economic benefits for the local fisheries.

In summary, the results show that there exists a transport for fish larvae from the spawning area off Northwest Africa to the Canary Islands illustrated in two occasions by the presence of Sardina pilchardus larvae in the coast of Gran Canaria Island in February and June 2001. Therefore, the transport of fish larvae in the upwelling filaments observed by Rodríguez et al. (1999) can lead to an African connection between the fisheries in the upwelling area and the Canary Islands. The presence of a lunar cycle in the abundance of fish larvae was also a striking result as it can suggest that the common observation of a lunar periodicity in the reproduction of many warm water fish species could be related to the recently observed moon cycle in zooplankton, in the food of fish larvae. Both the transport of fish larvae in the filaments and the lunar periodicity deserves further evaluation.

References


REGIME SHIFTS IN THE HUMBOLDT CURRENT ECOSYSTEM

Jürgen Alheit¹, Miguel Niquen²

¹Baltic Sea Research Institute, Seestr. 15, 18119 Warnemünde, Germany (juergen.alheit@io-warnemuende.de).
²Instituto del Mar del Peru (IMARPE), Esq. Gamarra y Valle s/n, Apartado 22, Callao, Perú.

Of the four major eastern boundary currents, the Humboldt Current (HC) stands out because it is extremely productive, dominated by anchovy dynamics and subject to frequent direct environmental perturbations of El Niño Southern Oscillation (ENSO). The extreme positive temperature anomalies caused periodically by ENSO events are unfavourable for anchovies, but enhance growth of the sardine population off Peru. The long-term dynamics of the HC ecosystem are controlled by shifts between alternating anchovy and sardine regimes which restructure the entire ecosystem from phytoplankton to the top predators. These regime shifts are caused by lasting periods of warm or cold temperature anomalies related to the approach or retreat of warm subtropical oceanic waters to the coast of the HC. Phases with mainly negative temperature anomalies parallel anchovy regimes (1950s-1970; 1985-up to now) and the rather warm period from 1970-1985 was characterized by sardine dominance. The transition periods (turning points) from one regime to the other were 1968-1970 and 1984-1986. Like an El Niño, the warm periods drastically change trophic relationships in the entire HC ecosystem exposing the Peruvian anchovy to a multitude of adverse conditions.

Positive temperature anomalies off Peru drive the anchovy population close to the coast as the coastal upwelling cells usually offer the coolest environment thereby substantially decreasing the extent of the areas of distribution and spawning of anchovy. This enhances the effects of negative density-dependent processes such as egg and larval cannibalism and dramatically increases its catchability. Increased spatial overlap between anchovies and the warmer water preferring sardines intensifies anchovy egg mortality further as sardines feed heavily on anchovy eggs. Food sources for juvenile and adult anchovies which prey on a mixed diet of phyto- and zooplankton are drastically reduced because of decreased plankton production due to restricted upwelling in warm years as demonstrated by lower zooplankton and phytoplankton volumes and the diminution of the fraction of large copepods, their main food source. Horse mackerel and mackerel, the main predators of anchovy, increase predation pressure on juvenile and adult anchovies due to extended intrusion into the anchovy habitat in warmer years.

In contrast to these periods of warm and cold temperature anomalies on the decadal scale, ENSO events do not play an important role for long-term anchovy dynamics as the anchovy can recover even from strong ENSO events within one to two years. Consequently, the strong 1972-73 ENSO event was not the cause for the famous crash of the Peruvian anchovy fishery in the 1970s.

Full paper available in:

Gabriel Claramunt¹, Jorge Oliva², Gustavo Herrera¹, Rubén Escribano³, Rodolfo Serra², Ruben Roa⁴

¹Departamento de Ciencias del Mar, Universidad Arturo Prat, P.O. Box 121, Iquique, Chile (gclaramu@unap.cl).
²Instituto de Fomento Pesquero (IFOP), Valparaiso, Chile.
³Center of Oceanography for the Eastern South Pacific (COPAS), Universidad de Concepción, Chile.
⁴Departamento Oceanografía, Universidad de Concepción, Concepción, Chile.

The DEPM was applied for the first time in 1992 for anchovy spawning biomass estimates in northern Chile. Thereafter, it has routinely been applied every year since 1995 to present (except for 1998) to estimate the spawning biomass. After 10 years the DEPM may provide valuable information to assess interannual variability in spawning biomass and its derived biological parameters for this important stock. For instance, the application of the DEPM can give much insight on how the population has responded to the ENSO (El Niño Southern Oscillation) cycle, characterized by alternating warm (El Niño) and cold (La Niña) periods in the last 10 years in northern Chile. Annual changes in “anchoveta” biomass are mostly thought to be driven by ENSO variability.

In each survey the area was covered by a sampling grid with parallel transects separated 10 nm and with stations each 3 nm. In some years an additional sampling effort was applied in the most important spawning area (ca. 21° - 22°S) (Fig. 1). In the last years a regular grid was applied. The transects extended 60 nm offshore and the sampling was performed using a CalVET net with 0.05 m² opening and 250 μm mesh, deployed in vertical tows from 70 meters depth to surface or from 5 meters above the sea bottom in shallow waters. The number of stations sampled during each survey, the number of positive station for eggs, the number of eggs obtained and an estimate of the surveyed area in nm² are shown in Table 1.

In parallel to the egg surveys, adults of anchoveta were sampled by purse seiner, fishing in the same area surveyed for eggs. An adequate design for the adult parameter is to sample at least 30 mature female from no less than 40 tows; this ensure a CV of no more than 0.20. The number of positive samples for adult anchovetas ranged between 32 and 60.

Table 1. The surveys results for each year: Total number of stations sampled (Stations); Number of positive stations (Stations (+)); Total number of eggs; average of eggs in stations (Density) in egg/0.05 m²; average number of egg in positive stations in eggs/0.05m²; Survey area and Spawning area in nm².

<table>
<thead>
<tr>
<th>Year</th>
<th>Stations</th>
<th>Stations (+)</th>
<th>Total eggs</th>
<th>Density</th>
<th>Density (+)</th>
<th>Survey area</th>
<th>Spawning area</th>
</tr>
</thead>
<tbody>
<tr>
<td>1992</td>
<td>542</td>
<td>212</td>
<td>10974</td>
<td>20</td>
<td>52</td>
<td>17055</td>
<td>10332</td>
</tr>
<tr>
<td>1995</td>
<td>578</td>
<td>208</td>
<td>7555</td>
<td>13</td>
<td>36</td>
<td>18137</td>
<td>13315</td>
</tr>
<tr>
<td>1996</td>
<td>752</td>
<td>176</td>
<td>6718</td>
<td>9</td>
<td>38</td>
<td>18353</td>
<td>10698</td>
</tr>
<tr>
<td>1997</td>
<td>800</td>
<td>209</td>
<td>8054</td>
<td>10</td>
<td>39</td>
<td>19627</td>
<td>14660</td>
</tr>
<tr>
<td>1999</td>
<td>598</td>
<td>132</td>
<td>7582</td>
<td>13</td>
<td>57</td>
<td>21734</td>
<td>7525</td>
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<tr>
<td>2000</td>
<td>502</td>
<td>212</td>
<td>10473</td>
<td>21</td>
<td>49</td>
<td>19539</td>
<td>13059</td>
</tr>
<tr>
<td>2001</td>
<td>514</td>
<td>60</td>
<td>7586</td>
<td>15</td>
<td>126</td>
<td>25921</td>
<td>4026</td>
</tr>
<tr>
<td>2002</td>
<td>589</td>
<td>310</td>
<td>18305</td>
<td>31</td>
<td>59</td>
<td>30264</td>
<td>23728</td>
</tr>
</tbody>
</table>
Geostatistical maps of egg density exhibited a fairly variable situation from year to year, that is well showed by years 2001 and 2002 (Fig. 1). In terms of spatial coverage, 2001 appeared as a year of very high concentration of eggs close to the shore. The highest egg density in a single station along the entire period was observed during this year inside the patch centered at 21°S (1987 eggs/0.25 m$^3$). At the other extreme of spatial coverage, the following year 2002 showed almost complete coverage of the whole survey area (Fig. 1). Regarding anisotropy, the year 1997 (ENSO event) reflected a clear elongation of the patches towards the north. There are signs of anisotropy in 2002 and probably also in incompletely observed patches in other years. It also seems clear that egg patches often extend towards unobserved areas to more oceanic waters. Spatial distribution of eggs consistently showed a spawning area in the nearby the Rio Loa (ca. 21° - 22°). Another area with a relative temporal stability is near the northern boundary. Normally, southernmost positive station were located in the vicinity of Tal-Tal (ca. 25°), but during 1997 (ENSO year) eggs were found as south as 26°S. In a longitudinal gradient, eggs were found as far as 60 nm from the coastal line. As a rule, the egg distribution of anchovy in northern Chile suggests a homogeneous spawn activity. Adults anchovies were found in the first 40 nm from the coastal line, but some positive tows were obtained in more oceanic waters.

The extents of the spawning area (nm$^2$) are related to population abundance index (Fig. 2). Interannual fluctuations in localization of the egg distribution could be related to changes in oceanographic features. The oceanographic data however have not provided a clear explanation. Interannual variability in the physical and chemical environment are mostly reflected in changes in sea surface temperature, sea level and thermocline depth (Blanco et al., 2001), changes in surface chlorophyll-a patterns (Thomas et al., 2001) and alterations in the extension and depth of the oxygen minimum zone (Morales et al., 1999). Variability in the biological environment, such as the rates of primary production, presence of predators and food resources for the spawning population has been much less studied. Year-to-year variation in circulation patterns has not received attention either. Both cross-shelf and alongshore currents might be key driving forces to determine spatial distribution of eggs and egg mortality subjected to advection during the spawning season.
The zone nearby the El Loa river has persisted as an important spawning site, where eggs aggregate nearshore. This site may deserve special attention, but oceanographic studies in the area have only recently begun (unpublished results).

Among other features, it is remarkable that during 1997, when strong El Niño event was present in the Eastern South Pacific, which drastically altered the physical environment in coastal waters off northern Chile, anchoveta eggs were abundant and widely distributed, not evidencing any dramatic decline in the spawning process. It appeared that the 1997-98 El Niño did not actually produced an ecological catastrophe in the Eastern South Pacific as compared to previous events (Chavez, 2003) and anchoveta spawned in a “normal” fashion. It is likely however that strong temperature anomalies or others alterations may have increased egg and larval mortality affecting recruitment, this because of the decline in spawning biomass and landing in the next two years (1998-99). The population seemed to have rapidly recovered however in 2000.

The application of the DEPM in northern Chile has become an important tool to not only obtain a rapid estimate of the anchoveta population size, but also to examine population responses to interannual variability in the environment.

References


Luis A. Cubillos\(^1\), Patricia Ruiz\(^1\), Sergio P. Núñez\(^1\), Gabriel Claramunt\(^3\), Jorge Oliva\(^4\), Ciro Oyarzún\(^2\), Santiago Gacitúa\(^2\), Aquiles Sepúlveda\(^1\), Leonardo Castro\(^5\)

\(^1\)Instituto de Investigación Pesquera, Casilla 350, Talcahuano, Chile (lucubillos@udec.cl).
\(^2\)Departamento de Oceanografía, Universidad de Concepción, Casilla 160-C, Concepción, Chile.
\(^3\)Departamento de Ciencias del Mar, Universidad Arturo Prat, Casilla 121, Iquique, Chile.
\(^4\)Instituto de Fomento Pesquero, Barrio Industrial s/n, Iquique, Chile.
\(^5\)Laboratorio de Oceanografía Pesquera y Ecología Larval (LOPEL). Departamento de Oceanografía, Universidad de Concepción, Casilla 160-C, Concepción, Chile.

Two small pelagic fish of clupeoids, locally known as common sardine (*Strangomera bentincki*) and anchovy (*Engraulis ringens*), are important fish resources for both an industrial and a small-scale fleet of purse-seiners in the central-south area off Chile (34°S - 40°S), with Talcahuano as the main port for landings (Cubillos *et al*., 2002). The spawning season of these species tends to occur in winter (Southern Hemisphere) and extends from July to September, with a peak between August and September (Cubillos *et al*., 1999). In this contribution, we communicate the first application of the daily egg production method (DEPM; Lasker, 1985) to assess the spawning stock biomass of common sardine and anchovy in central-south Chile.
The study area was located off central-south Chile (33°00′S – 40°00′S) covering 27836 km², from August 15 to September 9, 2002. The area was divided into three operational zones: a) northern zone, from Valparaíso to Constitución (33°00′S – 34°40′S), b) central zone, from Constitución to Golfo de Arauco (34°50′S – 37°10′S), and c) southern zone, from Bahía Carnero to Punta Galera (37°28′S – 40°00′S) (Fig. 1). In this area, 761 planktonic stations were distributed on a regular grid covering the continental shelf (200 m depth), with stations separated by 2 nautical miles along transects, and each transect separated by 5 nautical miles. Two ships were used to collect ichthyoplanktonic data using Pairovet nets through vertical tows from 70 m to surface. Ten artisanal boats collected adult fish by using purse-seine. Five boats were distributed in the central zone and five in the southern zone, completing 106 sets from which 17 were without fishing. Anchovy and common sardine were randomly sampled from 39 and 76 sets respectively. The tows covered a wide geographic area between Constitución and Punta Galera.

The spawning of both species revealed the absence of eggs in the northern zone. In the central zone, it was observed a higher average abundance of common sardine eggs (10.0 eggs/0.05 m²) than anchovy eggs (4.1 eggs/0.05 m²), and the distribution of the anchoveta spawning was more continuous along the coast. In the southern zone, the spawning of both species was very coastal and related to depth lower than 50 m. The average abundance of anchoveta (10.2 eggs/0.05 m²) was similar than the common sardine eggs abundance (12.6 eggs/0.05 m²). The spawning distribution of both species was fully covered (Plate 5, page xii).

The daily egg production was estimated in 30.8 and 45.2 eggs/0.05 m²/day for anchoveta (CV = 25.1%) and common sardine (CV = 29.1%), respectively. The daily mortality rate was estimated in 0.549 and 0.523 d⁻¹ for anchoveta (CV = 21.6%) and common sardine (CV = 36.6%), respectively. The main reproductive parameters as used in the DEPM were evaluated from 1348 females in 32 tows of anchoveta and from 1278 females in 57 sets of common sardine. During the surveys, females of both species were reproductively active. The batch fecundity was linearly related to the body weight for 158 anchoveta females and for 116 sardine females. Average batch fecundity for mature females was estimated in 6758 oocytes for anchovy (CV = 6.9%) and 9227 oocytes for common sardine (CV = 3.5%). The proportion of mature female spawned per day was estimated in 10.7% for the anchoveta (CV = 12.8%) and in 13.1% for common sardine (CV = 11.3%). It seems that the greater fraction of females spawned per day in common sardine can explain the higher daily egg production of this species. The proportion by weight of females was of 51% in anchoveta (CV = 3.7%) and of 47% in common sardine (CV = 3.3%), while the average weight of mature females was estimated in 18.6 g for the anchovy (CV = 5.8%) and in 21.4 g for the common sardine (CV = 3.6%).

The spawning area was more greater in the case of anchoveta, covering 26.2% of the study area, while the common sardine spawning covered only 15.3% of the study area. It must be mentioned that there was no spawning in the northern zone. The spawning stock biomass was estimated as 227 170 t for the anchovy (CV = 28.3%) and as 145 730 t for the common sardine (CV = 32.1%). These values are similar in magnitude with the estimates obtained through the hydroacoustic method in 2001 by Castillo et al. (2002) and from cohort analysis carried out between 1990 and 1998 by Cubillos et al. (2002).

Acknowledgements

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References


TOPOGRAPHIC CONTROL OF THE LARVAL CLUPEIFORM DISTRIBUTION IN THE COASTAL UPWELLING AREA OFF CONCEPCIÓN, CENTRAL CHILE

Marcus Sobarzo¹, Beatriz Yannicelli², Leonardo R Castro¹,², Mauricio Landaeta² and Wolfgang Schneider¹

¹Departamento de Oceanografía, Universidad de Concepción (msobarz@udec.cl).
²Laboratorio de Oceanografía Pesquera y Ecología Larval (LOPEL), Departamento de Oceanografía, Universidad de Concepción, Casilla 160-C, Concepción, Chile.

Local concentrations of plankton and fish are often enhanced in and around shelf-break canyons (Allen et al., 2001) and in coastal areas with a major retention time (gulfs, wide continental shelf, etc). Several arguments have been suggested to explain these patterns. i) Flow near the canyon rim is strongly influenced by non linear advective effects driving relative vorticity and aggregation areas; ii) Cross shore transport is enhanced due to submarine canyons; and iii) Upwelling fronts can be coupled with shelf-break canyon fronts. Some of these arguments are applicable to the coastal upwelling system in Central Chile (35°S to 39°S) because this is dependent, among others, on the local wind stress variability and the strong topographic control imposed by a complex submarine topography and coastal line.

In terms of the submarine topography in the coastal zone off Talcahuano, Central Chile, the coastal line changes its orientation from Punta Lavapie (37°12’S) northwards, originating an equatorward-facing embayment system and a wide continental shelf limited by two submarine canyons (Fig. 1). This particular disposition of the coastal line and of the continental shelf break causes that the main area of coastal upwelling of this zone (Punta Lavapie) to remain practically aligned or at the same longitude (73°40’W) that the shelf break located northward in front of Concepción. In these conditions, the local wind forcing at the daily (sea-breeze process) and weekly temporal scales (of the order of 4 to 10 days) interact with the submarine topography and with rather weak tides modulating the coastal ocean in terms of their dynamic, turbulence and stratification.

Figure 1. a) Maps of geopotential anomaly (relative to 70 m, in m²/s²). The isoline of 1 ml/l of dissolved oxygen and the isohaline of 34.5 at 80 m depth are included. b) Larval clupeiform (anchoveta and common sardine pooled) distribution showing the areas of highest concentrations associated with the canyons and upwelling points.
The aim of this study is to show the influence of the submarine topography on the larval distribution of small pelagic fishes. The hydrographic data utilized were obtained from a cruise carried out during November 2001 over the continental shelf of Central Chile between 35 and 37 degrees south. We sampled 69 stations (hydrography and zooplankton) in 11 equally spaced transects.

Surface distribution of geopotential anomaly relative to 70 m depth show a pressure gradient toward the coast with a northward predominant flow following the bathymetry (Fig. 1a). This northward flow is clearly affected by the Itata canyon driving onshore currents (at the south rim of the canyon) and offshore currents (at the north rim of the canyon) and, also influencing the along shore distribution of the Equatorial Subsurface Water (ESSW). According with Figure 1 at 80 meters depth, the isohaline of 34.5 and the isoline of 1 ml/l of dissolved oxygen (both values characteristic of ESSW) have similar alongshore distributions that follow the isobath of the 200 meters. This way, ESSW tend to be closest to the coast in the Itata canyon, although not necessarily near surface.

The Biobio submarine canyon does not show the same influence on the flow. Our sampling design did not have enough horizontal resolution at this canyon. However, it seems the Biobio canyon is too narrow and the northward flow tends to cross the isobaths without adjusting to the bathymetry, specially at the north rim.

In this scenario, high Clupeiform larval concentrations occur around the rim of the Biobio canyon and in the central coastal shelf (Fig. 1b). At the north of the Biobio canyon, the larval distribution seemed to be associated with a secondary upwelling region related to the shelf break. In this place, the change of curvature of the 200 m isobath is too abrupt for the northward flow to adapt and then the flow tends to cross isobaths into the shelf. On the other hand, the larval distribution in the central coastal shelf is related with the coastal upwelling front near to the shelf break of the Itata Canyon. This front moves along the SE – NW axis and can to arrive to the shelf break of the Itata canyon on a temporal scale of a few days. This front could be contributing with a major retention time of larvae near the coast.

Acknowledgements
Support was provided by the Fondecyt Project # 1010900.

Reference
Jack mackerel is a migratory species that carried out offshore migrations to spawn in oceanic waters off central Chile during the austral spring in October-December (Serra 1991; Arcos et al., 2001). In the spawning condition, the reproductive strategy of jack mackerel is to disperse over a large area off central Chile (30-40°S). This species has a spawning centered on the Subtropical Convergence Zone extending from Chile to between 150°W and 160°W, and characterized by small food, and warmer waters. In addition, because jack mackerel is fully mature at 3-4 years of age, and each mature female releases several batches of eggs during the reproductive season, it could be feasible to apply the Daily Egg Production Method (DEPM) to assess the spawning stock biomass (Lasker, 1985). In this contribution, the spatial spawning distribution, the relationships between jack mackerel eggs and habitat variables, and DEPM estimates of spawning stock biomass are discussed for jack mackerel on the basis of surveys carried out in oceanic waters off Chile during the main reproductive season from 1998 to 2001.

Data and methods

From 1998 to 2001, five surveys were carried out in the oceanic waters off central Chile using industrial fishing vessels, for determining the spatial distribution and abundance of jack mackerel eggs (Table 1). Surveys were conducted during the main spawning period for jack mackerel as determined from historical data. A pilot cruise was developed in 1998 with a systematic zig-zag tracking lines covering the wide spawning area. From 1999 to 2001, a regular grid of planktonic stations (separated by 18 nm) were carried out using a lineal-tracking design in the main spawning area (75°W-92°W) off central Chile by using 9-10 fishing vessels simultaneously in a 6-12 day period, producing a quasi-synoptic distribution of the jack mackerel spawning. In each cruise, WP-2 nets (0.6 m diameter, 0.33 mm mesh size) were used to collect planktonic samples by vertical tows. All jack mackerel eggs were sorted and counted (expressed by number of eggs/10 m$^2$). The environmental information corresponds to satellite-derived data for the spawning area (30-40°S; 75-92°W), considering the quasi-synoptical condition in eggs sampling. The environment variables are sea surface temperature (Pathfinder Program), wind (ERS and QuïSCAT), mean sea level anomalies (AVISO Program) and color (SeaWiFS). It was calculated thermal gradients, wind-derived parameters (speed and turbulence), and geostrophic velocities (Hormazábal et al., 2003).

Table 1. Sampling design for 1998-2001 surveys and cross-validation results for sectors and maximum number of points used during kriging.
Geostatistical techniques were used to describe the spatial structure of eggs distribution, to estimate the egg patches of jack mackerel, and mean egg density and precision. The spherical model was fitted according to the weighted least-square minimization criterion. Cross-validation was used to determine the number of sectors and the number of neighbouring points to be used in the interpolation by kriging. The geostatistical mean egg densities and precision (CV), were compared with the single arithmetic mean and CV. Also, bootstrap simulations were done to provide the possible biases in the single arithmetic mean and standard error. For exploring the relationships between eggs density and environmental conditions, data were analyzed using the cumulative frequency distribution method and Monte Carlo randomization for providing evidence of habitat-species association (Perry and Smith, 1994) and, the generalized additive model technique (GAM; Hastie and Tibshirani, 1990).

Results
The jack mackerel spawning took place on a huge oceanic area, with important high density egg patches covering several nautical miles. Spatial analysis of eggs showed an omnidirectional spherical variogram. The spatial continuity at short distances was solved with the range fluctuating between 143 and 250 nautical miles. The unsolved spatial continuity at short distances was very low (nugget < 36%), excepting for November 1998 survey (nugget of 43%). The cross-validation results are shown in Table 1. The mean egg density fluctuated between 372.1 and 734.9 eggs 10 m$^{-2}$ (14.35 - 2.49% CV). These estimates are comparable with the simple arithmetic mean and the bootstrap mean because of the high incidence of positive stations (>70%), although geostatistical estimates provided lower coefficients of variation. In general terms, for the 1999-2001 spawning period, the bulk of the jack mackerel spawning tends to occur offshore, from 80°W to 92°W. This is inferred from the most comparable surveys carried in November 1999, 2000 and 2001 (Fig. 1).

