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SMALL PELAGIC FISHES AND
CLIMATE CHANGE PROGRAMME

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

12-13 January 2004, Concepción, Chile

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No. 9. IGBP Report No. 40. Global Ocean Ecosystem Dynamics Science Plan.

No. 11. Small Pelagic Fishes and Climate Change Programme Implementation Plan.

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No. 21 Report of a GLOBEC/SPACC Workshop on Characterizing and Comparing the Spawning Habitats of Small Pelagic Fish, 12-13 January 2004, Concepción, Chile. van der Lingen, C.D., L. Castro, L., Drapeau and D. Checkley.

No. 22 Report of a GLOBEC/SPACC Meeting on Characterizing and Comparing the Spawning Habitats of Small Pelagic Fish, 14-16 January, Concepción, Chile. Castro L.R., P. Fréon, C.D. van der Lingen and A. Uriarte.

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PREFACE

This report documents a Workshop that was held under the auspices of SPACC Working Group 3: Reproductive Habitat Dynamics. The Workshop was hosted by the Universidad de Concepción, Chile, from 12-13 January 2004, and aimed to characterize and compare the spawning habitats of small pelagic fish from a variety of systems. The Workshop was sponsored by the Universidad de Concepción, GLOBEC, IRD, IDYLE, IAI, SCOR, Gobierno de Chile Subsecretaría de Pesca, Sociedad Chilena de Ciencias del Mar, and Lota Protein Ltd. Workshop convenors were C.D. van der Lingen, L. Castro, D. Checkley, Jr. and L. Drapeau. This report should be cited as:

> van der Lingen, C.D., Castro, L., Drapeau, L. and D. Checkley, Jr. (Eds.). 2005. Report of a GLOBEC-SPACC Workshop on Characterizing and Comparing the Spawning Habitats of Small Pelagic Fish. GLOBEC Report 21: xii, 33pp.

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List of Abbreviations and Acronyms

AZTI	Technological Institute for Fisheries and Food, San Sebástian, Spain
BENEFIT	Benguela Environment Fisheries Interactions and Training
CalCOFI	California Cooperative Oceanic Fisheries Investigations
CalVET	California Vertical Egg Tow Net (= PairoVET)
CICESE	Centro de Investigación Científica y de Educación Superior de Ensenada, Ensenada, Mexico
CUFES	Continuous, Underway Fish Egg Sampler
DEPM	Daily Egg Production Method
GLOBEC	Global Ocean Ecosystem Dynamics
IAI	Inter-American Agency for Global Change
IDYLE	Interactions and Spatial Dynamics of Renewable Resources in Upwelling Ecosystems
IEO	Instituto Español de Oceanografía, Spain
IFOP	Instituto de Fomento Pesquero, Valparaíso, Chile
IMECOCAL	Investigaciones Mexicanas de la Corriente de California
IMR	Institute of Marine Research, Bergen, Norway
INP	Instituto Nacional de la Pesca, México
INRH	Institut Nacional de Recherche Halieutique, Casablanca, Morocco
IPIMAR	Instituto do Investigaçao das Pescas e do Mar, Lisbon, Portugal
IRD	Institut de Recherche pour le Développement, Paris, France
MCM	Marine and Coastal Management, Cape Town, South Africa
MPDH	Método de Producción Dias de Huevos (= DEPM)
PairoVET	Pair of Vertical Egg Tow Nets (= CalVET)
SAGARPA	Secretaría de Agricultura, Ganadería, Desarrollo Rural, Pesca y Alimentación, Mazatlán, México
SCOR	Scientific Committee on Oceanic Research
SPACC	Small Pelagic Fishes and Climate Change Programme
SST	Sea Surface Temperature
SWAPELS	South West African Pelagic Egg and Larval Surveys
T-S	Temperature-Salinity

ABSTRACT

A Workshop to characterize and compare the spawning habitats of small pelagic fishes from a variety of ecosystems was held in Concepción, Chile, from 12th-13th January 2004, under the auspices of SPACC Working Group 3: Reproductive Habitat Dynamics. Spawning habitat was characterized in terms of environmental parameters using two standard methods; temperature-salinity plots, and single parameter quotient analysis performed on egg abundance data and concurrently-measured environmental parameters. The Workshop was attended by 25 participants from 12 countries, and the spawning habitats of anchovy (*Engraulis encrasicolus, E. mordax* and *E. ringens*), sardine (*Sardinops sagax* and *Sardina pilchardus*), mackerel (*Scomber australasicus* and *Trachurus symmetricus*) and round herring (*Etrumeus whiteheadi*) from the Benguela, Canary, California, and Humboldt Current systems, the Iberian Peninsula, the Bay of Biscay, the Mediterranean Sea, and eastern Australia, were examined and characterized.