![Figure 1. Spatial distribution of jack mackerel eggs density (egg 10 m$^{-2}$) for 1998-2001 spawning period as a result of the spatially stochastic process by kriging.](image)

The daily egg production of jack mackerel have been estimated as 41.4, 24.9 and 35.3 eggs/m²/day for 1999, 2000 and 2001 surveys, covering a spawning area of 630101, 746786 and 531196 km², respectively. Egg production estimates were very precise because of the high incidence of positive stations (> 70%). Sampling of adults was difficult because jack mackerel tend to disperse and the aggregations are not detected for fishing in the spawning condition. In this way, reproductive parameters for appropriate DEPM estimates come from few sets. Nevertheless, batch fecundity, spawning frequency, sex proportion and average weight were estimated, allowing to estimate spawning stock biomass, which have ranged between 2.1 and 3.8 million t in the spawning area. These estimates of spawning stock biomass are representing a relative biomass index because
the offshore boundary of spawning has not been covered during the surveys, and because jack mackerel also spawned in other areas in oceanic waters off Chile. However, because the higher egg densities it is concluded that the study area represents the main spawning area of the jack mackerel stock. DEPM estimates of spawning stock biomass are completely feasible for Chilean jack mackerel, and estimates will be improved with each annual repetition. The survey design could be adapted to cover a greater area because the egg patches are covering several nautical miles, but it is absolutely necessary the collaboration of the fishing industry because such vast oceanic spawning area can not be sampled adequately by a single research vessel.

Exploratory data showed associations between eggs density and SST and wind-derived parameters distributions. Higher egg densities were found in oceanic waters in comparatively warmer waters (16-19°C), intermediates values of wind speed (3-5 m s⁻¹), low current speed (< 15 cm s⁻¹) and low thermal gradients (< 0.3°C 10 km⁻¹). The cumulative frequency distributions between eggs density and environmental parameters revealed a significant association between eggs and SST (p<0.01) and wind speed (p<0.05, except for 1998). Turbulence index and SST gradients showed significant values only for 1999 (p<0.05), and current speed for 2000 (p<0.01). In contrast, the distribution of eggs did not show a significant association with chlorophyll-α. According to the GAM, the best model included latitude, longitude and SST. In general, the jack mackerel egg density exhibits a nonlinear dome-shape relationship with latitude and SST, while egg density along the longitude showed a continuous increases (Fig. 2). It can be inferred that jack mackerel spawning is confined between 35 to 37°S and associated to SST between 16 and 19°C. The offshore boundary of the spawning was not solved during the surveys due to continuous increases in egg density with longitude. GAM’s results did not show clear relationships for wind- and current-derived parameters.

Figure 2. Partial regression plots of GAM explaining the jack mackerel egg density. Solid line is the fitted model and dashed line are 95% confidence intervals.
Acknowledgements
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References


SYNTHESIS OF EARLY LIFE-HISTORY DYNAMICS AND SPAWNING HABITAT CHARACTERIZATION OF SMALL PELAGIC FISHES IN SOUTH-EASTERN AUSTRALIA: PAST AND CURRENT RESEARCH

Francisco J. Neira

Australian Maritime College, PO Box 21, Beaconsfield, Tasmania 7270, Australia
(f.neira@fme.amc.edu.au).

Data on spawning, and larval fish distribution and abundance at various locations across south-eastern Australia are provided based on broad- and fine-scale ichthyoplankton surveys conducted in 1995-99 and 2002-03 using a ranges of samplers and sampling strategies. Aims of these surveys have been to locate spawning areas of key species, and to relate ichthyoplankton concentrations with hydrographic and hydrochemical data in an attempt identify retention areas and advection pathways. Broad-scale surveys have covered shelf waters along northern Bass Strait (BS) (455 nautical miles; nm), and southern Queensland (Qld)-northern Tasmania (Tas) (1,050 nm). Fine-scale surveys have been conducted within Port Phillip Bay (PPB), a and in an eastern Bass Strait area containing oil/gas production platforms (Esso Australia-BHP).

Fishery-independent and dependant surveys of PPB during 1994-97 showed that this large, semi-enclosed marine embayment in Victoria (Vic) is a spawning/nursery area for anchovy (Engraulis australis), and a nursery area for pilchard (Sardinops sagax). Larval anchovy ranked second in abundance (16.7%) after gobids (54.2%) during an intensive ichthyoplankton survey in 95/96 that yielded ~17,200 larvae from 32 families. Mean anchovy egg concentrations were markedly lower than in a survey in 83/84, indicating expected interannual variability. However, it was proposed that major ecosystem changes in the bay, particularly increased fishing pressure, and the introduction and establishment of exotic marine species, could have led some of the main differences between the 83/84 and 95/96 larval fish assemblages.

Vertically-stratified surveys in BS in summer (January, December 1997) and winter (May-June, July 1998) yielded ca. 24,900 larval fishes belonging to 96 families. Larval clupeids (mostly pilchard) and carangids (jack mackerel, Trachurus declivis) dominated in summer, while scorpaenids, morids and myctophids dominated in winter. The greatest larval fish concentrations and number of taxa were obtained during January and December 1997 at the western and eastern ends of BS, respectively. High concentrations in western BS in January 1997 were largely due to pilchard, and were associated with a coastal, wind-driven upwelling at that time; upwelling was evident from SSTs and density profiles, and was accompanied by a moderate subsurface enrichment of inorganic nutrients in the area. By contrast, high concentrations and diversity in eastern BS in December 1997 were explained by the greater abundance of estuarine and inshore rocky reef habitats, coupled with a southwest current flow and an inshore anticyclonic eddy (corrected shipboard ADCP data) which is likely to favour ichthyoplankton retention in this region; hydrodynamic modelling did predict average westward current flows along eastern BS over summer, reflecting the greater incidence of easterly winds during that period.

Pilchard larvae in western BS in January 1997 were caught mostly 2-16 nm offshore in 14.5-18.0°C water, from the surface to 75 m. Mean larval concentrations were significantly greater in 25-0 m than at the surface (P<0.05), while no significant differences were found with distance from shore. Jack mackerel larvae were caught during summer in western (January 1997) and eastern (December 1997) BS (14.5-17.5°C). Larvae in eastern BS were relatively more abundant 8-32 nm offshore, in the 25-0 and 50-25 m depth strata.

Intensive sampling around oil/gas platforms in eastern BS (February 1998, 1999, August 1998) yielded >1,500 larval and early juvenile fishes from 45 families and 55 taxa. Larvae of pelagic/
mesopelagic species dominated the catches, whereas larvae of reef-associated species normally observed amongst platform structures in the area were unexpectedly rare. Jack mackerel dominated in February 1999 and were the most abundant species caught (55.6%). Mean jack mackerel concentrations did not vary significantly between surface and oblique tows (P<0.05), suggesting that they were evenly distributed throughout the water column. Of the ca. 560 specimens measured (3.0-26.7 mm BL), 28% were preflexion/flexion larvae (<7.0 mm), 27% postflexion larvae (7-13 mm), and the remaining 45% transforming/early juveniles. The approximate age of these specimens (days after first feeding) was 2-40 d, with 42% in the 25-31 d (12-16 BL mm). Despite similar sampling efforts during the February 1998 and 1999 surveys, the notably greater abundance of jack mackerel in February 1999 was associated with a distinct upwelling in the area. Intense, short-lived upwelling events bringing cool (14-15°C) subantarctic water to the surface are persistent features in this area around February-March, and appear to be enhanced by topographic features such as the deep Bass Canyon, as well as strong currents around anticyclonic eddies derived from the warm (nutrient-poor), south-flowing Eastern Australian Current (EAC).

The markedly low incidence of fish eggs during the 1997/98 BS study prevented locating spawning areas of key species. However, the high larval fish concentrations in shelf waters at the extremes of BS would indicate that both regions may be important spawning areas. The latter observation is supported by the findings from the oil/gas platform surveys in eastern BS. Given the typically low productivity of BS, the two extremes regions can be considered as “hot spots” following increased summer productivity resulting from often intense, short-lived upwelling events. The presence of high concentrations of jack mackerel larvae in both regions during summer suggests the presence of distinct spawning stocks, i.e. western South Australia (SA) and southern New South Wales (NSW)/eastern Victoria -Tasmania.

Intensive sampling of eggs and larvae of blue mackerel (*Scomber australasicus*) is currently underway along shelf waters off southeastern Australia designed to evaluate the use of DEPM for spawning biomass estimation. Surveys between southern Queensland and the NSW/Vic border in October 2002 and 2003 (spring) showed eggs and larvae confined to shelf waters between 27.5°S (southern Qld) and 33.5°S (northern NSW), with few occurrences past the break (Fig. 1). No eggs or larvae were found south of 33.5°S in October 2002 or 2003. Greatest egg concentrations (eggs per 100 m$^3$) in October 2002 (240) and October 2003 (698) occurred 6.5 and 17.3 nm offshore, respectively, in northern NSW. Larval distributions mirrored very closely those of eggs in both surveys. Preliminary results suggest that blue mackerel spawns predominantly within the continental shelf, an observation supported by July-August 1986 data on spatial distribution of larvae from the same area. In addition, egg and larval distributions during October suggest a strong link between spawning and the EAC incursion, as shown by the fact that the southern limits of egg distributions both in 2002 and 2003 coincided with the southern-most extension of the EAC on those occasions (Fig. 1 and Plate 6, page xii).

In general, season(s) and location(s) of spawning of small pelagics in subtropical and temperate waters of south-eastern Australia are strongly linked to major oceanographic features such as the EAC and associated gyres, as well as localised coastal upwelling events that trigger episodic “hot spots”. For example, major summer/autumn spawning of pilchard occurs in a known wind-driven upwelling area off eastern SA, while summer spawning of jack mackerel off eastern Tas occurs in deep shelf break waters at the peak flow of the EAC. Moreover, few species appear to migrate north to sub-tropical waters to spawn during winter/early spring, and their larvae then transported back to temperate nursery areas via the EAC. In fact, the two major Australian boundary current systems, namely the EAC and the nutrient-poor, southward flowing Leeuwin Current on the west coast, are known to play an important role in the transport of early stages of fishes and subsequent recruitment in temperate waters. The lack of permanent upwelling zones in temperate Australia, coupled with the low nutrient (nitrates) levels in upwelled waters (<20% of those in world richest systems), explain the comparatively small fisheries for small pelagics (<20,000 t in 02/03) in that region.
Figure 1. Distribution of blue mackerel eggs along southeastern Australia during October 2002 (A) and 2003 (B). Mean SST images from sampling periods were provided by CSIRO Marine Research, Hobart.
**SPawning of Small Pelagic Species in New Zealand Waters**

Paul Taylor

*National Institute of Water and Atmospheric Research Ltd., New Zealand.*

New Zealand is a productive archipelago in the southwest Pacific with a rich marine fauna. The most valuable fisheries are for species like orange roughy (*Hoplostethus atlanticus*), hoki (*Macruronus novaezelandiae*), and snapper (*Pagrus auratus*). There has been little development of fisheries for small pelagic species. Only pilchard (*Sardinops sagax*) is targeted, with a commercial catch limit of 2000 t and a current total annual catch of about 1200 t. Other small pelagics are anchovy (*Engraulis australis*), sprat (*Sprattus antipodum, S. muelleri*), and garfish (*Hyporhamphus ihi*).

By contrast, well-developed purse-seine and trawl fisheries operate for larger schooling pelagic species like blue mackerel (*Scomber australasicus*), trevally (*Pseudocaranx dentex*), kahawai (*Arripis trutta*), and the three jack mackerels found in New Zealand waters (*Trachurus declivis, T. symmetricus, and T. novaezelandiae*), which support approximate annual catches of 13,000 t (blue mackerel), 3,000 t (trevally), 3000 t (kahawai), and 30,000 t (the three jack mackerels combined).

The oceanography of New Zealand is highly varied, offering a range of habitats for pelagic fish species. For example, the northeast coast of the North Island is a known spawning area for a number of species, providing a strong upwelling system under El Niño conditions. Sea-current systems are well documented and produce clearly defined, persistent mesoscale eddies that, in one case at least, is known for its role in entraining larval stages of rock lobster (*Jasus edwardsii*). Potentially, this feature could act as a spawning/nursery area for pelagic finfish species, although no information is currently available.

Little information is available on the biology of small pelagic species in New Zealand and, apart from several studies that collected what was often incidental information on spawning distributions of anchovy, pilchard, and sprat in one or two years, no work has been done to collect systematic information over an extended time frame. One study used ichthyoplankton sampling techniques to collect data and determine egg and larval distributions of sprat, but sampling in any area occurred only once and the presence of eggs and larvae may be confounded by the degree of offshore transport during the sampling period. Thus, results from these studies provide information useful in determining minimum spawning distributions for these species, but they are too restricted temporally to provide definitive spawning distributions.

Based on this information, anchovy show a preference for spawning in sheltered bays and sounds, such as the Hauraki Gulf, Tasman Bay, Bay of Plenty, and Fiordland (Fig. 1), but will spawn on exposed coasts and offshore neritic waters with spawning grounds extending out to mid-shelf in some areas. Spawning occurs in dense schools, where, it has been suggested, the seawater is slightly diluted. Spawning has been observed over the range 16°C to 20°C, peaking at about 19°C in the Hauraki Gulf.

Figure 1. Map of New Zealand showing locations referenced in the text.
Generally, spawning occurs from spring to autumn and has been observed year round in at least one location - larvae have been found in northeastern New Zealand throughout the year, with a major peak in February.

Pilchard spawning occurs in most coastal waters of New Zealand with spawning events the most intense in large sheltered bays and sounds like the Hauraki Gulf and Tasman Bay. Spawning occurs at night in waters between 14.7°C and 20.9°C with eggs taking approximately 56 to 58 hours to hatch at optimal temperatures. Spawning events are year round in northern waters, and in late spring and summer in central and southern waters. The Marlborough Sounds and Tasman Bay exhibited a spawning peak in December to January and peak spawning in the Hauraki Gulf occurred in November.

Spawning of sprat occurs extensively in coastal waters of the South Island. Only minor spawning has been recorded from the North Island. A series of plankton surveys of South Island coastal waters, excluding Fiordland, in 1973 to 1975, found what was then believed to be a single species of sprat (S. antipodum) present in most areas at some stage during the winter months. Subsequent separation into two species suggested the survey data would have included both S. antipodum and S. muelleri. The spawning season for both species combined has been described as extended (May to December, peaking between June and August), but it is possible that the season for each species is shorter. The eggs are pelagic and take about 4-6 days to hatch. The key spawning areas observed were from north of Banks Peninsula to Otago Peninsula and a region around Hokitika on the West Coast of the South Island.

During the mid 1980s, the carangid mackerel I. symmetricus invaded New Zealand waters after migrating across the South Pacific from South America. Recent work concluded that New Zealand conditions are favourable for the establishment of a self-sustaining stock of this species. Given the widespread distribution of prey species and highly adaptable feeding strategy, it is unlikely that food is limiting.

However, it is aspects of the reproductive biology that were particularly interesting. Sampling from sites throughout the geographic range of New Zealand waters and throughout the year showed that this species was most often in spawning condition and usually indicated a high predominance of males. Specimens taken from schools where T. symmetricus was mixed with the other two jack mackerels, showed all three species to be running ripe simultaneously, sometimes during winter, well outside the known spring-summer spawning season for I. declivis and T. novaezelandiae.
AN OVERVIEW OF THE APPLICATION OF THE DAILY EGG PRODUCTION METHOD (DEPM) TO MEDITERRANEAN ANCHOVY STOCKS

Stylianos Somarakis¹, Isabel Palomera², Alberto Garcia³, Luis Quintanilla³ and Constantin Koutsikopoulos¹

¹University of Patras, Department of Biology, Laboratory of Zoology, 26500 Rio, Patras, Greece (somarak@upatras.gr).
²Departament de Recursos Marins Renovables, Institut de Ciències del Mar (CMIMA-CSIC), P. Marítim de la Barceloneta, 37-49, 08003 Barcelona, Spain.
³Instituto Español de Oceanografía (IEO), Centro Oceanográfico de Málaga, Puerto Pesquero s/n. 29640, Fuengirola, Málaga, Spain.

The Daily Egg Production Method has been applied to Mediterranean anchovy stocks in the Catalan Sea-Gulf of Lions, the Ligurian-Tyrrhenian Sea (Garcia and Palomera, 1996), the Sicilian channel (Quintanilla and Garcia, 2002), the SW Adriatic (Casavola, 1998), the central Ionian and Aegean Seas (Somarakis et al., 2002) and the northern Aegean Sea (Somarakis, 2004) (Fig. 1, Table 1). These applications were largely experimental and often opportunistic with the main aim to develop and test the method rather than provide spawning stock biomass estimates for the assessment of the stocks. Consequently, the DEPM has been applied once or twice in each area with a maximum of three successive applications for the Sicilian channel anchovy (Table 1). There was not any among-area standardization in techniques and many methodological differences existed in several aspects of the method.

The main differences in methodology were the following:

1. Some applications did not cover the entire spawning area of the respective stocks (they rather covered a particular, however distinct, spawning center)
2. Some applications were based on opportunistic adult sampling (commercial rather than research samples were collected)
3. Applications in the northern Aegean Sea used oblique rather than vertical plankton tows
4. One or two daily classes of postovulatory follicles were occasionally used to estimate spawning fraction
5. In the eastern Mediterranean, both eggs and yolk sac larvae were used for the estimation of the daily egg production.

Figure 1. Areas of application of the daily egg production method in the Mediterranean Sea.
Table 1. Applications of the Daily egg production method to Mediterranean anchovy stocks. 

<table>
<thead>
<tr>
<th>Region</th>
<th>Year</th>
<th>Application code</th>
<th>Month</th>
<th>P₀</th>
<th>R</th>
<th>W</th>
<th>F</th>
<th>S</th>
</tr>
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<tr>
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<td>1990</td>
<td>CAT90</td>
<td>May</td>
<td>57.16</td>
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<td>4958</td>
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<td>4894</td>
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<td>June-July</td>
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Estimated DEPM parameters varied greatly between stocks and year of application (Table 1). For example, the daily egg production in the spawning area ranged from 8.88 to 109.22 eggs/m² and the spawning frequency from 0.06 to 0.36. Such variability is uncommon for pelagic species in upwelling areas (e.g. Alheit, 1993) as well as the European anchovy in the Bay of Biscay (Motos, 1996). An amount of this variability could be attributed to differences in methodology and standardization problems, yet, this explanation is difficult to test.

An alternative explanation would be that variability in biological production among sub-basins or among seasons/years directly affects anchovy egg production. In other words, the trophic environment of reproducing stocks could directly impact anchovy reproductive effort. For example, in comparing the DEPM parameters between 1993 and 1995 in the northern Aegean Sea, Somarakis (in press) showed that adult food availability (mesozooplankton) was much higher in 1993, when waters were significantly cooler and fresher. Concurrently, female anchovies were in better condition, producing numerous eggs at a higher spawning frequency. These observations were consistent with a ration-related reproductive tactic in European anchovy (Somarakis, 2004). Likewise, indicative of the environmental influence on reproductive potential of anchovy, was the unusually high rates of atresia and amount of inactive females in the Sicilian Channel DEPM applications. Some adult anchovy samples showed more than 40% of inactive females, especially during the 2000 anchovy peak spawning season, which was attributed to unfavourable environmental conditions rather than finalization of spawning (Quintanilla and Garcia, 2002).

Some interesting points emerge when comparing adult parameters from the more southern Mediterranean areas. These areas are inhabited by small stocks with contagious distributions and are largely oligotrophic, receiving the influence of only small rivers. It is worth-noting the remarkable difference in batch fecundity between the central Aegean and Ionian stocks in 1999 (Table 1). However, the interplay of fecundity and spawning frequency seemed to eventually condition anchovy reproductive effort since the spawning frequency estimates showed an opposite trend (Aegean Sea: 0.15, Ionian Sea: 0.06) and resulting values for daily specific fecundity were almost equal for the two seas (about 18 eggs per gram of reproducing stock).
In comparing the correlation between the estimates of the daily egg production ($P_0$) and respective estimates of the daily specific fecundity (DSF) for the Mediterranean and the Bay of Biscay, a significant isometric relationship emerges (Fig. 2). The relationships for the Mediterranean and the Atlantic do not differ statistically and the pooled model has an exponent that equals 1 (t-test, $P>0.05$) explaining about 61% of the variation in the data. An isometric relationship between $P_0$ and DSF in European waters implies a density dependent use of the spawning habitat by the anchovy spawners. This has already been shown for the Bay of Biscay anchovy in which a strong linear relationship exists between the spawning stock biomass and spawning area (Uriarte et al., 1999).

The empirical relationships suggest that anchovy tend to maintain an upper level of spawning stock density in European waters. It seems likely that when biomass per unit area of the stocks in the main spawning grounds exceed a certain threshold (most possibly related to the trophic capacity of the European spawning grounds) fish tend to spread over a larger area in order to avoid intraspecific interactions, such as trophic competition and/or egg cannibalism.

**References**


IS THE DAILY SPAWNING FRACTION DEPENDENT ON FEMALE SIZE?

Gabriel Claramunt\textsuperscript{1}, Ruben Roa\textsuperscript{2}, Pedro Pizarro\textsuperscript{1} and Rodolfo Serra\textsuperscript{3}

\textsuperscript{1}Departamento de Ciencias del Mar, Universidad Arturo Prat, P.O. Box 121, Iquique, Chile. (gclaramu@unap.cl).
\textsuperscript{2}Departamento Oceanografía, Universidad de Concepción, Concepción, Chile.
\textsuperscript{3}Instituto de Fomento Pesquero (IFOP), Valparaíso, Chile.

Histological evaluations of ovarian tissues of \textit{Engraulis} indicate a daily spawning fraction (DSF) of 0.16 day\textsuperscript{-1} during peak spawning months (approximately once a week). Hunter and Macewicz (1980) found no relationship between size and percentage of mature female northern anchovy containing day\textsuperscript{-1} postovulatory follicles (DSF). However, Picquelle and Hewitt (1984) showed that female weight and spawning incidence were highly correlated in the northern portion of the central stocks range. They stated that this implied the larger females spawned more frequently or that the smaller females had a much shorter spawning season.

There are other studies that indicate dependence of spawning periods on female size: \textit{Engraulis mordax} (Parnsh et al., 1986), \textit{Sardinops ocellatus} (Le Clus, 1989), \textit{Seriphus pollitus} (DeMartini and Fountain, 1981), \textit{Clupea harengus} (Lambert, 1987), \textit{Gadus morhua} (Marteinsdottir and Thorarinsson, 1998), and \textit{Sardinops sagax} (Claramunt et al., 1994). However, the relationships between female size and DSF has not been established and in general this effect has been ignored. For comparative purposes the temperature in different habitats appears as the only factor that could influence spawning rate differences, because it is known that higher temperatures can accelerate postovulatory follicle degeneration (Fitzhugh and Hettler, 1995).

The problem is that the information concerning size-specific spawning fraction has not been available because it is estimated through the proportion of females with postovulatory follicles, which is a time-consuming and biologically intensive histological methodology that can only be applied on samples obtained over short periods and regardless of age or size structure. We have found only one study in the literature that clearly demonstrates the relationship between daily spawning fraction and length, this is Schaefer’s (1998) paper on \textit{Thunnus albacares} where the author fitted a von Bertalanffy equation, implying that the DSF increases to an asymptote.

Claramunt and Roa (2001) developed a theoretical and statistical argument for a new method, previously outlined by Claramunt and Herrera (1994), which utilizes the gonadosomatic index to estimate the daily spawning fraction and applied it to \textit{Sardinops sagax}. A consequence of this approach is that the DSF is dependent on female size (Fig. 1), but until now this prediction has not been tested.

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{Figure1.png}
\caption{Daily spawning fraction (DSF) estimated from Claramunt and Roa (2001) methodology by size strata. A long term (1975 to 1996) estimation for August (peak of spawning) is presented for \textit{Sardinops sagax} from northern Chile.}
\end{figure}
In addition to its biological importance the spawning rate is a key component for estimating the spawning biomass of small pelagic fishes through the daily egg production method (DEPM).

In this work we review the relationships between DSF and female size for Engraulis ringens, using the information derived from the DEPM applied in northern Chile (1995 through 2002). We also discuss the results from DEPM applications in different Engraulis species.

The results of the DEPM applications on E. ringens in Chile suggest that the DSF increases with average weight of mature females; although they are overall mean weights for each survey (Fig. 2). These relationships can be fitted with the following asymptotic model (Table 1):

$$Y_x = Y_\infty \left(1 - e^{-K(x-x_0)}\right)$$

Where $Y_x$ = daily spawning fraction at length $x$, and $Y_\infty$, $K$ and $x_0$ are parameters

The average female weight from DEPM could be influenced by the size structure in the samples of each survey. To discount the last effect we constructed a data base for anchovy females including all DEPM applications (1995 through 2002) in northern Chile, totalling 9,034 females. The sizes were aggregated in strata of 0.5 cm of total length and daily spawning fraction for each stratum was recalculated and an asymptotic relationship appears and the same model can be fitted (Table 1).

<table>
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Figure 2 shows the DSF and the average female weight from results of DEPM applications on different species of Engraulis. A dependence of DSF on average female weight is observed in all species, except for the Peruvian anchovy stocks that show a different tendency. An important aspect to take account of in this analysis is the assumption that DEPM is always applied during the peak of the spawning season. This assumption is very important because DSF has temporal variation. The dispersion around the general tendency could probably be explained by different temperature, growth rates, maximum size or weight reached by the different species or populations and/or habitats.

**Figure 2.** Daily spawning fraction and average female weight relationship come from daily egg production method applications in Engraulis species.


*E. ringens Peru*: Santander et al., 1984; Santander and Maldonado 1985; Guzmán et al., 1995; Ayón, 1996.


*E. anchoita*: Sánchez et al., 1996.
In general it is recognized that the DSF of females could be affected by the temperature of the environment (Fitzhugh and Hettler, 1995). Therefore, it has been recommended to investigate the temperature effects on this parameter. However, the effect of the size of the females has been ignored. The results obtained in this present study indicate that the larger females have a higher spawning frequency. Future comparisons of the DSF among years need to include the size structure of the stock of females for each year. In addition, this size dependent effect has important consequences on the stock. Changes in the size or age structure of the female population could have a huge impact on the estimated annual potential egg production.

Acknowledgements

Partial support was provided by the Fondecyt Project # 1030819.

References


EFFECT OF MAJOR ATRESIA ON THE EGG PRODUCTION OF PACIFIC SARDINE (SARDINOPS CAERULEUS) OF BAHÍA MAGDALENA IN THE 1999-2000 SEASON

J. René Torres-Villegas\textsuperscript{1}, Liduvina Perezgómez\textsuperscript{1} and Gustavo García-Melgar\textsuperscript{1}

\textsuperscript{1}Laboratorio de Morfofisiología. CICIMAR-IPN, La Paz BCS, Mexico (jvillega@ipn.mx).

Pacific sardine is an iteroparous species that develops on synchronised intraovaric oocytes. As occurs in many fish species, active germinal epithelium is present along the reproduction season, which indicates production of new sexual cells while the reproductive season advances. Polymodal diameter distribution of the oocytes in the ovary happens in the Pacific sardine. Often, a small fraction of oocytes stops their development and reabsorption occurs; this process is called atresia. In some species, presence of high atresia incidence justifies corrections in batch fecundity assessment. Atresia incidence in Pacific sardine spawning season has been documented to be around 2%. When this frequency reaches 5%, it is associated with the end of the spawning peak. Atresia major occurs after the reproductive season and indicates the end of the spawning season. Atresia major can be related to the suspension of spawning, from the first stages of maturity until spawning by the reabsorption of mature oocytes to low temperatures and nutritional conditions or starvation. Other conditions associated with stopping spawning are overcrowding and change in the sexual ratio, and pollution. Because in Bahía Magdalena a high incidence of Pacific sardine below the size of first maturity (< 150 mm) was recorded early in the fishing season 1999-2000. Research was done to establish the effect that this would have on the spawning season. The subject of this paper was to establish a reproductive status in the Pacific sardine population, and the possible inhibition of reproduction, using a histologic analysis in ovaries.

Monthly samples of Pacific sardine were taken during the 1999-2000 fishing season, on board a commercial sardine fleet of Bahía Magdalena. 70 to 100 sardines per fishing tow were sampled. Because Pacific sardine reproductive peak occurs between December and April sampling was increased as weather allowed. The field and laboratory procedures were described in Hunter and Macewicz (1985). All sampled specimens between December and April were analysed by histological methods. From 2,498 specimens, histological studies were done on 1,882 fish. To calibrate the monthly monitoring of Gonadosomatic Index (GSI) and Gonadoc Relative Index (GRI) outside of the spawning season, sub-samples of 20 specimens taken at random were histologically analysed. The samples were embedded in paraffin and slices between 0.003 and 0.005 mm thick.

Figure 1. Mean value ± standard deviation of the Gonadosomatic Index (GSI) in 2000 year (A). Seasonal analysis of the monthly mean GSI time series from October 1980 to December 1991 (B).
were made. Hematoxyline–Eosin, Mallory’s trichrome, or Van Gieson alternative techniques were used to stain slides. Frequency of atresia was recorded as females with some stage of oocyte re-absorption, which can be one atretic follicle in the exploration of the histological slide. Atresia major and atresia stage are oocyte re-absorption. But atresia major is a generalised process in the ovary, it shows that different stages of atresia may be found in a microscope field. Atresia stages are isolated re-absorption at low frequency. The morphological criteria used for the histological diagnosis are based on descriptions of pre-spawn and postovulatory stages in Fundulus fundulus, Engraulis encrasicolus and Sardinaes caeruleus. The atretic stages were identified with the criteria of Lambert (1970) and Hunter and Macewicz (1985). The active female frequency (Hunter et al., 1992) was used as an indicator of the spawning intensity in the season.

Juvenile specimens were recorded in December, and active females were not recorded. Adults were present in January. GRI and GSI indicated that the winter reproduction peak was attenuated in the season 1999-2000. The histological analysis of the ovaries showed the spawning season 1999-2000 began in January and ended in March. Active females frequency peak in this spawning season was in January, in February it declined, in March reabsorption was increased and the active females frequency was insignificant. Atresia was present frequently from January on yolked oocytes. Atresia major was recorded with frequently in February. In April, the reproductive activity had finished completely. In this study we found 7 fish with postovulatory follicles. Then only a few females reached spawning in the season. Because of the low frequency of postovulatory follicles, spawning frequency was not assessed.

A monthly time series of active female’s frequency along 10 years in Bahia Magdalena (Torres-Villegas et al., 1995) indicate that the Pacific sardine spawning season has a peak between December and April. During this period the frequency of active females ranges between 95 and 100%. A second peak of spawning of low intensity is described during June and July that is recorded irregularly and active females frequency range between 15 and 50%. The length of spawning season can be between 4 to 8 months.

Results of Pacific sardine reproduction during the 1999-2000 season indicate that spawning was reduced strongly in winter, and the maximum of the active female frequency was near half of the usual value for this season. On the other hand, the atresia incidence was premature in the season. We conclude that spawning season was terminating early and active females frequency was short. It is difficult to define the causes of reproduction to stop because atresia incidence is poorly documented in marine fish. We discuss environmental effects on atresia occurrence and conclude that an egg production disruption occurs in 1999-2000. We discuss the possibility of the egg production in the spawning population as a mechanism to drive the population size.

References


Sardine and anchovy reproduction includes asynchrony and spawning by batch. Methods to assess batch fecundity are counting hydrated eggs or oocytes of the most advanced modal group. The first method assumes that batch fecundity is defined when oocytes are hydrated or in migratory nucleus stage (Hunter et al., 1992). Hydrated or migratory nucleus eggs, appear just before spawning, then recruitment or loss of oocytes to the next spawning group are not significant (Hunter et al., 1985). Picquelle and Stauffer (1985) recommend the most advanced modal group technique only when the number of hydrated females is insufficient. Some cytological and histological changes in the oocyte and in the follicle might be associated with the physiological state prior to hydration. In the Pacific sardine, the granulosa layer formed changes to a columnar epithelium with mucous secretion when the oocyte group of the next spawn ends the secondary growth stage. Torres-Villegas et al. (2000) proposed that these categories might be a good index for assessing batch fecundity of Pacific sardine. The subject of this paper is to test if individual batch fecundity is defined in some step of the mature stage of the oocyte, before maturity ends, and diameter of the most advanced modal in the Pacific sardine (Sardinops caeruleus).

Sampling was done on board the commercial fleet based on Guaymas, Sonora, Mexico in 1984, 1986 (with determinations in November and December), 1987, 1988, and 1991. We sampled 100 specimens per tow during capture on 152 fishing tows. The schedules of commercial catch did not include time between 1100 and 2300. Gonads were removed in the laboratory, and morphometric variables were recorded for each fish. Histological process was applied to ovary, cuts by paraffin 5 µm thick were obtained and coloured by different techniques. The microscopic analysis was made using descriptions of postovulatory follicles; atretic and the oocyte development stages. Batch fecundity was estimated in sardines active females follow the criteria: a) females with gonadosomatic index (GSI ≥ 6.0); b) females without postovulatory follicles or major atresia at any age; c) those females of the most advanced largest oocyte modal group. Individual batch fecundity was calculated from three sub-samples of ovarian tissue without capsule by average to total weight of the ovaries.

The mature female group was post-classified using histological features of the stages of oocyte development. The diagnostic features in categories were (a) follicles with columnar epithelium in the granulosa layer. (b) Oocytes with initial yolk proteolysis and oil drop formation, which is seen as small vacuoles around the nucleus. (c) Nuclear membrane dissolved and the germinal vesicle in migration toward the animal pole, and (d) hydrated oocytes in the ovarian stroma. The group of mature sardine females was 7477 as independent result of both analyses. Finally they were compared with a Kruskal-Wallis test, where groups were morphological categories. Because of the possible variations in fecundity among assessments, this analysis was made separately for each sampling.
We find in the first classification 4532 fish were mature non-spawning females. But in the post sampling we found the same group of mature fish. No hydrated females were found in these samples for all periods. Although hydrated oocytes were recorded in some ovaries near spawning with day-zero postovulatory follicles; these females were rejected. The proportion of females with a migratory nucleus was too small, but by adding females in the other two categories, non-spawning mature females were increased. The high frequency columnar epithelium and initial yolk proteolysis, and formation of die oil drop, corresponds to 24 hours. The females with migratory nucleus oocytes were recorded between 20:00 and 11:00 hours the next day. The duration of migratory nucleus oocyte and hydrated egg stages together are then approximately 24 hours. The time from the appearance of the columnar epithelium until the appearance of hydrated eggs was approximately 72 hours.

A progressive increase was observed in the diameter of oocytes during the columnar epithelium, initial proteolysis, and migratory nucleus phases, and this difference is more important during the last two phases. This corresponds to the characteristic volume increase in the ooplasm when finishing vitellogenesis, and reaching maturity and hydration, and indicates a more rapid change in cellular volume during these stages, possibly related to hydration of the oocyte.

To investigate differences in individual batch fecundity among morphological categories, a Kruskal-Wallis test was done by sampling. We have found no significant differences among morphological categories (Fig. 1). Our results suggest that the group of oocytes of the next spawning is defined at the time the follicles show a columnar epithelium in the granulosa layer, 72 hours before spawning.

In the extensive sampling done for this work, hydrated females and specimens with migratory nucleus oocytes appeared with a low frequency. We believe the maximum incidence of hydrated females occurs during the period without samples. Histological descriptions have especially stressed the postovulatory phases because, based on this stage, spawning frequency is calculated as a parameter of the daily egg production method to assess spawning biomass. With the information available on postovulatory phases of the Pacific sardine (Torres-Villegas, 1986), ovarian follicle development apparently occurs about 75 hours before and after spawning. Hunter et al. (1985) proposed that estimates of batch fecundity obtained using both hydrated and migratory nucleus eggs are equivalent. Based on this supposition, they found that batch fecundity is defined by the oocyte 24 hours before spawning. However they do not discuss when the definition of batch fecundity occurs. Our results show that individual batch fecundity, assessed in any of the three proposed categories, yields equivalent values.

Figure 1. Results of the Kruskal-Wallis test for individual batch fecundity, groups are steps of the oocyte final maturity stage for the 1986 sampling. Granulosa layer with columnar cell (a), proteolysis and oil drop formation (b) and migratory nucleus.

Therefore, the oocyte group that constitutes the next spawning can be recognised when columnar cells appear in the granulosa layer. This histological information suggests that undefined fecundity could be defined in a stage before hydration. If this is true, several oocyte groups that would be spawned in independent events could be defined in the ovarian stroma. It would then be possible to assess batch fecundity of the Pacific sardine with more fish, not necessarily only females with both migratory nucleus and hydrated eggs. Another consequence is the increase in sampling period, from 24 hours for migratory nuclei and hydrated females, to 72 hours using our approach.
This way it becomes possible to use samples obtained from the commercial fleet sampling of hydrated females. When yolk proteolysis begins, followed by nucleus migration, the increase in diameter accelerates. Therefore, the threshold diameter could be used as an additional criterion in the selection of females to estimate batch fecundity, although it would be necessary to interpret its meaning appropriately, particularly if changes occur in the diameter of the oocyte during spawning season or among years. We conclude that the proposed morphologic criteria cannot be used directly for other species because the criteria are based on the specific characteristic morphology of the Pacific sardine. Histological approaches of this type can then be developed for other species, based on knowledge of their daily spawning cycle.

**References**


In order to assess spawning biomass of *Engraulis mordax* using daily egg production method, from 1991 to 1994 adult were collected along the both Gulf of California coasts according to the Small Pelagic Fishes National Program station plan (Line 140 to Line 430; Fig. 1), during four research trawl surveys in the peak spawning season.

Trawls were made wen anchovy schools were detected by video echo sounder, following the sampling criteria described by Picquelle (1985). The sea-surface temperature was recorded for each trawl.

At each station anchovies were randomly sampled from the catch. Up to 50 fishes collected were sexed, and standard length was measured to the nearest millimeter and individually weighed to the nearest gram at time of capture. Gonads were removed from the first 5 males and 25 females in each sample and preserved in 10% phosphate buffered formalin. Additional fish were selected after the random sample in order to increase the number of fecundity samples, but were not used to estimate spawning frequency. In the lab, a piece of each ovary was removed and processed for histological analyses with a traditional technique. All slides obtained were analyzed and classified; batch fecundity was estimated using female ovariess female with both hydrated oocytes and migratory nucleus oocytes stages (Wallace and Selman, 1981; Hunter and Macewicz, 1985; Hunter *et al.*, 1985).

For each year several parameters were estimated from reproductive adults: the mature female weight, the batch fecundity, the sex ratio, the spawning fraction and the variances and co-variances respectively using the Egg Daily Production Method (Piquelle and Stauffer, 1985).
The temperature incidence in the Gulf of California on all reproductive parameters of anchovy and their variability during the research was relevant and the effect El Niño in 1992, principally in the batch fecundity and spawning fraction was observed (Figs. 2 and 3) which had an important role in the biomass assessment each year.

References


TEMPERATURE-DEPENDENT DEVELOPMENT RATE OF EGGS OF THE SOUTHERN ANCHOVETA ENGRAULIS RINGENS

Samuel A. Soto¹, Gabriel Claramunt¹, Ruben Escribano²

¹Departamento de Ciencias del Mar, Universidad Arturo Prat, P.O. Box 121.
Iquique, Chile (ssoto@unap.cl).
²Center of Oceanography for the Eastern South Pacific (COPAS), Universidad de Concepción, Chile.

The development rate of fish eggs before they hatch as yolk-sac larvae is strongly dependent on environmental temperature. The temperature-development rate can have profound ecological implications for fish populations, because it will determine the rate at which larvae are supplied to the planktonic environment, as well as the extension of time over which the eggs are exposed to all sources of egg mortality, including predation.

In addition to its ecological importance the temperature-dependent development rate of eggs is a key component for estimating the spawning biomass of small pelagic fishes through the daily egg production method (DEPM). This method mostly applied for anchovy populations uses the survival curve of eggs in field conditions to derive the daily production of eggs. In northern Chile, the DEPM has been applied since 1992 to assess the northern stock of the *Engraulis ringens*.

In order to construct the egg survival curve the age of the eggs from spawning needs to be estimated from field temperature at time of sampling. Thus, egg age as a function of temperature is to be known. This function has never been established for *E. ringens*, so that the equation derived for *E. mordax* has been currently used. Although both species may exhibit some ecological similarities, because they inhabit similar coastal upwelling systems, it is not known if egg development rates respond in the same manner to temperature.

In the last three years adult *E. ringens* have been maintained under controlled conditions at the Ciencias del Mar laboratory in northern Chile. Induced spawning has been successful on several occasions. This allowed us to have fertilized eggs at age “0” and hence provided the opportunity to study the egg development of *E. ringens* under controlled conditions of temperature. In this work, for the first time we report the temperature-dependent development rate of *E. ringens* eggs from spawning to hatching and analyze the temperature-development rate function as compared to that previously derived for *E. mordax*.

Three experiments were performed corresponding to three different spawnings under same conditions. The first experiment was carried out in December 2000, the second in January 2001 and the third one in March 2001. For all of them the spawning took place at about midnight. Incubation temperatures were 12, 14, 16, 18, 19 and 20°C (±0.2°C). Once the adults spawned, 400 viable eggs were chosen for each thermoregulated bath.

Observed ages for each stage at all temperatures are shown in Table 1. In the first and second experiments the eggs incubated at the low temperature of 12°C only reached stage IX, but a complete development at this temperature was obtained in the third experiment. The effect of temperature on egg development rate is remarkable, resulting in 1.4 days and 3 days required for complete development at 20°C and 12°C respectively. There was also some variability between experiments, although one-way ANOVA showed not significant (F = 0.203; F₀.05,1,2,158 = 3.053; P = 0.82) differences between the three experiments. Therefore temperature-dependent models for egg development were fitted using pooled data from the three experiments.
Table 1. Observed age for each stage at all temperatures.

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</table>

The exponential model, $y = ae^{bt}$, where $y_i$ is the age of anchoveta eggs of the i-stage at a temperature $t$ (°C) and $a$, $b$ are parameters, was first fitted separately for each stage. Parameters from the regressions are shown in Table 2. The parameter $b$ increases through the stages, exhibiting three distinct phases. After log-linear transformation of equation 1, and pooling all data, an ANCOVA indicated significant differences among the regressions revealing that $b$ does not hold constant through stages ($F = 4.86; F_{0.05,14,10.13} = 1.86$).

The second model that includes both temperature and stage of development (Lo, 1985) contains four parameters, $y = a e^{(b+ct)}t^d$ was fitted and its results are shown in Table 3.

Table 2. Parameters for the exponential model.

<table>
<thead>
<tr>
<th>Stage</th>
<th>$a$</th>
<th>$Sa$</th>
<th>$b$</th>
<th>$Sb$</th>
<th>$R^2$</th>
<th>SSE</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>6.693</td>
<td>1.2164</td>
<td>0.063</td>
<td>0.01184</td>
<td>0.68</td>
<td>1.3812</td>
<td>15</td>
</tr>
<tr>
<td>II</td>
<td>16.893</td>
<td>1.5580</td>
<td>0.054</td>
<td>0.0059</td>
<td>0.87</td>
<td>2.9254</td>
<td>15</td>
</tr>
<tr>
<td>III</td>
<td>33.298</td>
<td>4.5463</td>
<td>0.067</td>
<td>0.0089</td>
<td>0.82</td>
<td>17.1461</td>
<td>15</td>
</tr>
<tr>
<td>IV</td>
<td>57.111</td>
<td>7.3890</td>
<td>0.081</td>
<td>0.0086</td>
<td>0.88</td>
<td>29.0796</td>
<td>15</td>
</tr>
<tr>
<td>V</td>
<td>77.450</td>
<td>7.3395</td>
<td>0.083</td>
<td>0.0063</td>
<td>0.94</td>
<td>26.7544</td>
<td>15</td>
</tr>
<tr>
<td>VI</td>
<td>97.756</td>
<td>8.9860</td>
<td>0.083</td>
<td>0.0061</td>
<td>0.94</td>
<td>40.8525</td>
<td>15</td>
</tr>
<tr>
<td>VII</td>
<td>125.022</td>
<td>13.8595</td>
<td>0.085</td>
<td>0.0074</td>
<td>0.92</td>
<td>90.1192</td>
<td>15</td>
</tr>
<tr>
<td>VIII</td>
<td>149.028</td>
<td>19.4340</td>
<td>0.086</td>
<td>0.0087</td>
<td>0.89</td>
<td>173.5895</td>
<td>15</td>
</tr>
<tr>
<td>IX</td>
<td>218.358</td>
<td>24.4820</td>
<td>0.102</td>
<td>0.0072</td>
<td>0.95</td>
<td>86.7020</td>
<td>13</td>
</tr>
<tr>
<td>X</td>
<td>246.644</td>
<td>24.4292</td>
<td>0.105</td>
<td>0.0064</td>
<td>0.96</td>
<td>78.1558</td>
<td>13</td>
</tr>
<tr>
<td>XI</td>
<td>261.600</td>
<td>21.2603</td>
<td>0.106</td>
<td>0.0052</td>
<td>0.97</td>
<td>57.6306</td>
<td>13</td>
</tr>
</tbody>
</table>

E. ringens distribute in coastal waters in temperate/warm environments and the population inhabits temperate/warm environments. Its development in cold waters in central/south of Chile (ca. 12°C) could be in the lower limit of tolerance (Tarifeño and Carmona, 2001). Off northern Chile E. ringens spawning may be triggered by low temperatures, associated with upwelling plumes (Escribano et al., 1996). In E. mordax, however a decline in egg density is related to temperatures lower than 13.5°C (Fiedler, 1983; Smith and Hewitt, 1985). Carmona et al. (2001) compared the results for E. ringens in the south of Chile (Iquique, 36°S), with those obtained by Escribano et al. (1996) in the north (Antofagasta, 23°S), finding that development was slower in the south at 30% at 20°C, 24% at 15°C and 14% at 11°C.
Table 3. Parameters for the second model.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Value</th>
<th>S</th>
<th>SSE</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>a</td>
<td>9.811</td>
<td>0.9778</td>
<td>845.323</td>
<td>159</td>
</tr>
<tr>
<td>b</td>
<td>0.094</td>
<td>0.0023</td>
<td></td>
<td></td>
</tr>
<tr>
<td>c</td>
<td>0.071</td>
<td>0.0138</td>
<td></td>
<td></td>
</tr>
<tr>
<td>d</td>
<td>1.632</td>
<td>0.0972</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The temperature range during the period of maximal reproductive activity in the northern area is between 14 and 17°C, whereas in the southern area this is 11° to 13°C. Therefore the differences in development rates between both populations may be reflecting temperature adaptation. Escribano et al. (1996) suggested that development rate of *E. ringens* is lower than that of *E. mordax*. However, the ages estimated by Lo (1985) for *E. mordax*, indicate that development rate of eggs of *E. ringens* in northern Chile are faster in according to our study (Fig. 1). Kamler (1992) pointed out that interspecific differences in development of eggs are probably very small to be detected. However, caution should be taken to make these comparisons, because variations may be reflecting differences in the experimental methods. In our experiments the tested eggs were obtained from laboratory adults, such that age “zero” is not subjected to error, so that we were able to obtain absolute ages.