Some participants brought data on more than one small pelagic species from the ecosystem in which they worked, which permitted a comparison of inter-specific differences in spawning habitats within that ecosystem. Because of time limitations however, comparisons of spawning habitat of similar (or the same) small pelagic fish species across ecosystems was not conducted. This report provides a brief description of the standard analysis methods employed to characterize spawning habitat, and contains summaries of the results obtained at the workshop for the various species and/or ecosystems examined.

ACKNOWLEDGEMENTS

The convenors and editors would like to extend their thanks and appreciation to Mr Luis Hückstadt of the Universidad de Concepción for his assistance and organizational expertise both before and during the workshop; to Dr Claude Roy for his initial ideas regarding the workshop; to the Universidad de Concepción for hosting the workshop; and to Miss Dawn Ashby from the GLOBEC International Project Office for her assistance in publishing this Report. Funding from GLOBEC, IAI, IDYLE, IRD, Lota Protein Ltd., SCOR, Sociedad Chilena de Ciencias del Mar, and the Universidad de Concepción, is gratefully acknowledged. CONICYT (Chile) and SubSecretaria de Pesca (Chile) also sponsored the workshop.

COLOUR PLATE LEGENDS

The colour plates in this volume all show temperature-salinity plots for species examined at the Workshop. In order to facilitate comparisons, the colour plates have been standardised such that anchovy (*Engraulis* spp.) are represented by red symbols, sardine (*Sardina pilchardus* and *Sardinops sagax*) are represented by blue symbols, and other species are represented by symbols of other colours.

Plate 1: Temperature-salinity plot showing concentrations of blue mackerel eggs, and mean temperatures and salinities at each positive station during surveys in 2002 and 2003 off southeastern Australia (mean values between 50 and 0 m). Circle sizes indicate the relative proportion of eggs in each sample. See contribution by Neira and Keane, "Preliminary data on spawning habitat characterization of blue mackerel, *Scomber australasicus*, in southeastern Australia" for details see page 7.

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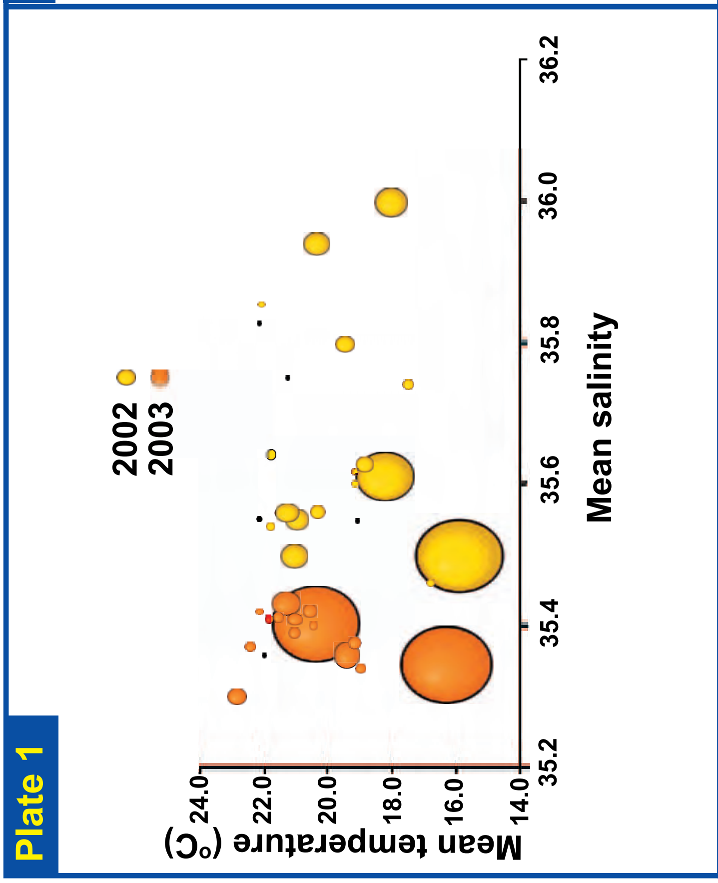