![Figure 1. Temperature-dependent development rate of anchovy eggs.](image)

**References**


TEMPERATURE-DEPENDENT EGG-DEVELOPMENT MODELS FOR STRANGOMERA BENTINCKI AND ENGRAULIS RINGENS IN THE AREA OFF CENTRAL-SOUTH CHILE

Aquiles Sepúlveda¹, Luis Cubillos⁴*, T. Mariella Canales, Doris Bucarey, Andrea Rojas

¹Instituto de Investigación Pesquera. Casilla 350, Talcahuano, Chile *(lcubillos@inpesca.cl).

Eggs of common sardine, Strangomera bentincki, and anchovy, Engraulis ringens, were collected from plankton samples taken from the coastal zone off Coliumo Bay (36°32'S; 72°57'W) during the spring spawning season of both species. In the laboratory, eggs were incubated at constant temperatures ranging from 10 to 18°C. The average observed age (in hours) of eggs for eleven embryonic stages was temperature-dependent and described by exponential functions, and a combination of exponential and potential function described the development curves at a given temperature. A combination of the previous models into a single model according to Lo (1985), explained very well all existing data available for each species. The estimated age of eggs through the development models obtained for E. ringens and S. bentincki were compared with the estimated ages of E. mordax through an ANOVA test. There were significant differences between the models of both species with E. mordax, but the development of E. ringens eggs was most close to the model of S. bentincki.

Reference
A TEMPERATURE DEPENDENT MODEL OF YOLK SAC LARVAL DEVELOPMENT AND THE EFFECTS OF THE ADDITION OF YOLK SAC LARVAE DATA ON THE ESTIMATIONS OF $P_0$ IN THE DEPM

Katty Riquelme$^{1,2}$, Alejandra Llanos$^1$, Luis Cubillos$^2$ and Leonardo R. Castro$^1$

$^1$Laboratorio de Oceanografía Pesquera y Ecología Larval (LOPEL), Departamento de Oceanografía, Universidad de Concepción, Casilla 160-C, Concepción, Chile.

$^2$Instituto de Investigación Pesquera (INPESCA), Casilla 350, Talcahuano, Chile.

The estimation of $P_0$ in the Daily Egg Production Method (DEPM) is based on the assignation of egg ages (after staging) utilizing a temperature dependent model of egg development (Lo, 1985). In order to improve the estimates of $P_0$ of the anchoveta *Engraulis ringens* in its southern spawning area, we increased the range of the dependent variable, adding the age frequency data of yolk sac larvae to the regular staged egg data obtained from the samples collected during the August 2002 DEPM survey. To age the yolk sac larvae collected from the field, we developed a temperature dependent model from larval rearing experiments in the laboratory (Plate 7, page xiii). This model incorporates the ratio between the yolk sac length and larval length ($R^1$). The viability of using this model is given by: $R^1$ varies non-linearly with time, $R^1$ is sensitive to temperature changes, there is a minimum variation in body proportions after preservation and is easy to measure. Previous studies in this spawning area reported anchoveta egg durations ranging from 2.4 to 3.9 days at temperatures between 18 and 11.5°C (Sepúlveda, 2000). The yolk larval duration estimated from our rearing experiments varied from 3 to 5.2 days at temperatures between 18 and 12°C (Llanos and Castro, in press). Thus, the entire age frequency data obtained was prolonged by a factor of about 2.3 by adding the yolk sac larval duration to the egg duration at both, the upper and lower temperatures (Fig. 1). We looked for potential differences in $P_0$ with and without yolk sac larvae data for the entire area, and also we split the data set from the entire area into two zones: a southern zone (37°10’S-40°00’S) where the peak egg density occurred and hence where we expected a larger number of yolk sac larvae and a wider age frequency distribution, and a northern zone (35°20’S - 37°10’S) where fewer eggs were collected.

![Figure 1. Eggs and yolk-sac larvae abundance for *E. ringens*, in relation to age, for the total area (central + southern zone).](image-url)
Our results show: a) the daily egg production \(P_0\) which was estimated by adding the yolk sac larvae data was higher in the southern zone (35,032 eggs/0.05 m\(^2\)/day) than in the central zone (15,17 eggs/0.05 m\(^2\)/day). This difference in \(P_0\) was also observed in the estimates without the addition of the yolk sac larvae data. The overall mortality rates obtained by combining both age frequencies (eggs and yolk sac larvae) were similar between areas. Therefore, the higher \(P_0\) and number of egg and larval survivors occurring in the southern area resulted from a higher initial egg abundance, that was influenced partially by an increase in egg concentrations close to the coast due to the predominance of northern winds, characteristic of the winter spawning season (Castro et al., 2000). b) Within a same area, no differences occurred between \(P_0\) estimated from the staged egg frequency data and from the egg and yolk sac larvae combined. However, a reduction in the variation coefficient (CV) for \(P_0\) was detected in each zone when the yolk sac larvae data were included (ca. 16% reduction). Also, we found a reduction of the CV for the biomass estimates (11% reduction) (Table 1). Similar results were obtained when the egg and yolk sac data from both zones were pooled. Consequently, the incorporation the yolk-sac larvae data improves the precision of the \(P_0\) estimates. c) The egg data (from north and south) and the yolk sac larvae data show that the egg mortality rate was higher than the yolk-sac larval mortality. Consequently, there is an increase in survival from the egg to the larval stage, as usually reported in the literature.

### Table 1. \(P_0\) estimated, and its CV, with and without yolk sac larvae data. Also, the biomass estimates are given, with their respective CV.

<table>
<thead>
<tr>
<th>(P_0) (eggs 0.05 m(^2) dia(^{-1}))</th>
<th>(P_0)</th>
<th>Std. Err</th>
<th>Var</th>
<th>CV (P0)</th>
<th>Biomass (ton)</th>
<th>CV (B)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eggs</td>
<td>27.9</td>
<td>6.84</td>
<td>46.80</td>
<td>0.25</td>
<td>205,781</td>
<td>0.28</td>
</tr>
<tr>
<td>Eggs + larvae</td>
<td>24.8</td>
<td>5.26</td>
<td>27.65</td>
<td>0.21</td>
<td>182,820</td>
<td>0.25</td>
</tr>
</tbody>
</table>

### References


Understanding and modelling the vertical distribution of fish eggs in the water column is a major challenge for future use of underway continuous egg samplers as estimators of the total egg abundance. This study presents modelling of field data of anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) egg vertical distribution obtained from LHPR sampling in the Bay of Biscay. Starting from the Sundby (1983) model, improvements were achieved through successive modifications concerning egg buoyancy and vertical propagation of wind-induced turbulence (Boyra et al., 2003; Coombs et al., 2004; Rueda et al., 2003). In addition, measurements of egg settling velocity and buoyancy by stages were included as inputs for the models (Table 1).

Table 1. Average densities and standard deviations of anchovy and sardine eggs obtained by three stages of development in the density gradient experiments.

<table>
<thead>
<tr>
<th></th>
<th>Anchovy</th>
<th></th>
<th></th>
<th></th>
<th>Sardine</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Total av.</td>
<td>No. embryo</td>
<td>Early embryo</td>
<td>Late embryo</td>
<td>Total av.</td>
</tr>
<tr>
<td>Density (sigma-t)</td>
<td>23.264</td>
<td>22.963</td>
<td>23.536</td>
<td>23.138</td>
<td>23.488</td>
</tr>
<tr>
<td>Standard deviation</td>
<td>0.629</td>
<td>0.158</td>
<td>0.587</td>
<td>0.647</td>
<td>0.445</td>
</tr>
</tbody>
</table>

The best model fitting was achieved through the adoption of a gradual turbulence vertical decay model (proportional to the inverse of the water density profile), a Gaussian variability of egg densities and adaptability of the egg densities to the surrounding water by means of permeability of the chorion. This led to neat improvements over the base Sundby original model. The coefficient of determination ($R^2$) of the modelled egg abundance profiles versus the observed ones was rather similar for sardine and anchovy (Fig. 1): around 80% (geometric mean of $R^2$ of the four hydrographical environmental scenarios considered). The model described successfully the vertical distributions of eggs for waters of high surface salinity ($R^2$ of almost 90%), but less so for waters of low surface salinity ($R^2$ of about 70%).

![Figure 1](image-url)

**Figure 1.** Predicted (continuous line) vs. observed (dotted line) vertical distributions of anchovy (a) and sardine (b) eggs for the 2000-2001 years total average, using the optimised model. N is the number of LHPR stations included and n is the total number of eggs found.
In order to study the adaptability more precisely, we also developed a 1D dynamic model, that included the permeability of the external membrane (or chorion) of the eggs, to simulate the movement of sardine eggs released at the top of a density gradient column. The permeability of the chorion would permit the flow of salted water inside or outside the egg, provoking the adaptation of egg density to the medium (especially for species of large perivitelline space, such as sardine), this affecting their actual vertical distribution. Experimental measures of settling velocities of eggs in a density gradient column were performed and compared to the modelled ones. Before being dropped in the gradient, half of the eggs were submersed in a low salinity solution and the rest in a high salinity one. The neat different trajectories of eggs from both solutions (Fig. 2) evidenced the different starting density conditions in each case, this proving the permeability of the egg membrane.

![Graph showing low and high density averages.](image)

**Figure 2.** Results obtained in the adaptability experiments and simulations. On the left graph the result obtained with low salinity eggs is shown, on the right, the result obtained with high salinity eggs. Discontinuous lines are the experimentally observed results, dotted lines correspond to the non-permeable model and continuous lines, to the permeable one.

**References**


FINE-SCALE SPATIAL VARIATION OF PELAGIC FISH EGGS IN RELATION TO ONTOGENETIC VARIATION OVER THE WESTERN AGULHAS BANK, SOUTH AFRICA

Mbulelo Dopolo¹, Carl van der Lingen¹, Laurent Drapeau¹² and Coleen Moloney³

¹Marine and Coastal Management, Private Bag X2, Rogge Bay, 8012, South Africa (mbdopolo@deat.gov.za).
²Institute for Research and Development, France.
³Marine Biology Research Institute, Zoology Department, University of Cape Town, Rondebosch 7701, South Africa.

Understanding the spatial distribution of fish eggs is important in fisheries science (Haug et al., 1986), because it: (i) affects the transport of eggs from spawning to nursery grounds, (ii) provides insights into the of reproductive strategies of fish, and (iii) allows one to design optimal sampling. However, because pelagic fish eggs are highly aggregated, it is difficult to infer distributions from studies conducted using coarse-scale data. Fine-scale quantitative studies to examine the spatial distribution of fish eggs have been lacking in the southern Benguela upwelling ecosystem and are scarce in many other ecosystems.

To address this, ichthyoplankton samples collected over 1 nautical mile intervals in an area of high egg densities (Fig. 1) were analyzed for anchovy, *Engraulis encrasicolus* (formerly known as *E. capensis*), sardine, *Sardinops sagax* and round herring (red-eye), *Etrumeus whiteheadi*. Samples were collected using a continuous, underway fish egg sampler (CUFES, Checkley et al., 1997) aboard the FRS Algoa in September 2000 over the western Agulhas Bank, South Africa (Fig. 1). In the laboratory, eggs were identified, grouped into three stage categories: (i) early-stage (i.e. no embryo- stages 1-3), (ii) middle-stage (early embryo, i.e. tail is still attached to the yolk- stages 4-7) and (iii) late-stage (i.e. tail has detached from the yolk- stages 8-11), and concentrations were standardized to numbers per cubic meter. Directional (anisotropic) variograms were computed for each category for each species using the EVA computer software package to quantitatively describe the spatial variation or correlation of the eggs in terms of distance and direction of each category for the three species.

The variogram results illustrate the spatial structure of the egg patches of the three species following spawning (Fig. 2; Plate 8, page xiii). Theoretically, stations that are far apart were expected to be less correlated, and to have large variances. Late-stage anchovy eggs showed no spatial structure in the inshore/offshore direction, but were spatially structured alongshore (Fig. 2). Early and middle-stage eggs were not collected from the CUFES samples, but were collected from the WP2 net hauled at vertical stations in the same area. Therefore, these results highlight the drawback of the CUFES sampler. It damaged about 68% of anchovy eggs beyond recognizable developmental stage, but the extent of damage
was less pronounced for sardine (14%) and round herring (16%). Sardine early-stage eggs were patchily distributed with a nugget effect (the distance between the origin and the value of the variance at an extremely small distance apart) generally large (Fig. 2). Middle-stage eggs were spatially structured, samples at close distances being spatially correlated and those at large distances apart less correlated with an influence range of about 5-6 nautical miles, whereas late-stage eggs had no spatial cohesion. Unlike for sardine, round herring early-stage eggs were relatively spatially structured with an influence range of about 3 nautical miles, whereas middle- and late-stage eggs had similar spatial structure to those of sardine.

Figure 2. Variograms of anchovy, sardine and round herring, eggs by stage category. The degrees indicate the directions that were given greatest weighting in constricting the variogram; degree 45 is inshore/offshore direction, and degree 90 is the alongshore direction.
These results suggest that the sardine spawning strategy is that of several dense spawning shoals over the spawning area, unlike round herring, which appears to be that of less dense spawning shoals. Similar results have been reported for the Australian sardine *S. sagax* (Fletcher and Sumner, 1999) using a similar sampling distance, but using vertically towed nets. Furthermore, these results indicate that the size of the egg patches (5-6 nautical miles) for all three species is smaller than the current sampling interval of 10 nautical miles between stations in the southern Benguela. These data are currently used to make inferences about the spawning strategies of the species, therefore this study suggest that such inferences could be inappropriate. In conclusion, the results obtained from this study suggest that these spatial properties would have serious implications for individual based modelling (IBM) studies, and would need to be incorporated.

**Acknowledgements**

This project was conducted under the auspices of the Interactions and Spatial Dynamics of renewable resources in upwelling Ecosystems (IDYLE) Programme, which funded our participation at the meeting.

**References**


VERTICAL DISTRIBUTION OF EGGS OF ANCHOVY (*ENGRAULIS CAPENSIS*) AND SARDINE (*SARDINOPS SAGAX*) IN THE NORTHERN BENGUELA

Erling Kåre Stenevik¹, Svein Sundby¹ and Anja Kreiner²

¹Institute of Marine Research, PO Box 1870 Nordnes, N-5024 Bergen, Norway.
²National Marine and Information Centre, Ministry of Fisheries and Marine Resources, PO Box 912, Swakopmund, Namibia.

Understanding and modelling the vertical distribution of fish eggs is an important component in the use of Continuous Underway Fish Egg Sampler (CUFES) to estimate total egg abundance. The vertical and horizontal distribution of eggs and larvae of sardine and anchovy have been investigated on a series of BENEFIT surveys in the Northern Benguela during the last 6 years (Table 1). Eggs and larvae have been observed both in September/October (1999), in January (2004), in February (2000 and 2003) and in April (2001 and 2002). The horizontal distribution of both eggs and larvae indicates that spawning in most of the years was located in a relatively limited area around Palgrave Point. In 2003, however, relatively high concentrations of both anchovy and sardine eggs were observed near Walvis Bay, an area which has historically been an important spawning area for these species. In 2004, sardine eggs were found both near Walvis Bay and Palgrave Point while anchovy eggs were observed between Palgrave Point and Tombua at 15°50'S.

Table 1. Anchovy and sardine eggs and larvae sampled on BENEFIT surveys with R/V Dr Fridtjof Nansen.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Anchovy eggs</td>
<td>27</td>
<td>35</td>
<td>0</td>
<td>0</td>
<td>3577</td>
<td>903</td>
</tr>
<tr>
<td>Anchovy larvae</td>
<td>0</td>
<td>168</td>
<td>481</td>
<td>63</td>
<td>103</td>
<td>54</td>
</tr>
<tr>
<td>Sardine eggs</td>
<td>477</td>
<td>147</td>
<td>3</td>
<td>114</td>
<td>5685</td>
<td>722</td>
</tr>
<tr>
<td>Sardine larvae</td>
<td>290</td>
<td>16</td>
<td>73</td>
<td>22</td>
<td>2844</td>
<td>562</td>
</tr>
</tbody>
</table>

Vertical distribution of eggs was observed using a Multinet plankton sampler with five nets. Various depths and depth resolutions were used during the surveys, but the results showed similar patterns. Here, results from the survey in 1999 and 2003 are presented. The eggs were staged and in this paper only the eggs older than about 10 hours are included since these are expected to have reached their equilibrium vertical distribution, where the upward-directed buoyancy forces balance the downward directed turbulent diffusive forces (Sundby, 1983). The anchovy eggs were generally concentrated in the upper 10 m and only few eggs were observed deeper than that (Fig. 1). Correspondingly, the sardine eggs had highest concentrations in the upper 10 m, but eggs of this species were also found in the deeper intervals down to 30 m.

![Figure 1. Mean vertical distribution of anchovy eggs (left panel) and sardine eggs (right panel) from February 2003. Only eggs older than 10 hours are included.](image-url)
The vertical distribution of sardine eggs was measured and modelled by Stenevik et al. (2001) based on data from 1999. The measured and modelled distributions compared well. Based on the vertical distribution of newly spawned sardine eggs, which have not reached their equilibrium vertical distribution, and buoyancy and size measurements of the sampled eggs, the spawning of sardine in 1999 was estimated to occur relatively deep (60 to 80 m). Buoyancy measurements showed that neutral buoyancy of the sardine eggs were at a salinity of 31.7, corresponding to a mean density difference of 0.0025 g cm\(^{-3}\) between the egg and the ambient seawater. Based on this, the mean ascending rate of the eggs was estimated to be 5.1 m hour\(^{-1}\). Also the measured and modelled vertical distributions of sardine eggs from the cruise in 2003 (Figs.1 and 2) fit very well with those presented in Stenevik et al. (2001). The measured vertical distribution of anchovy eggs, however, from both the cruises in 2003 and 2004 show differences from the modelled distributions. In 2003, the buoyancy of the anchovy eggs were measured and they were heavier than sardine eggs with mean neutral buoyancy at a salinity of 33.3, corresponding to a mean density difference of 0.0013 g cm\(^{-3}\) between the egg and the ambient seawater. The calculated mean ascending rate of 1.8 m hour\(^{-1}\) is based on that the eggs rise through the water column with the long axis vertically oriented (as observed in the laboratory). Using these input data to the model gave a considerably deeper distribution of anchovy eggs than sardine eggs. However, the observed vertical distributions of anchovy eggs show that they are more concentrated towards the surface layers than the sardine eggs. Presently, we have no reasonable explanation for the mismatch between the observed and modelled distributions of anchovy eggs. However, it is possible that the wild caught anchovy eggs get a too rough treatment in the Multinet if they are partly squeezed into the mesh holes of the net. The mesh size of the Multinet is 405 μm, while the short axis of the anchovy eggs are only slightly larger, i.e. 550 μm. Roughly treated eggs will lose their full potential of osmoregulation and will become heavier by loss of water. Further laboratory experiments measuring the buoyancy of artificially fertilized anchovy eggs in the laboratory are required to get reliable data on anchovy egg buoyancy.

References


VARIATION OF DAILY EGG PRODUCTION, SPAWNING AREA, AND INSTANTANEOUS MORTALITY RATE, NECESSARY PARAMETERS TO BIOMASS ESTIMATION OF NORTHERN ANCHOVY (ENGRAULIS MORDAX) IN THE GULF OF CALIFORNIA

Yanira Green-Ruiz\(^1\) Nancy C.H. Lo\(^2\), and L.M. Jacob-Cervantes\(^1\)

\(^1\) SAGARPA, Instituto Nacional de la Pesca, Centro Regional de Investigación Pesquera Mazatlán, Av. Sabalo Cerritos s/n Col. Estero Del Yugo, C.P. 82010 Mazatlán, Sinaloa, México (motagreen@yahoo.com.mx).
\(^2\) Southwest Fisheries Science Center P.O. Box 271 La Jolla CA, USA (Nancy.Lo@noaa.gov).

The reappearance of \(E. \text{ mordax}\) in the Gulf of California, detected through commercial capture and ichthyoplankton studies in 1985, and the presence of scales of anchovy in the Gulf of California in last century discovered in 1991 by means of pale ontological studies, created the necessity to know the biomass of this potential resource. Being this one of the objectives of the national program of small pelagic fish of the National Institute of Fishing, the Daily Egg Production Method was applied over four years in order to estimate the spawning biomass of \(E. \text{ mordax}\) in the Gulf of California. For this simultaneous investigation cruises were carried out for the collection of eggs, larvae, juvenile, and adults of anchovy in January-February of 1991 to 1994. For every year the daily egg production, spawning area, instantaneous mortality rate, and their coefficient of variation (CV) was obtained. In this work we analysed the temporary variation of these parameters.
EUPHAUSIID PREDATION ON ANCHOVETA (ENGRAULIS RINGENS) EGGS AND ITS INCIDENCE ON THE NATURAL EGG MORTALITY ESTIMATIONS IN THE SPAWNING ZONE OF NORTHERN CHILE

M. Cristina Krautz¹, Leonardo R. Castro¹ and Margarita Gonzalez²

¹Laboratorio de Oceanografía Pesquera y Ecología Larval (LOPEL), Departamento de Oceanografía, Universidad de Concepción, PO Box 160-C, Concepción, Chile (ckrautz@udec.cl; lecastro@udec.cl).
²Departamento de Bioquímica Clínica e Inmunología, Facultad de Farmacia, PO Box 237-C, Universidad de Concepción (magonzal@udec.cl).

In the highly productive upwelling systems of the California and Humboldt Currents, euphausiids and anchovies are extremely abundant and a key component of the pelagic community. Euphausiids channel much of the primary production to higher trophic levels (i.e. fishes) and export carbon and energy to the subsurface layers via pellet production or vertical migrations (Gonzalez et al., 2000; Escribano et al., 2000). Like other crustaceans, they are also active predators of copepods, fish eggs and larvae (Bailey et al., 1993; Theilacker et al., 1993). Anchovies, in turn, feed also on phytoplankton and extensively on zooplankton, reaching high biomass in upwelling systems of which they have been also considered key factor in structuring their communities (Cury et al., 2000). The relationship between these two major components of eastern boundary ecosystems, anchovies and euphausiids, although well known for a long time, have only recently been explored in more detail with the development of new immunochemical techniques that recognise the prey (anchovy eggs and larvae) in the predator gut (euphausiids) despite the lack of remnants of hard parts in the gut after the maceration of the prey. With the development of this technique, currently we can estimate not only predation rates exerted by euphausiids but also we may determine the relative importance of this type of mortality compared with other sources of mortality on egg and larvae of commercially important species in upwelling areas.

Euphausia mucronata is the most abundant and largest euphausiid in the Humboldt Current. This vertical migratory species has been documented as capable of withstanding very low oxygen concentrations in the Equatorial Subsurface Waters where they reside probably to reduce predation by fish. During their diel migration to the shallower layers at night, they usually become one of the most important phytoplankton consumers in the pelagic system in northern Chile (Gonzalez et al., 2000). E mucronata shares their nocturnal shallow residence with the anchoveta, Engraulis ringens, a coastal spawning species along northern and central Chile (Castro et al., 2000; Llanos and Castro, 2004) which is one of the most important fishery resources in northern Chile. During 2000, more than one million tons of anchoveta were captured in this north Chilean stock (SERNAPESCA 2002). Despite the previous knowledge on the euphausiids capability of predation over fish eggs and the obvious overlap in distribution at night between E. mucronata and E. ringens, no information existed on any potential relationship between these two key species of the upwelling systems in the Humboldt Current.