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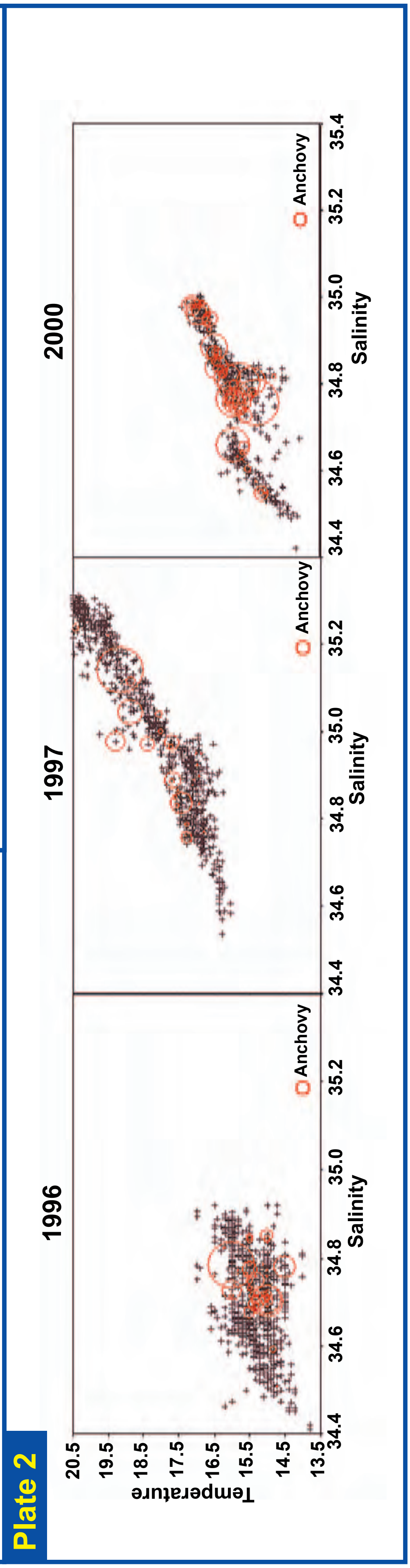

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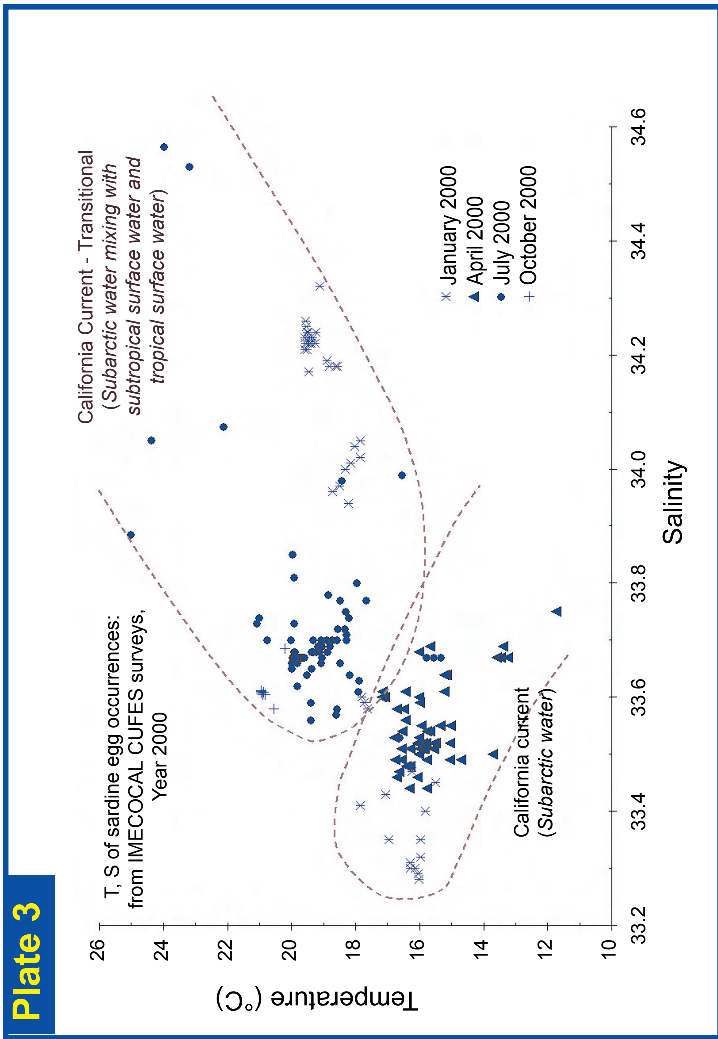

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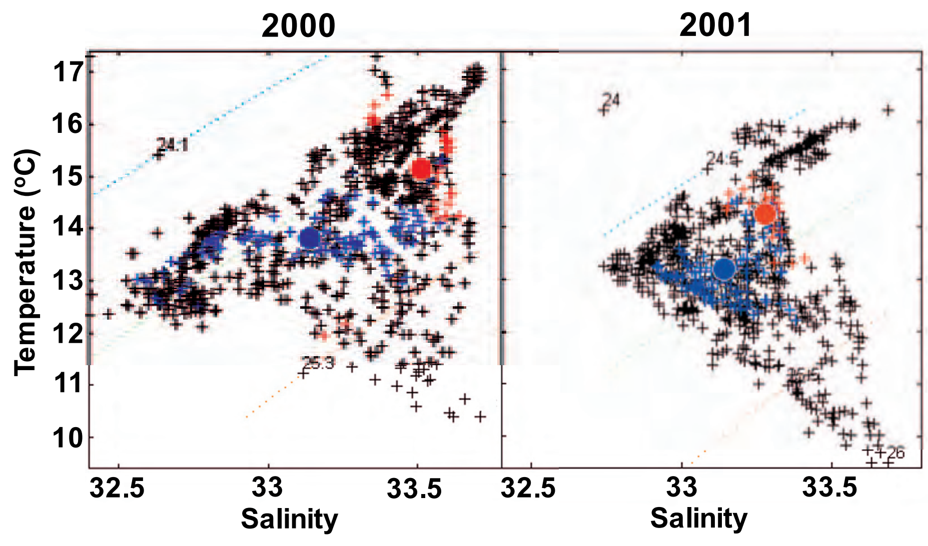

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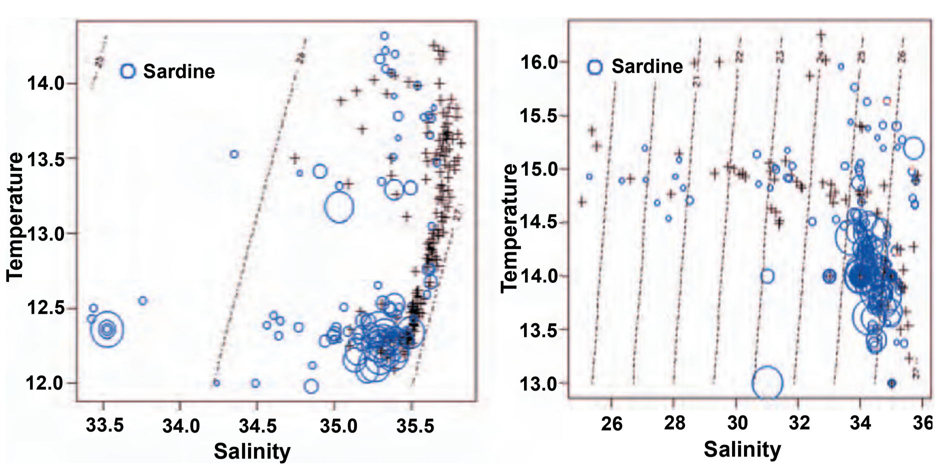