Daily egg production and natural mortality rates of anchoveta eggs have been estimated for several years from the application of the DEPM in northern Chile. However, the causes of natural mortality and their inter-annual variability have remained unexplored to date. In this study i) we considered the use of ELISA (Enzyme Linked ImmunoSorbent Assay) in the detection and quantification of euphausiids predation (Euphausia mucronata) on anchoveta eggs (Engraulis ringens) in Northern Chile during the winter peak spawning season 2000 and, ii) we estimated the fraction of the total natural mortality of anchoveta eggs in that area produced by euphausiids predation.
The use of immunoassays considered the production of a high titre (1:15000) polyclonal antibody that allowed the detection of 0.1 µg of anchoveta egg proteins. Potential cross-reactions with proteins of coastal fish eggs, and differences in the reactivity to the antibody between the eggs off Northern and Central Chile, were discarded after the use of electrophoresis, Western blotting and ELISA. The time estimated from laboratory experiments in which it is possible to detect remainders of egg protein in the euphausiids guts (protein retention time, PRT) was 9 hours (13°C), and the decay rate (exponential model) of the egg protein in the euphausiids guts was -0.0385 h\(^{-1}\).

Geostatistical analysis was utilized to define the nuclei of egg abundance within the area covered in the DEPM sampling grid (Fig. 1). The area of spatial influence (range of the exponential variogram) was equivalent to 28 nm and two spawning nuclei were identified. Eighteen percent of the total captured euphausiids within the main nucleous of eggs in the spawning area presented positive reaction of anchoveta egg proteins in their guts. Preliminary estimates of natural mortality calculated at the principal spawning nucleus was -1.029 d\(^{-1}\), while the value of \(P_0\) (Daily Egg Production) was 43.84 eggs day\(^{-1}\) (Iquique - Antofagasta; Table 1). The total euphausiid consumption of eggs estimated at the main spawning nucleus was 3.90 x 10\(^{12}\) eggs (based on algorithms proposed by Bailey et al., 1993) and 4.42 x 10\(^{12}\) eggs (based on algorithms proposed by Theilacker et al., 1993). The incidence of euphausiid predation on the egg natural mortality calculated in this study based on euphausiid abundance reported for this area reached 22%.

These are the first and still preliminary estimates of mortality induced by predation of the very abundant \textit{Euphausia mucronata} on early stages of the extremely abundant anchoveta \textit{Engraulis ringens} in the Humboldt Current.
Table 1. Mortality of anchovy eggs by euphausiid predation in the spawning area of northern Chile. \(M_p\) = Mortality due to predation; \(Z\) = total natural mortality in the area indicated (d\(^{-1}\)).

<table>
<thead>
<tr>
<th>Method of estimation</th>
<th>Spawning area (mn(^2))</th>
<th>Egg consumption (eggs (x) 0.05 m(^{-2}) (x) d(^{-1}))</th>
<th>Total consumption</th>
<th>Egg production (egg (x) 0.05 m(^{-2}) (x) d(^{-1}))</th>
<th>Total production</th>
<th>(M_p)</th>
<th>% (M_p/Z)</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. Based on Bailey et al. (1993)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Main nucleus</td>
<td>6301.39</td>
<td>0.842</td>
<td>3.90E+12</td>
<td>43.837</td>
<td>1.89E+13</td>
<td>0.206</td>
<td>20.59</td>
</tr>
<tr>
<td>Main and secondary nucleus</td>
<td>7963.02</td>
<td>0.842</td>
<td>4.93E+12</td>
<td>44.142</td>
<td>2.41E+13</td>
<td>0.204</td>
<td>18.38</td>
</tr>
<tr>
<td>B. Based on Theilacker et al. (1993)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Main nucleus</td>
<td>6301.39</td>
<td>0.953</td>
<td>4.42E+12</td>
<td>43.837</td>
<td>1.89E+13</td>
<td>0.233</td>
<td>22.65</td>
</tr>
<tr>
<td>Main and secondary nucleus</td>
<td>7963.02</td>
<td>0.953</td>
<td>5.58E+12</td>
<td>44.142</td>
<td>2.41E+13</td>
<td>0.231</td>
<td>20.81</td>
</tr>
</tbody>
</table>

References


GROWTH AND MORTALITY OF JACK MACKEREL \textit{Trachurus symmetricus} LARVAE IN THE SOUTHERN EAST PACIFIC

Maximiliano Reyes$^1$, Aquiles Sepúlveda$^1$, Leonardo R. Castro$^2$.

$^1$Instituto de Investigación Pesquera, Talcahuano, Chile (inpesca@inpesca.cl).

$^2$Laboratorio de Oceanografía Pesquera y Ecología Larval (LOPEL), Departamento de Oceanografía, Universidad de Concepción, Casilla 160-C, Concepción, Chile (lecastro@udec.cl).

The growth pattern of jack mackerel larvae in the oceanic area off central Chile (32°06'-37°48'S; 75°-92°W) is analysed. Larvae were obtained in November 2000 during a survey conducted on 20 transects separated each 18 nm by the simultaneous operation of 10 fishing vessels. At each transect of ca. 950 nm in extension, vertical plankton samples were systematically collected every 18 nm from the 100 m depth to the surface by using a WP-2 plankton net provided with a mesh size of 333 µm and a diameter of 0.6 m. A total of 880 samples were collected.

The size structure in length of larvae was obtained and corrected by shrinkage and sampling time (Fig. 1). A total of 1906 larvae were measured with a size range between 1.6 to 14.8 mm SL and 118 otoliths were used for counting of microincrements. Growth was modelled applying a linear and the Gompertz growth model. The daily growth rate of jack mackerel larvae was estimated as 0.258 mm.d$^{-1}$ and the hatching size ca. 2 mm. The principal mode in the size structure was between 2.5 and 3.5 mm. Considering this information, the birth date of the collected larvae was estimated and the distribution of birth dates was reconstructed. According to these results, the main spawning occurs between the 25 to 28 November. The mortality process was inspected dividing the spawning area into 6 sub-sectors (Fig. 2) and statistical differences were found between the mortality rate based on the analysis of catch curves for each sub-sector. Mortality rate estimates oscillate between 0.105 and 0.359 individual.d$^{-1}$ (Table 1).

Figure 1. Length distribution (%) of larval \textit{Trachurus symmetricus} over the entire area surveyed.

Figure 2. Positive stations with larval \textit{Trachurus symmetricus} in the area surveyed. For the statistical analyses, the entire area was divided in 6 sub-sectors.
Table 1. Larval mortality rates ($Z$) in each sub-sector of the area surveyed. (n) is the number of ages intervals considered in the mortality curve, number in brackets is the minimum larval age utilized in that particular sub-sector, (A) is the initial larval abundance. (IC 95%) interval of confidence of $Z$.

<table>
<thead>
<tr>
<th>Sub-sector</th>
<th>n</th>
<th>A</th>
<th>Z</th>
<th>(IC 95%)</th>
<th>r²</th>
</tr>
</thead>
<tbody>
<tr>
<td>North West</td>
<td>18</td>
<td>5574</td>
<td>0.359</td>
<td>0.421 - 0.296</td>
<td>0.961</td>
</tr>
<tr>
<td>North Central</td>
<td>21</td>
<td>4919</td>
<td>0.104</td>
<td>0.161 - 0.046</td>
<td>0.543</td>
</tr>
<tr>
<td>North East</td>
<td>18</td>
<td>19435</td>
<td>0.372</td>
<td>0.473 - 0.270</td>
<td>0.915</td>
</tr>
<tr>
<td>South West</td>
<td>21</td>
<td>5481</td>
<td>0.142</td>
<td>0.199 - 0.085</td>
<td>0.735</td>
</tr>
<tr>
<td>South Central</td>
<td>19</td>
<td>6184</td>
<td>0.215</td>
<td>0.307 - 0.124</td>
<td>0.724</td>
</tr>
<tr>
<td>South East</td>
<td>11</td>
<td>2649</td>
<td>0.272</td>
<td>0.331 - 0.214</td>
<td>0.963</td>
</tr>
<tr>
<td>TOTAL</td>
<td>108</td>
<td>4877</td>
<td>0.157</td>
<td>0.200 - 0.114</td>
<td>0.462</td>
</tr>
</tbody>
</table>

A strong relationship was found between mortality estimates with the average sea surface temperature of each sector. High mortality rates were found in the north west (oceanic) sub-sector with warm temperature (20°C) and in two east (coastward) sub-sectors of temperatures around 16°C. The intermediate zones characterized by temperatures between 18 and 19°C show significantly lower mortalities. This result suggests a dome-shaped relationship between larval survival rates of jack mackerel and surface temperature with an “optimal range” at medium temperatures in the main spawning habitat of this species in oceanic waters.
INTER-POPULATION DIFFERENCES IN EARLY LIFE HISTORY
TRAITS OF THE ANCHOVETA ENGRAULIS RINGENS ALONG
CHILE: ANY RELATIONSHIP WITH THE SPAWNING HABITAT
CHARACTERISTICS?

Leonardo R. Castro¹, Alejandra Llanos¹², José Luis Blanco³,
Mauricio Landaeta¹, M Cristina Krautz¹, Ruben Escribano⁴ and
Eduardo Tarifeño⁵

¹Laboratorio de Oceanografía Pesquera y Ecología Larval (LOPEL), Depto
Oceanografía, Universidad de Concepción, Chile.
²Programa de Doctorado en Zoología, Universidad de Concepción, Chile.
³Center for Coastal Physical Oceanography, Old Dominion University, USA.
⁴Centro COPAS, Depto Oceanografía, Universidad de Concepción, Chile.
⁵Depto Zoología, Universidad de Concepción, Chile.

The anchoveta, Engraulis ringens, presents a wide latitudinal distribution (4 - 42°S) along most of the Humboldt Current. In this study we assessed whether differences in early life history characteristics differ among individuals spawned along this wide range and also we discuss whether these differences matched the life history expectations based on the latitudinally-driven differences in environmental characteristics of the spawning habitat.

First, we assess three physical and two biological aspects of the environment that may affect the young larvae chances of survival: sea surface temperature, turbulence, seaward Ekman transport, potential gelatinous predators and feeding conditions. For the physical aspects, we utilized temperature and wind data collected over the last 30 years along the Chilean coast (18-42°S), and for the biological data we have analyzed information obtained from two locations within the central (Antofagasta, 23°S) and southern (Talcahuano, 36°30'S) major anchoveta spawning areas from 1995 to 2000. Our results show that in the central spawning area, the continuous upwelling during winter (and narrow continental shelf) sustain an ichthyoplankton community formed by relatively few coastal species and provides the larvae with a rich food environment affected by low turbulence levels. These benign feeding conditions, along with the higher water temperature, should be beneficial for the eggs and young larvae which could attain faster development and growth rates to counteract the higher probability of seaward exportation in the Ekman layer. The offshore transport in the surface Ekman layer and the high reproductive capacity of the gelatinous predators might represent a potential trade-off for the early life stages of the anchoveta at these low latitudes. At the southern spawning area, in turn, the winter coastward surface transport favours the development of a coastal-fish dominated ichthyoplankton community, and its retention over the wider continental shelf (Castro et al., 2000). The mean food concentrations in the water column seem high enough to support the young larvae except during the winter storms when turbulence in the water column may preclude larval first feeding success. During the rest of the winter spawning season, the lower temperature of the water might retard the egg development and larval growth. In this environment, therefore, our results suggest the anchovy populations should produce larger eggs, and their larvae should hatch at larger sizes, with a larger yolk content to facilitate their survival especially during the winter storm season (Fig. 1). Contrasting with the northern population and as a potential comparatively advantageous environmental characteristic at this southern spawning area, the potential trade-off represented by the gelatinous predators during the spawning season does not seem as significant as in northern Chile (Llanos and Castro, 2004). In the southern area, gelatinous predators are mostly located offshore in winter and they increase in number at the coastal zone mainly in summer when the main anchoveta reproductive season is over.
Secondly, from field collected eggs we assessed a) latitudinal variations in egg size during the peak spawning season, and b) inter-population differences in hatch size under their normal temperature conditions. Finally, from rearing experiments and information in the literature we determined c) temperature effects on egg development rates and the Q10 physiological parameter. Our results show that during the peak spawning season, the egg size and larval length at hatch increases with latitude. Conversely, the egg development and larval growth rates are slower in higher latitude populations, even at the same laboratory temperature-controlled conditions. Q10 values are >3 at temperature ranges below 15°C suggesting that anchovy populations at 37°S are living close to the lower tolerance limit for normal egg development which agrees with the observed temperature range at the species southern limit of spawning in winter. The results of this study therefore, suggest differences exist in early life history parameters among individuals spawned at different latitudes.

Thirdly, in rearing experiments of egg and yolk sac larvae from two anchovy populations located 13 degrees of latitude apart (Antofagasta 23°S, Talcahuano 36°S), we evaluated the effect of temperature in early life history traits such as: larval length at hatch, yolk volume at hatch, larval length at yolk-absorption, duration of yolk-sac stage, yolk consumption rate and yolk sac larval growth rate. Our results show that egg size had an effect on the larval length at hatch, initial yolk volume and larval length at yolk-absorption, since the values obtained were always larger in larvae hatched from Talcahuano (from larger eggs) than from Antofagasta (smaller eggs). Duration of yolk-sac phase, yolk consumption rate and larval growth rate until yolk exhaustion showed high thermic dependence in both populations. However, these traits showed no difference between populations when larvae were reared at the same temperature in the range between 12 and 20°C (Fig. 2). Therefore, when extrapolated to the environmental conditions in each nursery area (i.e. 15°C Antofagasta and 12°C Talcahuano), our results suggest that the anchoveta populations from Talcahuano compensate their lower larval growth rates mainly by increasing their initial egg and hatch sizes as they are larger than Antofagasta larvae at the end of the yolk sac stage. This increased larval length should enhance their chances of survival (especially during their first feeding period) under adverse environmental conditions such as high turbulence, lower temperature and lower food availability during winter, which is typical of the anchoveta southern spawning area.
Figure 2. Net larval length increase from hatch to the end of the yolk sac period, of anchoveta larvae from two locations (Antofagasta, 23°S and Talcahuano 36°S) reared at different temperatures.

Acknowledgements
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References

SPATIAL SPAWNING STRATEGY OF JACK MACKEREL
(Trachurus symmetricus murphyi) OFF THE CENTRAL-SOUTH REGION OF CHILE

M. Angel Barbieri1,3, J. Córdova1, Francois Gerlotto2 and M. Espejo1

1Instituto de Fomento Pesquero, Blanco 839, Valparaíso, Chile (mabarbieri@ifop.cl).
2IRD, c/o Instituto de Fomento Pesquero, Blanco 839, Valparaíso, Chile.
3Pontificia Universidad Católica de Valparaíso, Chile.

Jack mackerel is a middle-sized pelagic species that inhabits the southern Pacific Ocean. This species performs a seasonal migration that would explain its availability along the Chilean coast, this seasonal migration has been related to feeding and spawning processes, with an offshore migration for spring spawning in oceanic waters, and an onshore migration during end summer-autumn for feeding.

From 1997 until 2001 acoustic surveys are performed during spring in order to study the spawning zone of jack mackerel. From 1997 until 2001 acoustic surveys are performed during spring, in order to study the spawning zone of jack mackerel, Trachurus symmetricus murphyi, off the Central South region of Chile. Knowing that the spawning of jack mackerel is related to sea surface temperature (SST), the survey area is located between the shore and up to 800 nautical miles from the coastline.

A specific survey design, called “Rastrillo” was conceived and Rastrillo surveys were held in November in 1997, 2000 and 2001, and December 1998 and 1999. These surveys are performed using a set of fisheries vessels achieving simultaneous E-W parallel (linear or zigzag) transects. Each vessel performs two transects from the coastline up to 800 nautical miles offshore. Eggs and larvae are collected during plankton stations each 15 nautical miles using a WP2 plankton net; an acoustic survey is performed using the fleet echo sounders, i.e. only relative values (occurrence of aggregation echo types) can be recorded. They are classified according to their abundance (high: >200t, medium: 20-200t, low: <20t) and their type (defined during ECOS Project C97B06: dense schools, dense layers, dispersed layers and small schools). From these results a series of density and distribution indexes are calculated, such as the occupation surface index (OSI) (nb of positive ESDU over total nb of ESDU), for the whole detection and for each class of echo type. Similarly a series of indexes are calculated for the eggs (4 classes: “no eggs”; “low”: 1-249 eggs/10 m²; “medium”: 250-499; “high”: >500 eggs/10 m²) and abundance index.

In 1997 and 1999, the occupied surface indices (OSI) were high (15% and 15.5% respectively) and the egg abundance index (EAI) low (4.3 and 14.8%). In 1998, 2000 and 2001, OSIs were low (2, 4 and 4.3%) while EAIs were high (21.5, 36.8 and 39.4%). During all surveys, the highest abundance of eggs and the highest abundance of fish school echoes were located in different areas. Figure 1 describes the distribution of eggs and fish during the 2000 survey. It can be noted that high abundance of eggs occurs in the low fish abundance area, and vice versa. Geostatistical variograms were calculated on both egg and fish distributions. In the case of jack mackerel, 47.7% of variance is due to a nugget effect (76.4% for egg distribution); jack mackerel distribution presents spatial structures of 4.8 and 14.4 nautical miles. For egg distribution, the spatial structure is much wider, and above 42 nautical miles.

Lorenz curves were calculated on eggs and fish data. They describe the distribution heterogeneity in the surveyed area. Results show that the egg distribution is much more homogeneous than fish distribution. Moreover, they present an opposite tendency: the egg distribution is the most homogeneous when the fish distribution is the most heterogeneous.
From these results a series of hypothesis are drawn, the principal one being that in the spawning area, jack mackerels do not maintain compact aggregation and stays scattered, which make them invisible to the fleet echo sounders. A behavioural strategy of spawning jack mackerel is described: contrarily to many pelagic fish, this species favour a high dispersion of eggs by developing a highly scattered spawning behaviour, in ultra-oligotrophic areas (72.3ng/l). We hypothesize that the ecological implications of such spawning behavior are: reduced risks of predation on larvae and eggs (low abundance of predators); reduced intraspecific competition (dimension of the spawning area); and low interspecific competition for food during larval stages.

Acknowledgements

We would like to acknowledge support from the following grants: Proyectos FIP 97-05b, FIP 99-14, FIP 2000-10, FIP 2001-12, ECOS Project C97B06.
Pacific sardine nearly disappeared in the early 1960s off the west coast of the American continent and reappeared in the middle 1980s, with the estimates reaching over 1 million mt in recent years. The Daily Egg Production Method (DEPM) has been used to estimate the spawning biomass of sardine since 1996 (Lo, 2003). The underway fish egg sampler (CUFES) has been used during the ichthyoplankton surveys off California since 1997 (Checkley et al., 1997; Lo et al., 2001). This presentation reports results of the 2003 CUFES-aided ichthyoplankton survey, compared to the 1994 conventional survey. The spatial distributions of Pacific sardine, jack mackerel and anchovy eggs from recent cruises are also presented together with sea surface temperature.

Sardine eggs from CalVET net, and yolk-sac larvae collected with CalVET and Bongo nets have been included to model the sardine embryonic mortality curve since 2000. During the 2003 survey, RV Jordan and Revelle were used. Sardine eggs collected by the CUFES were used only to map the spatial distribution of the sardine spawning population and to allocate extra CalVET tows when eggs/min ≥ 1 in CUFES collections for the Jordan only (Lo, 2003); Revelle conducted routine CalCOFI sampling. The survey area was post-stratified into two regions: Region 1, the high density area (eggs/min ≥ 1), and Region 2, the low density area, the remaining area (Fig. 1).

Total numbers of CUFES and CalVET samples are given in Table 1. Egg densities from the CalVET, and from the CUFES samples taken within an hour before and after the CalVET tow, were paired and used to derive a conversion factor (E) from eggs/min of CUFES sample to CalVET catch E=U_y/U_x. We used a regression estimator to compute the ratio of mean eggs/min from CUFES to mean eggs/tow from CalVET: y is the eggs/min and x is eggs/tow.

![Figure 1](image-url)  
Figure 1. Sardine eggs from CalVET (solid circle denotes positive catch and open circle denotes zero catch) and from CUFES (stick denotes positive collection) in April 2003 survey. The numbers on line 93 are CalCOFI station numbers. Region 1 is the stippled area.
For Region 1, sardine egg density for each developmental stage was computed based on CalVET samples. A temperature-dependent stage-to-age model (Lo et al., 1996) was used to assign age to each stage. Yolk-sac larvae are larvae ≤ 5mm in preserved length. Daily yolk-sac larval production was obtained by the standing stock divided by its duration. Eggs younger than 3h old and eggs older than 2.5 days were excluded because of possible bias. The average temperature for CalVET tows with ≥ 1 egg was 13.8◦C.

The sardine embryonic mortality curve was modeled by an exponential decay curve (Lo et al., 1996):

\[ P_t = P_0 \exp(-zt) \]  

(1)

where \( P_t \) is either eggs/0.05m\(^2\)/day from CalVET tows or yolk-sac-larvae/0.05m\(^2\)/day from CalVET and Bongo tows, and \( t \) is the age (days) of eggs or yolk-sac larvae from each tow. A weighted nonlinear regression was used to estimate two parameters in equation (1) where the weights are 1/SD.

For Region 2, 11 tows 5 of 59 CalVET collections had ≥ 1 sardine egg. We estimated daily egg production (\( P_{0,2} \)) as the product of the egg production in Region 1 (\( P_{0,1} \)) and the ratio of egg density in Region 2 to Region 1 (\( q \)) from CUFES samples.

The estimate of 6\( P_0 \) for the whole survey area was computed as a weighted average of \( P_{0,1} \) and \( P_{0,2} \) where weights are the regional area sizes.

The spawning biomass (\( B_s \)) was computed according to

\[ B_s = \frac{P_0AC}{RSF/W_f} \]  

(2)

where \( A \) is the survey area in unit of 0.05 m\(^2\), \( S \) is the proportion of mature females that spawned per day, \( F \) is the batch fecundity (number of eggs per mature female), \( R \) is the fraction of mature female fish by weight (sex ratio), \( W \) is the average weight of mature females (gm), and \( C \) is the conversion factor from gm to mt. The denominator (RSF/\( W_f \)) is the daily specific fecundity (number of eggs/population weight gm/day), which was estimated from 2002 survey data (Lo, 2003): 22.94 eggs/gm/day.

Table 1. Sardine daily egg production (\( P_0 \)) from a conventional survey (1994), compared to a CUFES/DEPM survey (2003)

<table>
<thead>
<tr>
<th>1994 Conventional DEPM survey Area: 380,175 km(^2)</th>
<th>2003 CUFES/DEPM survey Area: 365,906 km(^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>CalVET tows</td>
<td>CalVET tows</td>
</tr>
<tr>
<td>Total</td>
<td>684</td>
</tr>
<tr>
<td>Positive for eggs</td>
<td>72</td>
</tr>
<tr>
<td>Percent positive</td>
<td>11%</td>
</tr>
<tr>
<td>CUFES samples</td>
<td>none</td>
</tr>
<tr>
<td>Total</td>
<td>1,287</td>
</tr>
<tr>
<td>Total positive</td>
<td>Percent positive</td>
</tr>
<tr>
<td>Percent positive</td>
<td>87%</td>
</tr>
<tr>
<td>High density stratum</td>
<td>87%</td>
</tr>
<tr>
<td>Daily egg production</td>
<td>Daily egg production</td>
</tr>
<tr>
<td>( P_0 )</td>
<td>0.169/0.05m(^2)</td>
</tr>
<tr>
<td>CV</td>
<td>0.22</td>
</tr>
<tr>
<td>Spawning biomass</td>
<td>11,493 mt</td>
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</tbody>
</table>
The daily egg production in Region 1 ($P_{0,1}$) was $6.05 \pm 0.05$ m$^2$/day (CV=0.18) and egg mortality was $Z=0.48$ (CV=0.08) for an area of 82,578 km$^2$ (equation 1). The ratio ($q$) of egg density between Region 2 and Region 1 from CUFES samples was 0.033 (CV=0.025). In Region 2, the egg production ($P_{0,2}$) was $0.2 \pm 0.05$ m$^2$/day (CV=0.322) for an area of 283,328 km$^2$. The estimate of the daily egg production for the entire survey area was $1.52 \pm 0.05$ m$^2$ (CV=0.18) for an area of 365,906 km$^2$. The estimate of spawning biomass of sardine in 2003 (equation 2) was 485,121 mt (CV=0.36) (Fig. 1). The catch ratio (E) of eggs/min to eggs/0.05m$^2$ was 0.39 (CV=0.11).