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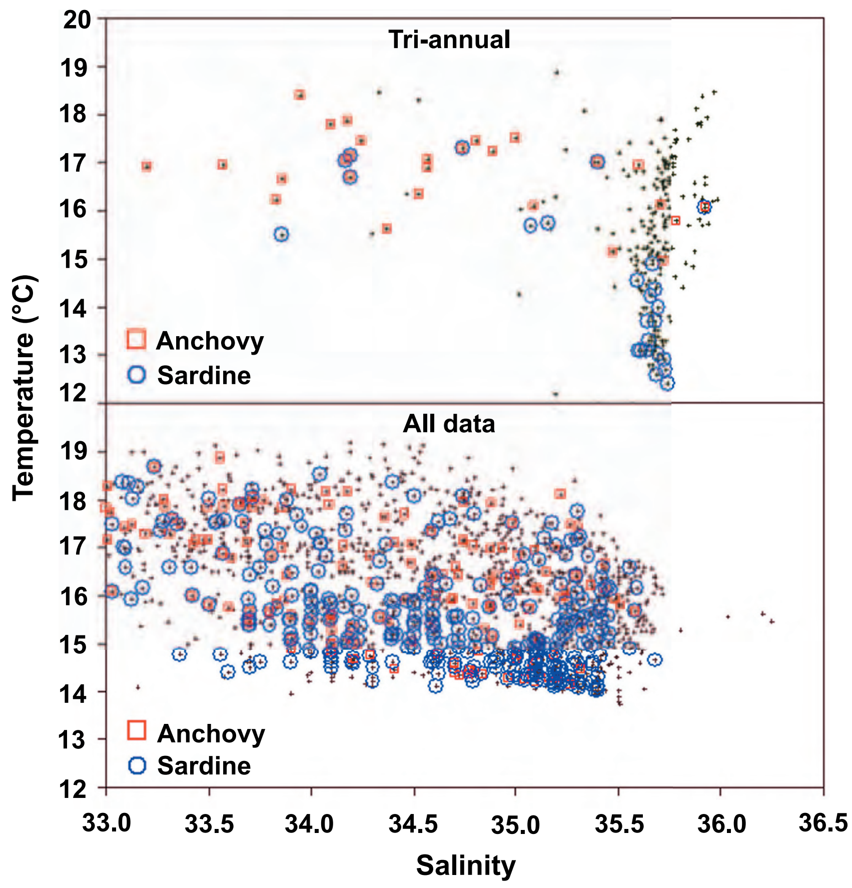

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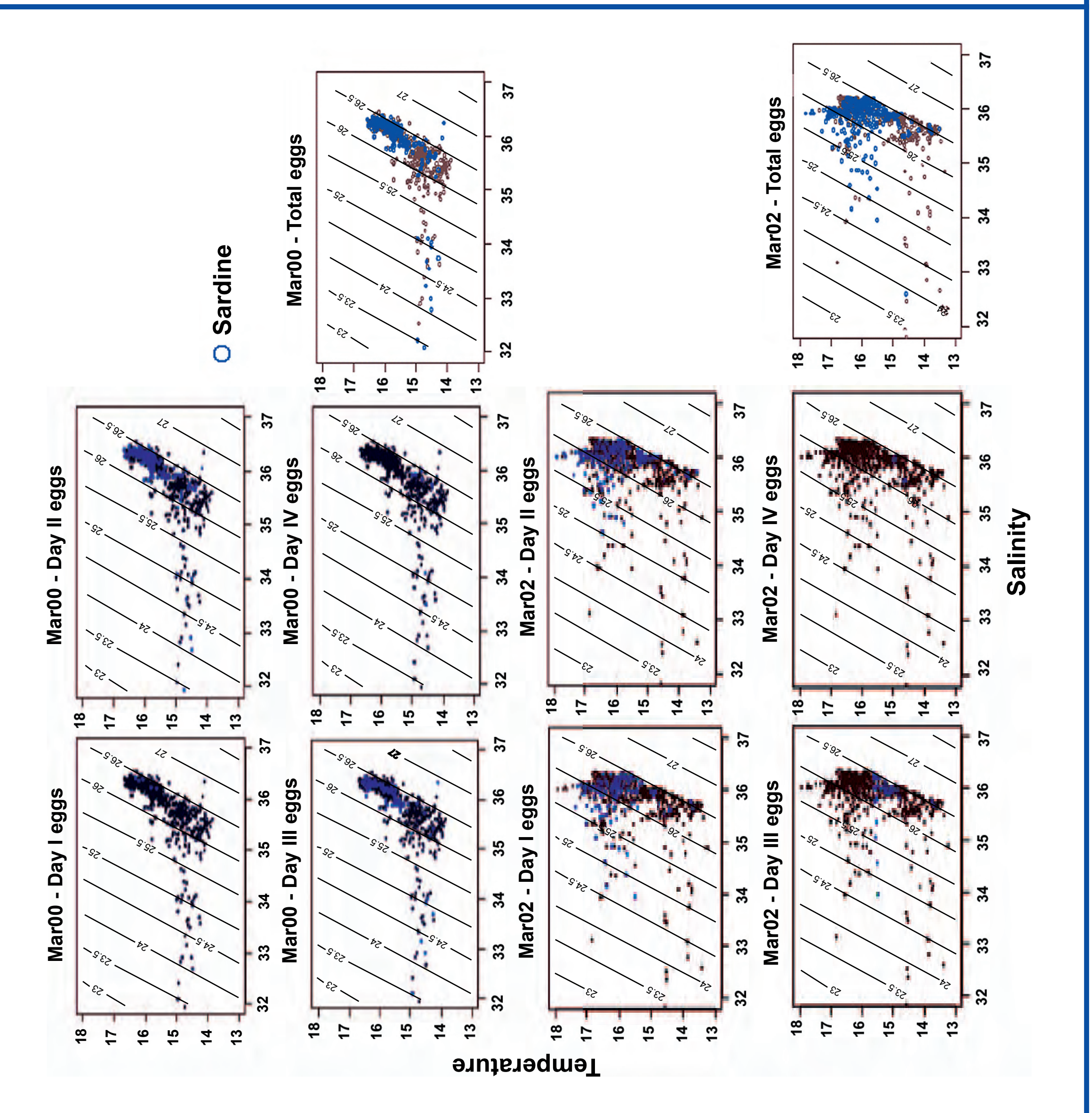