The comparison between the results of CUFES-aided ichthyoplankton survey in 2003 with a conventional ichthyoplankton survey in 1994 shows a large difference in percent of positive tows: only 11% (74/684) of CalVET samples were positive for sardine eggs in 1994 whereas in 2003, 66% (127/192) were positive (Table 1). Thus, CUFES was effective in allocating CalVET samples and thereby reducing ship time costs. The CVs of the estimates of $P_{0}$ were similar. The allocation of CalVET tows would be most useful when the population is low and concentrated in small areas as it was in 1994 (Table 1). In addition, the high resolution maps of pelagic fish eggs provided by CUFES, i.e. sardine, anchovy and jack mackerel, will enhance future survey designs and the understanding of the population distributions and oceanographic conditions (Plate 9, page xiv). Although CUFES is useful to delineate the spawning area of pelagic fish, the estimate of spawning biomass is still best based on data collected with traditional ichthyoplankton samplers.

References


Comparing the Abundance of Pelagic Fish Eggs Estimated Using the CalVET Net and the CUFES

Carl D. van der Lingen¹ and David M. Checkley, Jr²

¹Marine and Coastal Management, Pvt Bag X2 Rogge Bay 8012, South Africa.
²Scripps Institution of Oceanography, La Jolla, 92093-0218 USA.

Since its development in the mid-1990s, the CUFES has become an established tool for ichthyoplankton sampling, principally for the eggs of small pelagic fish such as anchovy (*Engraulis* spp.), menhaden (*Brevoortia tyrannus*), mackerel (*Scomber* and *Trachurus* spp.) and sardine (*Sardinops sagax* and *Sardinia pilchardus*). Currently, the CUFES is used in several regions of the world’s oceans, including the Benguela, California, Canary and Humboldt Current systems, the Bay of Biscay, the Canadian east coast, the Norwegian west coast, and the east coast of the United States. Designed to sample whilst the research vessel is both on-station and underway, the major advantages of the CUFES are its ability to collect near-surface samples at a high level of spatial resolution for shipboard analysis (which facilitates adaptive sampling), and the increased number of samples it provides compared to standard ichthyoplankton sampling gear such as the CalVET net. The major disadvantage of the CUFES is its inability to sample the entire egg vertical distribution range. Because the eggs of pelagic fishes typically are positively buoyant and abundant near to the surface, near-surface samples allow inference about the areal abundance and distribution of pelagic fish eggs. However, such inference depends on the assumption that egg concentration at the CUFES pump depth (eggs.m⁻³, ~3m) is significantly related to areal (eggs.m⁻²) egg concentrations.

Estimates of volumetric egg abundance made using a CUFES are significantly correlated with estimates of areal egg abundance from vertically hauled nets for small pelagic and other species from several regions, with coefficient of determination ($r^2$) values ranging from 0.03 to 0.92 (Table 1). These relationships demonstrate the efficacy of CUFES as a sampler of pelagic fish eggs; generally, $r^2$ values are higher for sardine eggs than those of other species of small pelagic fish (anchovy and round herring). Additionally, relationships between egg abundance estimates derived from CUFES and those from CalVET net samples within the same region (the southern Benguela) show consistent differences in slope values between anchovy eggs and those of other small pelagic species (mean slope values of 0.26, 0.89, and 0.75 for anchovy, sardine and round herring, respectively; Fig. 1), most likely a result of inefficient retention of the smaller anchovy eggs by the 500 µm mesh of the CUFES concentrator. This result indicates that a mesh of less than 500 µm should be used if anchovy (or other, small) eggs are the target, although decreasing mesh size increases the likelihood of clogging.

Additionally, there is some evidence for a “configuration” effect on CUFES-CalVET regressions. The survey in the southern Benguela during 2001 employed a sea-chest CUFES pumping from 6 m depth, as compared to a hull-mounted system pumping from 3m depth that was used in previous surveys. The slope values of the CUFES-CalVET net regression equations for 2001 were the lowest yet observed for all three small pelagic species, substantially so for sardine (Fig. 1b), although $r^2$ values for these equations were not noticeably different compared to other years. The reduction in slope value indicates that the CUFES collected fewer eggs per unit volume in 2001 compared to previous years, which may have been due to the different CUFES configuration used. A similar reduction in egg concentration from inboard (sea-chest) compared to outboard (hull-mounted) CUFES configurations has also been observed for anchovy and sardine in the Bay of Biscay (B. Planque, IFREMER, pers. comm.).
Table 1. Species and regions where significant linear relationships between CUFES- and CalVET net-derived estimates of egg density (eggs.m$^{-3}$ and eggs.m$^{-2}$, respectively) have been reported for small pelagics and other fish. BoB is the Bay of Biscay; PairoVET is a double CalVET net; VT indicates vertical tow; and HT indicates horizontal tow. Regression equations are log-transformed in most but not all cases. The number of data points and $r^2$ value are given. From 1Bez et al. (1999); 2Santos et al. (2000); 3van der Lingen (unpub.); 4Checkley et al. (1997); 5Watson et al. (1999); 6 Waton et al. (2002); 7Braun and Osses (2000); 8Ayon and Sanchez (2000); 9van der Lingen et al. (1998) and 10Lo et al. (2001).

<table>
<thead>
<tr>
<th>Species</th>
<th>Region and year</th>
<th>Net sampler</th>
<th>n</th>
<th>$r^2$</th>
<th>Ref.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Engraulis encrasicolus</td>
<td>France (BoB), 1998a</td>
<td>PairoVET (VT, 100-0m)</td>
<td>620</td>
<td>0.85</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Spain (BoB), 1998b</td>
<td>PairoVET (VT, 100-0m)</td>
<td>466</td>
<td>0.68</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Spain (BoB), 1998c</td>
<td>Bongo (VT, 200-0m)</td>
<td>43</td>
<td>0.88</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>South Africa, 1998</td>
<td>CalVET (VT, 100-0m)</td>
<td>355</td>
<td>0.30</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>South Africa, 1999</td>
<td>CalVET (VT, 100-0m)</td>
<td>304</td>
<td>0.34</td>
<td>3</td>
</tr>
<tr>
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<td>CalVET (VT, 100-0m)</td>
<td>294</td>
<td>0.49</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>South Africa, 2001</td>
<td>CalVET (VT, 100-0m)</td>
<td>231</td>
<td>0.40</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Engraulis mordax</td>
<td>California, 1996</td>
<td>CalVET (VT, 100-0m)</td>
<td>91</td>
<td>0.85</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>California, 1998</td>
<td>Bongo 70 (VT, max-0m)</td>
<td>-</td>
<td>0.33</td>
<td>5</td>
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<tr>
<td></td>
<td>California, 1999</td>
<td>Bongo 70 (VT, max-0m)</td>
<td>-</td>
<td>0.63</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Engraulis ringens</td>
<td>Chile, 1999</td>
<td>CalVET (VT, 10-0m)</td>
<td>128</td>
<td>0.32</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td>Peru, 1999</td>
<td>CalVET (VT, 10-0m)</td>
<td>128</td>
<td>0.32</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sardinops sagax</td>
<td>South Africa, 1996</td>
<td>CalVET (VT, 70-0m)</td>
<td>153</td>
<td>0.92</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td>South Africa, 1998</td>
<td>CalVET (VT, 100-0m)</td>
<td>356</td>
<td>0.62</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>South Africa, 1999</td>
<td>CalVET (VT, 100-0m)</td>
<td>311</td>
<td>0.45</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>South Africa, 2000</td>
<td>CalVET (VT, 100-0m)</td>
<td>317</td>
<td>0.78</td>
<td>3</td>
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<tr>
<td></td>
<td>South Africa, 2001</td>
<td>CalVET (VT, 100-0m)</td>
<td>231</td>
<td>0.65</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>California, 1996a</td>
<td>CalVET (VT, 70-0m)</td>
<td>91</td>
<td>0.62</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>California, 1996b</td>
<td>CalVET (VT, 70-0m)</td>
<td>91</td>
<td>0.55</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>California, 1999</td>
<td>CalVET (VT, 70-0m)</td>
<td>128</td>
<td>0.57</td>
<td>10</td>
</tr>
<tr>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Etrumeus whiteheadi</td>
<td>South Africa, 1996</td>
<td>CalVET (VT, 70-0m)</td>
<td>153</td>
<td>0.88</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td>South Africa, 1998</td>
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<td>356</td>
<td>0.38</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>South Africa, 1999</td>
<td>CalVET (VT, 100-0m)</td>
<td>311</td>
<td>0.28</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>South Africa, 2000</td>
<td>CalVET (VT, 100-0m)</td>
<td>317</td>
<td>0.41</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>South Africa, 2001</td>
<td>CalVET (VT, 100-0m)</td>
<td>231</td>
<td>0.55</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Brevoortia tyrannus</td>
<td>North Carolina, 1994</td>
<td>Bongo 70 (HT @3m)</td>
<td>13</td>
<td>0.92</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lagodon rhomboides</td>
<td>North Carolina, 1994</td>
<td>Bongo 70 (HT @3m)</td>
<td>10</td>
<td>0.61</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Citarichthys stigmacus</td>
<td>California, 1998/99</td>
<td>Bongo 70 (VT, ?-0m)</td>
<td>379</td>
<td>0.41</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Paralichthys californicus</td>
<td>California, 1998/99</td>
<td>Bongo 70 (VT, ?-0m)</td>
<td>443</td>
<td>0.03</td>
<td>6</td>
</tr>
</tbody>
</table>

The results obtained from comparing CUFES-CalVET net regressions for small pelagic fish across a range of systems suggest that CUFES may be better suited to sampling larger than smaller pelagic eggs, but that for both cases, CUFES may provide a good index of abundance with which to infer the areal distribution of eggs.
References


CATCHING CAPABILITIES OF CUFES VS PAIROVET AND IMPLICATIONS FOR ITS USE IN EGG SURVEYS

M. Santos, Andrés Uriarte, L.Ibaibarriaga

Fundación AZTI, Food and Fish Technological Institute, Herrera Kaia Portualdea z/g, 20110 PASAIA (Gipuzkoa) Basque Country, Spain (msantos@azti.es).

The Daily Egg Production Method (DEPM) is a widespread method used to estimate the biomass of multiple spawning pelagic fish, particularly clupeids (Lasker, 1985). In this method, the biomass is estimated from the ratio of the daily egg production to daily specific fecundity. Therefore an essential parameter is the egg abundance in the water column. Traditionally, vertical plankton samplers have been used to obtain egg abundance and spatial distribution.

The Continuous Underway Fish Egg Sampler (CUFES) has been proposed as a complementary sampling method (Checkley et al., 1997) and is progressively being incorporated (Van der Lingen et al., 1998; Checkley et al., 2000; Lo et al., 2001). This system operates continuously and in nearly all sea conditions during the surveys, providing a real-time estimate of the volumetric abundance of pelagic fish eggs, at 3m depth. Vertical samplers are reliable in terms of egg capture, but sampling is time consuming since require the vessel to stop. CUFES improves the cost/precision relationship in the estimation of the spawning area of pelagic fish and the egg production in relation to the DEPM as well as allowing us to obtain accurate horizontal egg distribution maps.

On the other hand, the major limitation of CUFES is that it collects samples from a fixed depth of 3m and the vertical distribution of fish eggs may vary in space according to changes in environmental conditions. It is therefore necessary to obtain an optimal relationship between CUFES and PAIROVET samples (Boyra et al., 2003) before being able to apply CUFES as a routine egg abundance estimator. 

The objective of this work is to analyse the differences in the detection capability of anchovy (Engraulis encrasicolus L.) and sardine (Sardina pilchardus) eggs by the two samplers, to study the quantitative relationship PAIROVET – CUFES and to test whether calibrations between both systems hold for different years and vessels.

Data used in this study were obtained during the 2000 and 2001 BIOMAN cruises on board R/V Investigador (AZTI) and PELGAS 2000 and 2001 cruises on board R/V Thalassa (IFREMER). The two surveys BIOMAN and PELGAS overlapped each year. The sampling on board R/V Investigador was performed taking samples continuously day and night. PAIROVET hauls were taken 3 miles apart using a 150μm net, at a maximum depth of 100m. At PAIROVET stations, a CUFES sample was taken for a minimum period of 4 minutes, or the duration of the PAIROVET if it was more than 4 minutes. Two CUFES samples were taken for a mile and a half before and after every PAIROVET station. Each of them usually lasted for about 10 minutes. The sampling carried out on board R/V Thalassa was different during night and day. During night, the scheme was similar to the one followed onboard R/V Investigador and during the day the sampling was concentrated on acoustic data acquisition, so a small number of PAIROVET hauls were carried out and those data have not been used in the present study.

From these surveys a subset of paired PAIROVET-CUFES samples were selected from all over the surveyed area in order to match different environments. Data were transformed on standardised values to 0.1 m² for PAIROVET and to 1 m³ for CUFES. It is desirable to obtain a sample with CUFES underway related with PAIROVET to carry out the survey without stopping the vessel so in the following analyses the CUFES mean was used before and after PAIROVET.
Table 1. Absence-presence table in percentages for PAIROVET and CUFES separated by vessels and species.

<table>
<thead>
<tr>
<th>Vessel</th>
<th>Anchovy</th>
<th>Sardine</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>CUFES</td>
<td>PAIROVET</td>
</tr>
<tr>
<td></td>
<td>0</td>
<td>&gt;0</td>
</tr>
<tr>
<td>Inv</td>
<td>20%</td>
<td>3%</td>
</tr>
<tr>
<td>Thala</td>
<td>42%</td>
<td>5%</td>
</tr>
</tbody>
</table>

The presence/absence of eggs was analysed (Table 1). For anchovy eggs the results show that the probability for CUFES or PAIROVET of detecting an egg while the other system does not, is the same, while for sardine the power of detection is higher for CUFES. This favours the use of CUFES for delimitation of the spawning area for both species especially for sardine.

A lineal regression was performed by gathering data from different years and vessels to analysed the relationship between CUFES and PAIROVET. The results showed that CUFES gives a poor representation of the egg abundance in the whole water column, with $R^2=0.32$ for sardine and $R^2=0.39$ for anchovy. These poor relationships are due to the existence of significant vessel and year effects that disturbed the above simple relationship.

Multiple linear regression models were used to test whether there were differences between vessel and years for sardine (Fig. 1) and anchovy (Fig. 2). The relationship between PAIROVET and CUFES changes by vessel (probably due to the type of hull) and year. Therefore a calibration is required for each vessel and year for quantitative use of CUFES.

Moreover a direct experiment was carried out in 2001 to compare the CUFES taken on board R/V Thalassa with those taken on board R/V Investigador. The two vessels navigated at 9 knots in parallel during two hours, taking samples each 10 min in a high abundance anchovy area between 45°49'N 3°22'W and 45°40'N 3°38'W. A proportional lineal model and log lineal model were fitted to check the relationship between CUFES sampling on board R/V Investigador and R/V Thalassa. The results showed that the R/V Thalassa took 80 to 90% more anchovy eggs per m$^3$ than R/V Investigador. This corroborates the analysis described above.

Figure 1. Multiple linear regression model for sardine.
Another element analysed was the stage distribution in samples collected by CUFES in comparison with PAIROVET. This was analysed classifying the eggs in 11 stages and in 3 stages (NE: no embryo, EE: early embryo and LE: late embryo) and considering the damaged eggs. The results showed that for the 11 stages the fraction of eggs damaged was higher in CUFES than in PAIROVET for both species, and higher in anchovy than in sardine. In addition we showed that in CUFES the most vulnerable eggs were the youngest and the most resistant ones the oldest. Only the use of 3 stages overcome this situation and prevent the huge loses of information. For these reasons any use of egg stages obtained with CUFES should be based on three stage classification.

The results of the study favour the use of CUFES for egg mapping and studies of spawning habitat of these pelagic species, particularly for sardine, but warns about the use of CUFES in a quantitative manner unless a good set of paired CUFES-PAIROVET samples were collected in each survey in order to standardize the relative catch efficiency of these two samplers.

References
Anchovy is a highly valuable resource in the bay of Biscay area for both Spanish and French Fleets. Scientific basis for management is required by the EU through ICES (WGHMSA). The evaluation of the status and dynamics of this short life, small pelagic population is namely made through direct, fishery independent estimates of population abundance.

Two consecutive, independent anchovy DEPM surveys (Lasker, 1985) were performed during the peak spawning season (in May and June) of 1989 and again in 1990, in order to get estimates of spawning biomass (SSB) and population at age for the Bay of Biscay anchovy population. The purpose of this exercise was to check the consistency of this assessment method through consecutive independent surveys with a short delay in the same spawning season. The foundation for this was the suspicion that partially different stock fractions might be spawning along the spawning season, as different authors pointed out a marked delay in the maturation process of 1 year old anchovy with respect to older anchovies.

Egg surveys were carried out along the Bay of Biscay area, to the south of 47°N latitude and to the east of 5°W longitude (Fig. 1). Adult samples were collected over the same area by a chartered commercial purse-seiner. Opportunistic samples were also collected by a set of commercial fishing vessels operating in the area (Fig. 2). For the four surveys, a post stratification of the area was always required for biomass estimation, because anchovies were spatially segregated by size.

Figure 1. Distribution of anchovy eggs in the Bay of Biscay during DEPM surveys in May (left) and June (right) of 1989 (top) and 1990 (bottom). Egg abundance is given in numbers per sample (individuals per 0.1 m²).
The spatial distribution of anchovy eggs changed substantially from May to June. However, whereas the spawning area (SA) increased between periods, the total daily egg production remained in the same order of magnitude (Table 1).

No female anchovy with exclusively unyolked oocytes (immature) occurred either in May or June, and only 10 of them presented partially yolked oocytes with no presence of yolked oocytes (histological analysis of 2,072 ovaries). This evidences that almost the entire Bay of Biscay anchovy population reaches sexual maturity at peak spawning as indicated in prior investigations (Lucio and Uriarte, 1990; Motos et al., 1991).

In 1989, point estimates for May and June indicate biomasses of 11,860 t (cv=0.41) and 10,058 t (CV= 55%). In May about half of that biomass was composed of 2 year old anchovies or older. In June the adult sampling was too poor as to infer the age composition of the spawning stock. Daily fecundity estimates were also rather close (62 and 55 eggs/day/g respectively, Table 2), although the values achieved in June were highly uncertain due to sampling deficiencies.

Table 1. Results of the consecutive DEPM anchovy surveys carried out in May and June 1989 and 1990. SST is sea surface temperature, $P_o$ is daily egg production for unit area, $cv$ is coefficient of variation, $P_{tot}$ is daily egg production in the whole spawning area, DF is daily specific fecundity.

<table>
<thead>
<tr>
<th>Year</th>
<th>Dates</th>
<th>SST °C</th>
<th>$P_o$ eggs/0.05m²</th>
<th>cv%</th>
<th>SA km²</th>
<th>Ptot e²/²</th>
<th>DF eggs/g</th>
<th>SSB t</th>
</tr>
</thead>
<tbody>
<tr>
<td>1989</td>
<td>10 - 21 May</td>
<td>16.6</td>
<td>2.08</td>
<td>27%</td>
<td>17546</td>
<td>0.7299</td>
<td>62.3</td>
<td>11861</td>
</tr>
<tr>
<td>1989</td>
<td>14-24 June</td>
<td>20.8</td>
<td>1.5</td>
<td>30%</td>
<td>27917</td>
<td>0.8263</td>
<td>54.8</td>
<td>10058</td>
</tr>
<tr>
<td>1990</td>
<td>4 -15 May</td>
<td>16.9</td>
<td>3.78</td>
<td>20%</td>
<td>59757</td>
<td>4.5176</td>
<td>52.2</td>
<td>97237</td>
</tr>
<tr>
<td>1990</td>
<td>29 May-15 June</td>
<td>17.7</td>
<td>5.21</td>
<td>13%</td>
<td>69471</td>
<td>7.2389</td>
<td>90.1</td>
<td>77254</td>
</tr>
</tbody>
</table>
Table 2. Estimates of adult parameters from the consecutive DEPM anchovy surveys carried out in May and June 1989 and 1990. DF is daily specific fecundity, R is sex ratio, S is spawning frequency, F is batch fecundity and Wf is mean weight of females.

<table>
<thead>
<tr>
<th>Year</th>
<th>Month</th>
<th>DF</th>
<th>cv</th>
<th>R (%)</th>
<th>cv</th>
<th>S</th>
<th>cv</th>
<th>F</th>
<th>cv</th>
<th>Wf</th>
<th>cv</th>
</tr>
</thead>
<tbody>
<tr>
<td>1989</td>
<td>May</td>
<td>62.3</td>
<td>0.13</td>
<td>0.54</td>
<td>0.07</td>
<td>0.26</td>
<td>0.10</td>
<td>12977</td>
<td>0.04</td>
<td>29.65</td>
<td>0.01</td>
</tr>
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<td>1989</td>
<td>June</td>
<td>54.8</td>
<td>0.28</td>
<td>0.51</td>
<td>0.12</td>
<td>0.17</td>
<td>0.23</td>
<td>15307</td>
<td>0.07</td>
<td>23.69</td>
<td>0.06</td>
</tr>
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<td>1990</td>
<td>May</td>
<td>52.2</td>
<td>0.36</td>
<td>0.53</td>
<td>0.04</td>
<td>0.28</td>
<td>0.04</td>
<td>7039</td>
<td>0.05</td>
<td>19.69</td>
<td>0.06</td>
</tr>
<tr>
<td>1990</td>
<td>June</td>
<td>90.1</td>
<td>0.12</td>
<td>0.58</td>
<td>0.11</td>
<td>0.30</td>
<td>0.06</td>
<td>8993</td>
<td>0.03</td>
<td>1713</td>
<td>0.02</td>
</tr>
</tbody>
</table>

In 1990, SSB estimates in May and June were 97,239 (cv=0.17) and 77,254 tons (cv=0.19), respectively. The decrease of biomass between surveys is explained by commercial catches, migration of big anchovies to non-surveyed areas and errors of the estimates. One year old anchovies accounted for 96% of the spawning stock (in numbers) in 1990. This relevant recruitment explains the big difference from the 1989 SSB estimate. Daily specific fecundity of the stock increased from May till June (from 52 to 90 eggs/day/g respectively, Table 2).

Mean weight of females decreased from May to June in both years, from 29.7 to 23.7 g in 1989 and from 19.7 to 17.1 g in 1990 (Table 2). It also evidenced a stronger reduction in 2+ anchovy numbers than in 1 year old anchovies from May to June. This fact could be explained either by a biased sampling of adults in June, or by a bigger fishing pressure on 2+ anchovies or, eventually by migration of 2+ anchovies to outside the survey area. The latter would imply that 2+ anchovy would be underestimated by the June survey.

A clear increase of batch fecundity between surveys was observed (Table 2). It increased from 438 eggs/g per batch in May to 646 in June for 1989 and from 357 eggs per batch and gram in May to 525 in June in 1990. However, no significant differences in specific BF (eggs per gram) was found between big and small anchovies within any of the periods/years sampled.

The substantial increase in DSF from May (52 eggs/g, cv=0.08) to June (90 eggs/g, cv=0.12) recorded in 1990 was namely related to the above mentioned increase of batch fecundity between surveys. In addition, a higher than expected sex ratio in June 1990 (0.58) contributed to that increase.

Clearly the DEPM appears to be a very robust estimator of the spawning biomass of pelagic species, regardless the particular date of application around peak spawning season. Although the spawning area increased between May and June in both years, the consecutive estimates of spawning biomass were very consistent. There was a good agreement between May and June SSB estimates for both years. For example, the 20,000 t difference observed in 1990 (97,000 t in May vs 77,000 t in June) can be explained by the catches of the commercial fishery (10,000 t) and an annual instantaneous natural mortality rate of 1, which could account for an additional 10,000 t).

For the case of the Bay of Biscay anchovy these surveys served also to conclude that May surveys are more suitable than June surveys for the DEPM application. In May, anchovy spawning is at its peak and both adult anchovy and eggs are distributed in a more reduced area than later on the season, simplifying the spatial coverage of the spawning stock by the survey. In addition, at this season all year classes are present in the spawning area and all of them are already mature.

Acknowledgements

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References


ASSESSING THE BAY OF BISCAY ANCHOVY POPULATION BY DEPM: A REVIEW 1989-2001

Lorenzo Motos¹, Andrés Uriarte¹, P. Prouzet², M. Santos¹, Paula Alvarez¹, Yolanda Sagarminaga¹.

¹AZTI, Food and Fish Technological Institute, Marine Research Unit, Herrera Kaia Portualdea z/g, 20110 PASAIA(Gipuzkoa), Basque Country, Spain (lmotos@pas.azti.es).
²Laboratoire Halieutique d’Aquitaine, Institut Français de Recherche pour l’Exploitation de la Mer, Technopole IZARBEL, Côte Basque, Maison du Parc, 64210 Bidart, France.

This paper reviews the basis for application and describes the realization of the Daily Egg Production Method (DEPM) to the Bay of Biscay anchovy population during the period 1989 to 2001. The main problems found are highlighted and the developments derived from this application listed and explained. Methodology, technological developments and shortcuts, which can be applied to other similar populations are discussed.

Since VPA-like assessment methods are not an adequate tool for pelagic, short living, species such as anchovies, direct surveying methods are required to assess the status of these stocks. For the Bay of Biscay anchovy the DEPM (Lasker, 1985) is used to monitor the population on an annual basis. For that purpose, concurrent egg surveys have been conducted every year (except in 1993) along the putative spawning area of this stock at peak spawning time (May-June). Adult sampling over the spawning area was obtained for most of the years either through direct fishing from the egg sampling vessel (as in 1991 and 1992) or by collaboration with a French parallel acoustic survey (1994, 1997, 1998, 2001). This sampling is complemented with opportunistic samples collected from the commercial fleet operating in the area. The surveys are aimed to get estimates of realised spawning area, egg production, population fecundity and population biomass and age composition.

Table 1. Historical series of spawning stock biomass, total egg production ($P_{tot}$), daily egg production, spawning area (SA) and daily fecundity (DF) estimates for the period 1989-2001.

<table>
<thead>
<tr>
<th>Year</th>
<th>Period</th>
<th>SSB t</th>
<th>$P_{tot}$ eggs $10^{12}$</th>
<th>$P_{0}$ eggs/0.05m²</th>
<th>SA km²</th>
<th>DF eggs/g</th>
</tr>
</thead>
<tbody>
<tr>
<td>1989</td>
<td>10 - 21 May</td>
<td>11,861</td>
<td>0.73</td>
<td>2.08</td>
<td>17,546</td>
<td>62.30</td>
</tr>
<tr>
<td>1990</td>
<td>4 - 15 May</td>
<td>97,237</td>
<td>4.52</td>
<td>3.78</td>
<td>59,757</td>
<td>52.20</td>
</tr>
<tr>
<td>1991</td>
<td>16 May - 07Jun</td>
<td>19,276</td>
<td>1.24</td>
<td>2.55</td>
<td>24,264</td>
<td>67.50</td>
</tr>
<tr>
<td>1992</td>
<td>16 May -13 Jun</td>
<td>90./70</td>
<td>5.79</td>
<td>4.27</td>
<td>67./796</td>
<td>71.60</td>
</tr>
<tr>
<td>1994</td>
<td>17 May – 3 June.</td>
<td>60,062</td>
<td>3.83</td>
<td>3.93</td>
<td>48,735</td>
<td>62.85</td>
</tr>
<tr>
<td>1995</td>
<td>11 - 25 May</td>
<td>54,701</td>
<td>3.09</td>
<td>4.96</td>
<td>31,189</td>
<td>56.72</td>
</tr>
<tr>
<td>1996</td>
<td>18 - 30 May</td>
<td>51,176</td>
<td>2.77</td>
<td>4.87</td>
<td>28,448</td>
<td></td>
</tr>
<tr>
<td>1997</td>
<td>9 - 21 May</td>
<td>101,976</td>
<td>5.59</td>
<td>3.83</td>
<td>73,131</td>
<td>56.54</td>
</tr>
<tr>
<td>1998</td>
<td>18 May - 8 June</td>
<td>3.59</td>
<td>3.52</td>
<td>51,019</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1999</td>
<td>22 May - 5 June</td>
<td>2.61</td>
<td>3.45</td>
<td>37,883</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2000</td>
<td>2 - 20 May</td>
<td>124,132</td>
<td>8.48</td>
<td>5.89</td>
<td>72,022</td>
<td>70.75</td>
</tr>
</tbody>
</table>
The magnitude of the realised spawning area changes with the abundance (biomass) level of the population, leading to substantial inter-year variation on this parameter (Table 1). However, spawning area increases as the spawning season progresses due to a centrifugal migration from the recurrent main spawning centres in SE Biscay. In a similar way, total egg production rates changes proportionally with biomass, although egg production rates per surface unit appears much more stable (Table 1). These phenomena evidence a density dependent occupation of the habitat by anchovy in the Bay of Biscay.

Daily Specific Fecundity (DSF), and particularly the determination of the Spawning Frequency (S) appear to be problematical due to the interaction between sampling and special features of the reproductive biology of this species. In addition to the already noticed oversampling of spawning females (Santiago and Sanz, 1992), we also found that pre-spawning females are oversampled between 32 and 6 hours before spawning. This finding has forced to modify the standard procedures to estimate this parameter.

![Figure 1. Historical series of spawning stock biomass estimates for the Bay of Biscay anchovy. Vertical lines represent ±2SD confidence intervals. No DEPM survey was carried in 1993.](image1)

![Figure 2. DEPM estimated age composition of the Bay of Biscay anchovy population from 1989 to 2001. Age categories are 1, 2 and 3+ year old. In 1996, 1999 and 2000 no adult survey was carried out. No DEPM survey was carried in 1993.](image2)
Biomass estimates fluctuates within a eightfold factor during the 1987-2001 time series (from 16,000 t to 120,000 t). Figure 1 shows the total spawning stock biomass estimates along with their correspondent confidence intervals. The recruiting 1 year old anchovy usually accounts for the major portion of the population, fluctuating between 27% and 97%, and it is the responsible of the bouncing dynamics of this stock (Fig. 2).

One year old anchovy are usually prevalent in the coastal spawning grounds along the French coast associated to areas influenced at surface by river outflows (Motos et al., 1996). However, peculiar distributions are observed some years, as in 1997 when unusual concentrations of 1 year old anchovy were found in the oceanic spawning grounds. The biggest sized 1 year old and older aged anchovies usually occur further apart from the coast, close to the shelf break or associated to oceanic gyres and fronts.

During the development of the survey series, new improvements have been introduced to the former procedures originally established by Lasker (1985). These developments include the use and testing of an adaptive sampling design, including for that purpose as well the complementary use of CUFES; extending the DEPM to the estimation of spawning population in numbers at age, spatio-temporal modelling techniques (GAM and geostatistics) for egg production and adult fecundity parameter estimates, correction of bias for S estimates and others. These developments are crucial for minimizing bias and maximizing the precision and reliance of the DEPM.

Acknowledgements
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References


APPLICATION OF GENERALISED ADDITIVE MODELS TO THE DAILY EGG PRODUCTION METHOD FOR THE BAY OF BISCAY ANCHOVY (ENGRAULIS ENCRASICOLUS L.)

Leire Ibaibarriaga¹, M. Santos¹, Andrés Uriarte¹, D. L. Borchers², C.E. Dixon², M.E. Lonergan², S.N. Wood³

¹AZTI Foundation, Fisheries and Food Technological Institute, Herrera Kaia Portualdea z/g, 20110 Pasai, Basque Country, Spain, (libaibarriaga@pas.azti.es).
²CREEM, University of St. Andrews, The Observatory, Buchanan Gardens, St. Andrews, Fife, KY16 9LZ, Scotland, UK.
³Department of Statistics, University of Glasgow, Glasgow, G12 8QQ, Scotland, UK.

The traditional Daily Egg Production Method (DEPM) has been applied since 1987 for the Bay of Biscay anchovy (Engraulis encrasicolus L.). Recently, following the work by Borchers et al. (1997), new methodology and software for the estimation of the daily egg production and mortality rates have been developed as part of the EU project (Study 99/080).

Staged egg frequencies are first transformed into daily cohort densities using a new ageing method. This method is developed from the ageing method described in Bernal et al. (2001), in which information on the spawning synchronicity is introduced via a probabilistic resampling method. From the Bayes’ theorem the posterior distribution of age ($a$) given stage ($i$), temperature ($t$) and sampling time ($τ$), $f(a | i,t,τ)$, is proportional to the prior distribution of age, $f(a | τ)$, times the likelihood of the stages given age and temperature, $f(i | a,t)$:

$$f(a | i,t,τ) \propto f(i | a,t)f(a | τ)$$

The first term on the rhs of (1), the probability function of stages given age and temperature, is estimated from a multinomial model fitted to the incubation experiment data. The second term on the rhs, the prior distribution of age given the sampling time $τ$, is based on the distribution of spawning times, $S(τ-a)$, multiplied by a mortality term, $e^{-Zτ}$. In the case of the Bay of Biscay anchovy, spawning time distribution per day is assumed to be normal with mean at 23 hours and standard deviation of 1.25 hours, based on histological analysis and incidence of stage I eggs on the historical data series.

The number of eggs and average age expected in each daily cohort are computed integrating the posterior distribution of age over the age range within each of the daily cohorts.

The expected number of eggs per daily cohort in sample $i$ is modelled as

$$μ_i = R_iP_0e^{-Zα_i}$$

where $μ_i$ denotes the expected number of eggs per daily cohort, $R_i$ the effective sea surface area sampled, $P_0$ the daily egg production per m$^2$, $Z$ the egg mortality rate per day and $α_i$ the expected average age per daily cohort. The model is fitted by means of a generalised additive model (GAM) with over dispersed Poisson error distribution and log link, in which the log daily egg production and mortality rates are smooth functions of spatial and environmental variables. The model with lowest generalized cross validation score (Wood, 2000; 2003) is selected.

Total daily egg production is computed as the sum of the predicted values over a regular grid that covers the survey area. Variance is estimated by non-parametric bootstrap from the original incubation experiment and survey data. This allows quantifying the variability due to the sampling and the ageing process.
This methodology was applied for the Bay of Biscay anchovy from 1996 to 1999. In the selected model daily egg production consisted of a bivariate smooth of longitude and latitude aiming to describe the spatial location, a bivariate smooth of salinity and temperature for characterising the environmental situation and a bivariate smooth of depth and alongdist (distance along the coast to a given point), indicating that the effect of depth changed in space. On the other hand, daily mortality rate was assumed constant all over the space for comparison with the traditional approach.

Figure 1 shows the daily egg production estimates for 1996-1999 given by the traditional DEPM and by the new GAM methodology, with their correspondent confidence intervals. Point estimates from both approaches are consistent, differences being from 1 to 20%. Contrary to expectation, the new GAM methodology did not reduce the estimated uncertainty associated with $P_0$. However it must be borne in mind that the traditional variance estimates were unrealistically small, reaching a CV of 5% in 1997, whereas the GAM method estimates were plausible, CV between 13% and 21%, suggesting that the traditional precision could be negatively biased. Currently the variance estimation process in the traditional method is being revised.

An advantage of the GAM methodology is that it provides predicted egg production surfaces that allow tracking historical changes of the spawning in space and analysing its relationship with environmental covariates.

The first attempt to use GAM’s for studying the structure of the daily specific fecundity (DF) in space was done using data from the 2002 survey. The key adult parameters for the Bay of Biscay anchovy are female weight (W) and spawning fraction (S) - since batch fecundity (F) is directly dependent on W (by a linear model) and expected sex ratio in weight (R) can also be inferred from W under the hypothesis of 1:1 sex ratio in numbers. W was fitted using a GAM with normal distribution, identity link and a bivariate smooth of latitude and longitude in an attempt to capture any spatial cline. The model explained 88% of the deviance. Similarly, S was fitted using a GAM with binomial distribution, logit link and a bivariate smooth of latitude and longitude. However, the smoother was almost flat and the explained deviance was very small (3%), suggesting little spatial structure in this parameter. Therefore, S was assumed constant all over the space. F and R surfaces were derived from the surface of W. Finally, maps of SSB were obtained by dividing the total daily egg production and DF predicted surfaces. Figure 2 shows maps of the predicted surfaces of SSB.
References


Figure 2. Fitted SSB surface derived from the egg production and DF surfaces for 2002.
APPLYING NEW STATISTICAL TOOLS TO IMPROVE DEPM-BASED ESTIMATE OF SPAWNING BIOMASS OF IBERO ATLANTIC SARDINE (SARDINA PILCHARDUS, WALB.)

M. Bernal¹, Y. Stratoudakis², M. Lonergan³, A. Lago de Lanzós⁴, L. Valdés⁵, D. Borchers³ and S. Wood⁶

¹Instituto Español de Oceanografía, C.O. de Málaga, Puerto pesquero s/n 29640 Fuengirola, Spain (miguel.bernal@ma.ieo.es).
²Instituto das Pescas e do Mar. INIAP/IPIMAR, Avenida de Brasilia, s/n, Lisboa, 1449-006, Portugal.
³CREEM, University of St. Andrews, Buchanan Gardens, St. Andrews KY16 9LZ, Scotland.
⁴IEO, C.O de Madrid, Avenida de Brasil, 31, 28020, Madrid, Spain.
⁵IEO, C.O de Gijón, Avenida Príncipe de Asturias 70 bis, 33212 Gijón, Spain.
⁶Department of Statistics, University of Glasgow, Glasgow G12 8QQ, Scotland.

In this work, a new implementation of the Daily Egg Production Method (DEPM) to estimate spawning biomass (SSB) of Ibero-Atlantic sardine (Sardina pilchardus, Walb.) is presented. The new methods include an improved model of incubation data, together with a Bayesian ageing method, and spatially explicit models of both egg production and adult parameters, based on improved Generalised Additive Models (GAMs). The new DEPM have been developed under the EU study 99/080 and provide a general framework in which to obtain final estimates of Spawning Stock Biomass (SSB) as a function of geographical and/or environmental covariates. Also, bootstrap-based confidence intervals of the SSB estimates that accounts for variability accumulated through the implementation of the DEPM can be obtained within the new DEPM framework. Two aspects of the new implementation are discussed in this abstract. First, the use of multinomial models to fit data from sardine incubation experiments is discussed, and its advantages in comparison with the traditional way of analysing the incubation experiments (Lo, 1985; Miranda, 1990) are briefly discussed. On the second part of the abstract, spatial explicit DEPM-based sardine SSB estimates for recent Iberian DEPM surveys are shown. They are obtained by fitting GAMs to both egg production and some adult parameters, like mean weight and spawning frequency. Scientific papers explaining the whole new DEPM based SSB estimation procedure are on preparation.

Figure 1 shows the result of applying multinomial models to fit data from a sardine incubation experiment. Multinomial models allow to describe egg development by fitting the probability of being at any given stage as a function of age and temperature, and allow the variability of observed ages at given stages and temperatures to be extracted directly from the data. In the figure, each stage is represented by a line which describes a bell-shape trajectory, in which the probability of being in a given stage increases after certain age up to a certain maximum and afterwards decreases when next stage probability increases. For stage I, only the decreasing part of the curve is observed, while for stage XI, the decrease is forced by the transition of all eggs to larvae, which was recorded on the experiment but was not plotted on the figure. For certain stages like stage II, V or VI, the probability becomes one, indicating ages at which all eggs are in those stages, while for other stages, specially for stages III and IV, there is a large degree of overlapping with other stages, indicating that the transition between those stages and the next ones is fast, and so it is impossible to observe all eggs in those stages. The degree of overlapping also increases for old stages and specially for increasing temperatures. In comparison with traditional models of egg development (Lo, 1985; Miranda, 1990), the multinomial models described here allow a flexible fit to the data, without having to assume monotonous trends between stages, while modelling the duration of each stage as a monotonous function of age and temperature. Also, the traditional models use age as the response and stage and temperature as the independent covariates, while the multinomial models appropriately uses stage as the response variable of the incubation experiment, and uses temperature and stage as a continuous independent variable and a factor respectively. The appropriate statistical use of the observed variables allows interpreting the summary statistics of the multinomial models in a more informative way than in the case of the traditional models.
Figure 1. Multinomial model of Iberian sardine incubation data. Each line (in grey scale) represent one stage, and numbers 1 to 9 and letters a and b represent the 11 stages. On the x axis is the observed ages (i.e. elapsed times from the start of experiment) and y axis is the probability of a given stage. Each panel represent a different temperature.

Plate 10 (page xiv) shows the new SSB estimates, based on spatial models of egg production and adult parameters. The new estimates can thus take into account the spatial structure of the population, and are of special interest when there are strong spatial trends in some of the DEPM parameters. The new SSB estimates are in general similar to the ones estimated by the traditional DEPM, when adequate post-stratification was performed. Nevertheless, adequate post-stratification is not always easy to perform when the spatial structure of the population is not analysed in depth, and a correct post-stratified traditional estimate has not always been available for the case of Iberian sardine. As for precision of the SSB estimates, the confidence intervals of the new estimates are narrower than previous ones, even when more sources of uncertainty (egg ageing) are included in the estimation. For the first time, the estimated spatial distribution of DEPM-based SSB can be compared with other independent sources, like acoustic densities, and although some discrepancies exist, both sources of data show general similar patterns.

References

RECOMMENDATIONS FROM THE DISCUSSION SESSION: CHARACTERIZING SPAWNING HABITAT

Discussions held during this session have been grouped into six major themes, namely (1) Defining spawning habitat; (2) Characterizing spawning habitat; (3) Selection of spawning habitat; (4) Population size and distribution effects on spawning habitat; (5) Climate change and spawning habitat; and (6) Future research directions. Each of these is described in detail below.

1. **Defining spawning habitat** - Data on the abundance and distribution of eggs (and occasionally larvae) are generally used to define and delineate spawning habitat, primarily because these early life history stages are relatively easy to sample compared to later stages such as actively spawning adults. Other definitions may be used, however, and a continuum of three, nested definitions of spawning habitat was proposed at the session. These were (i) “Potential spawning habitat” – habitat where the hydrological and/or physical conditions are suitable for fish to spawn; (ii) “Realized spawning habitat” - habitat where spawning actually occurs, and (iii) “Successful spawning habitat” - habitat where fish have spawned and from where successful recruitment has resulted. Under these definitions, the delineation of spawning habitat based on the abundance of spawn products therefore identifies realized spawning habitat and can be used to demarcate potential spawning habitat, but cannot identify successful spawning habitat. Given that the vast majority of eggs spawned do not survive to recruitment, the identification and detailed study of successful spawning habitat was considered to be of critical importance and a necessary requisite for improving understanding of variability in the population dynamics of small pelagic fish (suggested approaches to this are listed in the section on future research directions). However, examination of areas that qualify as potential spawning habitat but are never realized was also considered important, since this may allow the identification of factors that contribute to successful spawning habitat.

2. **Characterizing spawning habitat** – Changes in the productivity of small pelagic fish populations may be caused by changes in ocean climate that affect the extent, or spatial and temporal location of, suitable spawning habitat (Hunter and Alheit, 1997). Hence characterizing the spawning habitats of small pelagic fishes in terms of environmental variables will permit evaluation of this hypothesis. Accurate characterization of spawning habitat should take cognizance of the spawning strategy of the species in question, determined in part from data collected during DEPM assessments.

Temperature/salinity plots and single parameter quotient analysis (see van der Lingen et al., 2005) are considered to be “bottom-up” approaches to objectively characterize and quantify potential spawning habitat, and enable the incorporation of such quantification into models. Temperature and salinity are the aquatic equivalents of latitude and longitude, and hence can identify water mass characteristics. A disadvantage of this approach is that temperature and salinity may not necessarily be important per se for spawning habitat selection, but may be proxies for other variables (e.g. productivity) that may be more relevant to spawning habitat selection. Additionally, temperature/salinity plots may provide information at too large a resolution, and the use of this method may miss mesoscale features such as eddies and filaments that fish may use as cues for selecting spawning habitat. Because the quotient analysis is relative, full characterization of potential spawning habitat using this method will require large amounts of data to ensure complete coverage of the spawning area. In addition, data from areas where spawning does not occur, and has not occurred, are also required, in order to ascertain the upper and lower parameter thresholds for potential spawning habitat. Approaches that use other biological indices in the “bottom-up” characterization of spawning habitat should be further investigated, including phytoplankton biomass (e.g. Twatwa et al., 2004) and/or production, and zooplankton biomass (e.g. Lynn, 2003) and/or size structure. Additionally, “top-down” approaches to quantifying spawning habitat which examine predation and mortality on both spawning fish and their spawn products should be promoted and applied.
3. **Selection of spawning habitat** – Small pelagic fish are indeterminate spawners that spawn repeatedly over a protracted reproductive season, and often in a variety of environments. The number of eggs produced per spawning season depends both on energy (lipid) reserves and the quantity and quality of food available during the season, and hence is not fixed at the beginning of the reproductive season. Additionally, small pelagic fish can cease spawning and reabsorb their eggs if conditions become unfavourable, a process known as atresia. Given the above, weak or no selection for temperature/salinity optima or for other environmental proxies could perhaps be expected. However, spawning is both a physiological and behavioural process, and fish need to receive specific inputs for these at specific times in order for spawning to occur. A fish with sufficient energy reserves will swim eastwards (for example), until it reaches water of suitable hydrographic and biological characteristics that will trigger the next behavioural response which will lead to spawning. Hence spawning is the end result of a complex chain of behavioural activities that must occur in the proper sequence and at the correct time in the fish’s life. Whereas fish can only sense presently-occurring stimuli via the brain, there may also be genetic imperatives and/or teleonomic imprinting (Cury, 1994) that could impact on their selection of spawning habitat.

Absolute values of hydrographic parameters are probably not as important for the selection of spawning habitat as are changes in those values, suggesting that rates of change (gradients) in hydrographic parameters may be useful in assessing spawning habitat selection. For some species/populations of small pelagic fish the selection of spawning habitat may depend more on geography than on hydrography. For example, far eastern sardine (*Sardinops sagax*) are conservative in that they always select a specific geographic location for spawning (upstream of the Kuroshio Current) that encompasses a wide range of environmental variability. Hence characterization of the spawning habitat of this population using temperature/salinity plots or quotient curve analysis would likely indicate weak or no selection for environmental optima. Such fidelity to a particular geographical location of spawning habitat may have more to do with population memory than with present selection.

Whereas some consistency in the environmental characteristics of spawning habitat selected by small pelagic fish is observed (see Rebstock, 2002, who analysed a 50 year time series of ichthyoplankton and hydrographic data that indicated that northern anchovy *Engraulis mordax* spawn at relatively high salinities over a wide range of temperatures whereas Pacific sardine *S. sagax* spawn at lower temperatures over a wide range of salinities), substantial inconsistency is also seen, in particular at the interannual scale. This suggests that there is no single environmental key to spawning habitat selection, and that different environmental characteristics and/or processes may differ in their relative importance to spawning habitat selection from year to year. Additionally, spawning habitat selection by the same species (e.g. *S. sagax*) or genus (e.g. *Engraulis* spp.) is likely to be different in different systems; for example, advection (and loss of spawn products via this process) is likely to be a more important process in upwelling systems than in non-upwelling systems, and selection of spawning habitat is likely to reflect this.

4. **Population size and distribution effects on spawning habitat** – Population size and structure, and population distribution patterns, are considered to exert significant impacts on spawning habitat selection. Many studies have shown that small pelagic fish populations expand their area of distribution at high biomass levels, and “retreat” into refugia at low biomass levels. The increase in the area of distribution at high biomass levels presumably increases the range of environmental variability encountered by the population as a whole, and also means that fish at the extremes of the population distribution are likely to encounter sub-optimal environmental conditions compared to those at the centre. This suggests that the relative importance of environmental parameters used to select spawning habitat may vary over their distributional range, and that realized spawning habitat may well differ for stocks/populations at the mid-point of their distributions compared to those at the extremes. Furthermore, it is considered likely that environmental influences will be more important to spawning habitat selection for fish at the
extremes than those in the centre. The occupation at low biomass levels of refugia that appear to be consistently located in space emphasizes the need for accurate characterization of spawning habitat in these areas, and the sometimes marked discrepancy in prevailing environmental conditions between refugia and areas occupied at high biomass indicates that characteristics of spawning habitat at low biomass levels should not be extrapolated to high biomass scenarios. Additionally, biomass effects may be important in determining the ratio of potential to realized spawning habitat.

Older, larger fish can migrate further, and hence can colonize a wider range of potential spawning habitats than can younger, smaller fish. Additionally, because they spawn larger batches, spawn more frequently, and spawn for a longer period during the spawning season, larger fish contribute substantially more to total reproductive output than do smaller fish. This suggests that age structure should be considered in conjunction with spawning habitat selection and characterization, and that spawning habitats of first-time spawners be examined separately, where possible, from those of repeat spawners. Since overexploitation tends to reduce population age structure by preferentially removing older, larger fish, this practice will likely have significant impacts on spawning habitat selection.

5. Climate change and spawning habitat – The goal of SPACC is to better understand and ultimately predict the effects of climate change on the productivity of small pelagic fish populations, and scenarios regarding climate change need to be built and assessed to address this goal. Scenarios regarding possible effects of climate change on oceanography can be (and have been) constructed, but linking such scenarios and the biological response of small pelagic fish to these scenarios is considered to be a major challenge. Providing definitions of spawning habitat in terms of oceanographic criteria that can be incorporated into such scenarios was seen as a useful output of the SPACC Workshop and Meeting that could go some way to providing such linkages. Predicting changes in the relative abundance of small pelagic fish arising from climate change is considered difficult at this stage, whereas predicting changes in potential spawning habitat may well be easier. Long-term climate changes were not considered likely to have the same effect on spawning habitat selection as interannual changes in oceanography. Particular emphasis was placed on assessing, via modeling, how climate change could affect the critical environmental processes (Bakun’s (1996) triad of enrichment, concentration and retention) associated with the survival and recruitment of small pelagic fishes.

6. Future research – The following research regarding the characterization of the spawning habitats of small pelagic fish is recommended:

- Examine the utility of identifying successful spawning habitat through linking IBMs with hydrodynamic model outputs and assessing whether particular spawning areas are consistently successful in terms of pre-defined criteria pertinent to recruitment (e.g. Huggett et al., 2003; Mullon et al., 2002).

- Examine the utility of identifying successful spawning habitat through analysis of fish otoliths microchemistry to “backtrack” where and when eggs were spawned (note that because small pelagic fish populations are often very large, particularly in upwelling systems, large sample sizes will be required to obtain meaningful results). This could be coupled with a backward-running hydrodynamic model in order to link otolith microchemistry and structure (i.e. daily rings, which provide information on growth rate and, indirectly, survival; e.g. Allain et al., 2003) to environmental variability (note that realistic back-tracking will require data assimilation and a time-scale of 3-5 years to resolve mesoscale features and variability).

- Compare the characteristics of realized spawning habitat (i) at the centre and edges of a population/species distribution; (ii) for different age classes within a population; (iii) at low and high biomass levels; and (iv) at the beginning and the end of the reproductive season. This
may be best achieved via a meta-analysis conducted for a single stock; for different stocks and/or populations of small pelagic fish within one system; for stocks and/or populations of the same genus (or species) across a variety of systems; or for all stocks of small pelagic fish across a variety of systems.

- Conduct a meta-analysis in which realized spawning area (using a variety of threshold egg abundance values) is plotted against biomass for a variety of small pelagic fish stocks. Stocks that show a significant relationship between spawning area and biomass are considered likely to be less affected by environmental variability than those which do not show a significant relationship, as are stocks having a higher slope value (assuming a linear fit) compared to those showing a lower slope value. Additionally, analysis of the error structure of such relationships may possibly be used to infer differences between species.

References


RECOMMENDATIONS FROM THE DISCUSSION SESSION: DEPM APPLICATIONS AND METHODOLOGICAL ADVANCES IN THE SPACC CONTEXT

The DEPM, when applied regularly, provides a sampling framework which in the long term allows for studying the role of environmental factors (such as temperature, El Niño events, etc.) on the reproductive biology of small pelagic fish species. In addition the mapping of spawning areas required by the DEPM is used to analyse the selection of spawning habitats made by these species. The combination of egg and adult sampling help to understand the spatial structuring of the population by sizes or ages and its spawning behaviour in relation to the environment (maturing cycle, size-selection of spawning habitats, migration patterns etc.). Finally, the levels of (DEPM) biomass estimates and their inter-annual changes reflect the productivity of the ecosystems and their variation in time, potentially related to fluctuating environmental conditions.

The SPACC sub-group on DEPM discussed several issues: First, the problems of estimating the reproductive parameters of small pelagic fish and how environment can influence them. Second, the incorporation of improved sampling tools as CUFES, in terms of their advantages and weaknesses to improve survey designs and egg mapping. Finally, recent advances in egg production estimates ($P_0$) were reviewed, including topics such as application of GAMs, inclusion of yolk larvae, analysis of egg incubation data, etc. The summary of those discussions follows (with some quotations of authors in brackets referring to abstracts included in this GLOBEC report).

1. Reproductive parameters and environment

Temperature may affect the rates of atresia, batch fecundity and spawning fraction. If the percentage of atresia is relevant, the estimation of the spawning frequency ($S$) can be problematic and that percentage should be checked for each region, as it is the usual practice in South Africa, Aegean Channel, etc. In the Gulf of California, it seems that the rate of atresia could be affected by temperature (Cotero, this issue). In general the effect of temperature on atresia rates could be studied either by examination of routine DEPM adult samples or by ad hoc experimental opportunistic sampling at changing environmental conditions.

Atresia can also influence the batch fecundity even after the hydration occurs (Ochoa et al.; Cotero, both in this issue), although generally it is not important at peak spawning time. Batch fecundity might also be estimated prior to the hydrated state of oocytes, for instance for *Sardinops caeruleus* (Ochoa) and this feature could be used to check consistency between successive spawning batches and to check whether temperature dependent atresia can affect realized batch fecundity.

Usually spawning time and maturation changes with size and age of fishes. In general small fishes have higher incidence of atresia (Torres-Villega et al., this issue) and probably smaller spawning frequency than big ones (Claramount et al., this issue).

Temperature could also affect directly spawning fraction ($S$). For instance in El Niño events tend to decrease $S$ compared to other years in the Gulf of California (Cotero; Torres-Villega et al., both in this issue). Good adult food availability however, regardless of temperature, can enhance the condition of fishes inducing higher spawning frequency than usual (Somarakis, 2004). When checking for potential effects of temperature on spawning frequency care should be paid not to confound the effect of temperature on POFs degeneration rates with its effect on $S$ itself. Fitzhugh and Hettler (1995) assessed the effect of temperature on menhaden POFs degeneration rates in aquariums, showing that an increase in temperature accelerates POFs degeneration. The daily vertical migration of anchovies and sardines, will minimize the changes in the temperatures affecting POFs degeneration among years or regions, because they will be far less important than the changes occurring in surface temperatures. Nevertheless, this is a line of research that deserves further work.
In general, problems in S determination might be shown by examining the statistical distributions of occurrence of day 1 and 2 POFs throughout the day. They should be consistent at all times whenever the likely over-sampling of active spawning females is duly removed.

2. CUFES application for egg mapping and in DEPM surveys

Different uses of the Continuous underway Fish Egg Sampler (CUFES) (Checkley et al., 1997) were discussed:

**CUFES for egg mapping spawning areas:** CUFES capacity in detecting eggs (presence/absence) is similar or better than that of CalVET, but its detection properties change slightly between species and depends as well upon the local hydrographic conditions. CUFES is however more efficient for mapping sardine than anchovy eggs (Van der Lingen and Checkley; Santos et al., both in this issue). This is probably due to the fact that sardine eggs do not show extrusion through the 500 μm mesh net of CUFES, while for anchovy significant extrusion seems to exist.

CUFES, by allowing fast continuous egg sampling, has the potential of monitoring the effect of changes in environment on spawning areas, through for instance, repeated surveys during the spawning season.

**CUFES can be used for optimal allocation of sampling effort in adaptive surveys:** The allocation of CalVETs according to CUFES egg abundance has the drawback of being labour intensity, since requires real time continuous work with the CUFES. In California (Lo et al., 2001 and in this issue) CUFES has been used to calibrate the P₀ between regions of low and high CUFES egg abundances, by setting a raising factor between the two areas. CalVET is only used at high abundance spawning areas. This can be applied to other areas and particularly where wide geographical potential spawning area must be covered during the cruises. When starting this procedure a minimum CalVET sampling should be implemented in the low CUFES egg abundance areas in order to verify that post stratification was correctly applied.

Further quantitative use of CUFES as to infer total egg abundance in the water column requires proper calibration with integrated vertical samplers (as CalVET nets). The position of the pump (in the bottom or aside the hull) can affect the sampling properties of CUFES (B. Planque, pers. comm.). In addition, year and vessel effects arise often (Van der Lingen and Checkley, Santos et al., both in this issue) which imply that for any quantitative use of CUFES, a year to year inter-calibration with CalVET must be done and also an inter-calibration among vessels if several vessels participate in the same survey.

**Standardization of CUFES** as an estimator of total egg abundance in the water column is being devised by modelling of the vertical distribution of eggs. Current models of vertical egg distribution (Boyra et al., Stenevik and Sundby, both in this issue) allow for obtaining raising factors of egg abundances at three meters depth over the total water column, but still with poor precision particularly in areas of low surface salinity. Therefore this issue deserves further development.

**CUFES shows a different egg-stage selectivity vs. CalVET** as in California (Lo et al., 2001) and other areas. In the Bay of Biscay these differences could potentially be modelled (Santos et al., this issue). But this must be checked for each application. Part of the differences in egg stages can result from the relevant percentage of sardine and anchovy eggs that are damaged by CUFES. The earlier the stage the more the percentage of damaged eggs (Santos et al., this issue).

**Calibration of CUFES vs CalVET** is difficult given that both gears are subject to observation errors: stochastic errors can affect both gears, but systematic errors may particularly relate to CUFES, given the differences in the relative percentages of eggs at surface that may occur at different hydrographic environments (Boyra et al., this issue). Functional regression lines could be used to establish
quantitative relationships. In order to get an estimate of the errors associated to each technique some experimental intensive sampling design could be devised for both gears in small selected areas within the range of the variogram (Dopolo, this issue). But different environments should be covered by the experiments. Alternatively a more general approach would consist in comparing the average egg abundances obtained by each gear over the whole spawning area; bias would appear in case of systematic errors and could be related to particular hydrographic environments.

3. Advances in egg production estimates (P₀)

Incorporation of General Additive Models (GAM) for P₀ estimates: Egg production in DEPM applications has been usually based on a non-linear regression of egg abundance at age for simultaneous estimation of P₀ and Z over the whole sampled area (or strata) (Picquelle and Stauffer, 1985). A new method is nowadays available based on a recently developed GAM application to egg production (Borchers and Wood, 2003), which produces spatial estimates of P₀ and potentially allows for a spatial variation in Z. Proper publication of the method and a manual for application is in progress. Application of this method requires some statistical skills, since potentially several slightly different estimates could result depending upon the final selection of covariates and model setting. In any case solutions should be close enough each other to those obtained with the standard procedure. The method forces the user to analyse in detail the data he is handling before achieving a sensible result.

Adult parameters can also be modelled and hence biomass be estimated and visualised in space (Ibaibarriaga, et al.; Bernal et al., both in this issue). For the standard DEPM procedures, it is important to have a good stratification of the spawning area with rather homogenous environmental conditions, so that Z and adult parameters can be considered constant over the spawning area for which P₀ is estimated. For practicality this cannot often be done. In the cases of high spatial heterogeneity of egg or adult parameters, GAM becomes a powerful tool for analysing that information and obtaining highly spatially resolved P₀ and SSB estimates (Bernal et al., this issue; ICES, 2003) because it deals with these parameters in its proper spatial context and, hence, not requiring any post stratification of the area.

Although the standard procedure will probably remain as a basic reference of P₀ and biomass estimates, GAMs allow for a spatial modelling of the egg production and adult parameters which are very useful for ecological analysis in the context of SPACC.

The inclusion of yolk larvae improves precision in P₀ estimates. This procedure will be unbiased provided natural mortality keeps constant over the whole range of eggs and larvae entering into the regression estimate: larvae at the stage of escaping the net should not be included (5 mm long are used as reference for sardine in California, based on bongo net). In Aegean Sea, larvae with pigmentation in the eye are rejected for P₀ estimates (Somarakis et al., 2004). A model of temperature dependent development of larvae will then be required (Riquelme et al., this issue).

Analysis of incubation experiments, for modelling the development rates of eggs (and subsequent larvae) at different temperatures, is a basic requisite for correct egg or larvae ageing. This is usually made by fitting Lo’s development rate model (1985) (Soto et al.; Sepúlveda et al., etc., all in this issue). But recently a multinomial model for the occurrence of stages by ages depending upon temperature it is being implemented to the analysis of incubation data (Ibaibarriaga et al.; Bernal et al.; both in this issue). Bayesian methods which combine the above multinomial model with the knowledge about the probability distribution of spawning time allows for new egg ageing procedures (Borchers and Wood, 2003).
Cutting the tails in both sides of the $P_0$ curve is important in order to assure that all eggs of different ages are sampled with equal probabilities. For the tail of old ages, a minimum cutting point of about 15-20% of the average hatching age might be necessary. Temperature has a major impact on the life of eggs before hatching of the larvae. If egg abundance and/or mortality can be related to temperature (see experimental results for $Z$ in Sepúlveda et al., this issue), then the allowed range of egg ages could affect the $P_0$ estimates. In these cases, a rule for cutting the ending tail of $P_0$ curve could be devised based on the hatching time for the upper range of temperatures at positive stations, but deserves detail consideration for each case. An initial study can be made by comparing inter-annual or regional variability of $P_0$ and $Z$ estimates and its relationship with environmental covariates (GAM software would help here).

References


LIST OF PARTICIPANTS

*author presenting a paper

Alheit, Juergen*
Baltic Sea Research Institute
Rostock University
Seestrasse 15, D-18119
Warnemünde
GERMANY
Email: juergen.alheit@io-warnemuende.de

Angélico, Maria Manuel*
IPIMAR
Av. Brasilia
Lisboa 1449-006
PORTUGAL
Email: angelico@ipimar.pt

Arcos, Dagoberto
Instituto de Investigación Pesquera
Casilla 350
Talcahuano
CHILE
Email: inpesca@inpesca.cl

Barange, Manuel*
GLOBEC
Plymouth Marine Laboratory
Prospect Place
Plymouth, PL1 3DH
UK
Email: m.barange@pml.ac.uk

Barbieri, M Angela*
Instituto de Fomento Pesquero
Blanco 839
Valparaíso
CHILE
E-mail: mabarbieri@ifop.cl

Bernal, Miguel*
Instituto Español de Oceanografía
Centro costero de Málaga
Puerto pesquero s/n
Fuengirola, Málaga
SPAIN
Email: miguel.bernal@ma.ieo.es

Bustos, Claudia
LOPEL
Department Oceanografía
Universidad Concepción
P.O. Box 160-C
Concepción
CHILE
Email: cbustos@udec.cl

Carrasco, Franklin*
Department Oceanografía
Universidad Concepción
P.O. Box 160-C
Concepción
CHILE
Email: fcarrasco@udec.cl

Castro, Leonardo*
LOPEL
Department Oceanografía
Universidad Concepción
P.O. Box 160-C
Concepción
CHILE
Email: lecastro@udec.cl

Chandía, Christian
LOPEL
Department Oceanografía
Universidad Concepción
P.O. Box 160-C
Concepción
CHILE
Email: crchandi@udec.cl

Checkley, David M. Jr.*
Integrative Oceanography Division
Scripps Institution of Oceanography
University of California San Diego
La Jolla, CA 92093-0218
USA
Email: dcheckley@ucsd.edu

Claramunt, Gabriel*
Departamento de Ciencias del Mar
Universidad Arturo Prat
P.O. Box 121
Iquique
CHILE
Email: gclaramu@unap.cl

Cotero, Eva*
SAGARPA
Instituto Nacional de la Pesca
Centro Regional de Investigación Pesquera-Mazatlán
MÉXICO
Email: cecotero@yahoo.com
Cubillos, Luis*
Instituto de Investigación Pesquera
Casilla 350
Talcahuano
CHILE
Current address:
Departamento de Oceanografía
Universidad de Concepción
PO BOX 160-C
Concepción
CHILE
E-mail: lucubillos@udec.cl

Dopolo, Mbulelo T.*
University of Cape Town
Private Bag
Rondebosch 7700
SOUTH AFRICA
Email: mbdopolo@deat.gov.za

Drapeau, Laurent*
IRD/MCM
Marine and Coastal Management
Private Bag X2
Rogge Bay 8012
SOUTH AFRICA
Email: ldrapeau@deat.gov.za

Escribano, Rubén
COPAS
Departamento de Oceanografía
Universidad Concepción
P.O. Box 160-C
Concepción
CHILE
Email: rescriban@udec.cl

Fréon, Pierre
Centre de Recherche Halieutique Méditer-
ranéenne et Tropicale
IRD - IFREMER & Université Montpellier II
Avenue Jean Monnet
BP 171
34203 Sète Cedex
FRANCE
Email: preon@attglobal.net

Green-Ruiz, Yanira A.*
SAGARPA
Instituto Nacional de la Pesca
Centro Regional de Investigacion
Pesquera-Mazatlán
MÉXICO
Email: motagreen@yahoo.com.mx

Hernandez-Leon, Santiago*
Facultad de Ciencias del Mar
Universidad de Las Palmas de GC
35017 Las Palmas de Gran Canaria
Canary Islands
SPAIN
Email: shernandez@dbio.ulpgc.es

Hormazabal, Samuel
Departamento de Física del Océano y la Atmosfera
Universidad de Concepción
Concepción
CHILE
Email: sam@profc.udec.cl

Ibaibarriaga, Leire*
AZTI
Herrera kaia portualdea z/g
20110 Pasaia
Guipúzcoa
SPAIN
Email: libaibarriaga@pas.azti.es

Inostroza, Pedro
LOPEL
Department Oceanografía
Universidad Concepción
P.O. Box 160-C
Concepción
CHILE
Email: peinostr@udec.cl

Irigoyen, Xabier*
AZTI
Herrera kaia portualdea z/g
20110 Pasaia
Guipúzcoa
Basque Country
SPAIN
Email: Xirigoien@pas.azti.es

Krautz, M Cristina*
LOPEL
Department Oceanografía
Universidad Concepción
P.O. Box 160-C
Concepción
CHILE
Email: ckrautz@udec.cl
Landaeta, Mauricio
LOPEL
Department Oceanografía
Universidad Concepción
P.O. Box 160-C
Concepción
CHILE
Email: mlandaeta@udec.cl

León, Roxana
LOPEL
Department Oceanografía
Universidad Concepción
P.O. Box 160-C
Concepción
CHILE
Email: rleonl@udec.cl

Llanos, Alejandra
LOPEL
Department Oceanografía
Universidad Concepción
P.O. Box 160-C
Concepción
CHILE
Email: alllanos@udec.cl

Lo, Nancy C.H.*
Southwest Fisheries Science Center,
La Jolla CA,
USA
Email: nancy.lo@noaa.gov

Motos, Lorenzo*
AZTI
Herrera kaia portualdea z/g
20110 Pasaia
Guipúzcoa
Basque Country
SPAIN
Email: lmotos@pas.azti.es

Muñoz, Maria Inés
LOPEL
Department Oceanografía
Universidad Concepción
P.O. Box 160-C
Concepción
CHILE
Email: mariaimu@udec.cl

Neira, Francisco J.*
Australian Maritime College
P.O. Box 21
Beaconsfield
Tasmania 7270
AUSTRALIA
Email: f.neira@fme.amc.edu.au

Núñez, Sergio
Instituto de Investigación Pesquera
Casilla 350
Talcahuano
CHILE
Email: inpesca@inpesca.cl

Oyarzún, Ciro
Department Oceanografía
Universidad Concepción
P.O. Box 160-C
Concepción
CHILE
Email: coyarzun@udec.cl

Pizarro, Pedro
Departamento de Ciencias del Mar
Universidad Arturo Prat
P.O. Box 121
Iquique
CHILE
Email: pedro.pizarro@unap.cl

Riquelme, Katty*
LOPEL
Department Oceanografía
Universidad Concepción
P.O. Box 160-C
Concepción
CHILE
Email: kriquelm@udec.cl

Roa, Rubén
Department Oceanografía
Universidad Concepción
P.O. Box 160-C
Concepción
CHILE
Email: rroa@udec.cl

Roy, Claude*
Centre IRD de Bretagne
29280 Plouzané
FRANCE
Email: claude.roy@ird.fr
Santos, Maria*
AZTI
Herrera kaia portualdea z/g
20110 Pasaia
Guipúzcoa
Basque Country
SPAIN
Email: msantos@azti.es

Sepúlveda, Aquiles*
Instituto de Investigacion Pesquera
Casilla 350
Talcahuano,
CHILE
Email: inpesca@inpesca.cl

Sobarzo, Marcus*
Department Oceanografia
Universidad Concepcion
P.O. Box 160-C
Concepcion
CHILE
Email: msobarzo@udec.cl

Somarakis, Stylianos*
Department of Biology
University of Patras
26500 Rio
Patra
GREECE
Email: somarak@upatras.gr

Soto, Samuel
Departamento de Ciencias del Mar
Universidad Arturo Prat
P.O. Box 121
Iquique
CHILE
Email: sasoto@udec.cl

Stenevik, Erling Kåre*
Institute of Marine Research
Bergen
NORWAY
Email: erling.stenevik@imr.no

Taniguchi, Akira*
Laboratory of Aquatic Ecology
Division of Environmental Bioremediation
School of Agriculture
Tohoku University
Aoba-ku, Sendai
Miyagi 981-8555
JAPAN
Email: Atani@bios.tohoku.ac.jp

Torres-Villegas, René*
Laboratorio de Morfofisiología.
CICIMAR-IPN.
La Paz B.C.S.
MEXICO
Email: jvillega@ipn.mx

Taylor, Paul*
National Institute of Water and Atmospheric Research Ltd
NEW ZEALAND
Email: p.taylor@niwa.co.nz

Uriarte, Andres*
AZTI
Herrera kaia portualdea z/g
20110 Pasaia
Guipúzcoa
Basque Country
SPAIN
Email: auriarte@pas.azti.es

van der Lingen, Carl D.*
Marine and Coastal Management
Private Bag X2
Rogge Bay 8012
SOUTH AFRICA
Email: vdlingen@deat.gov.za

Vásquez, Sebastián
LOPEL
Department Oceanografia
Universidad Concepcion
P.O. Box 160-C
Concepcion
CHILE
Email: sevasque@udec.cl

Yannicelli, Beatriz
LOPEL
Department Oceanografia
Universidad Concepcion
P.O. Box 160-C
Concepcion
CHILE
Email: byannice@udec.cl
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