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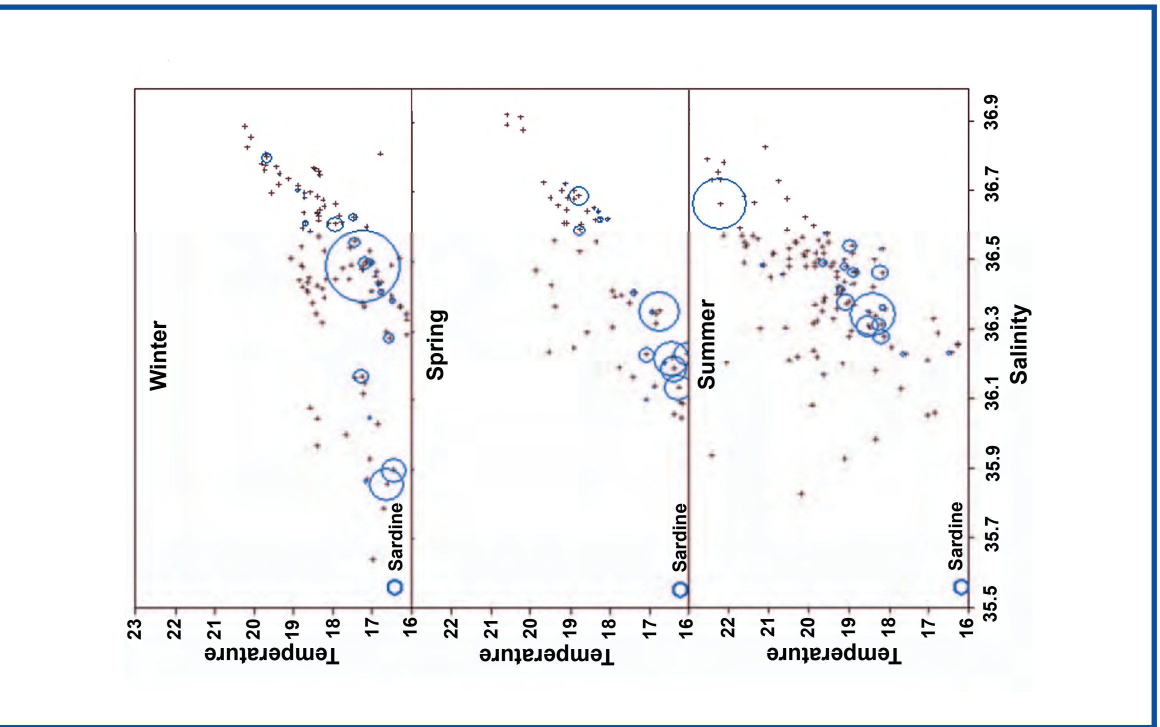

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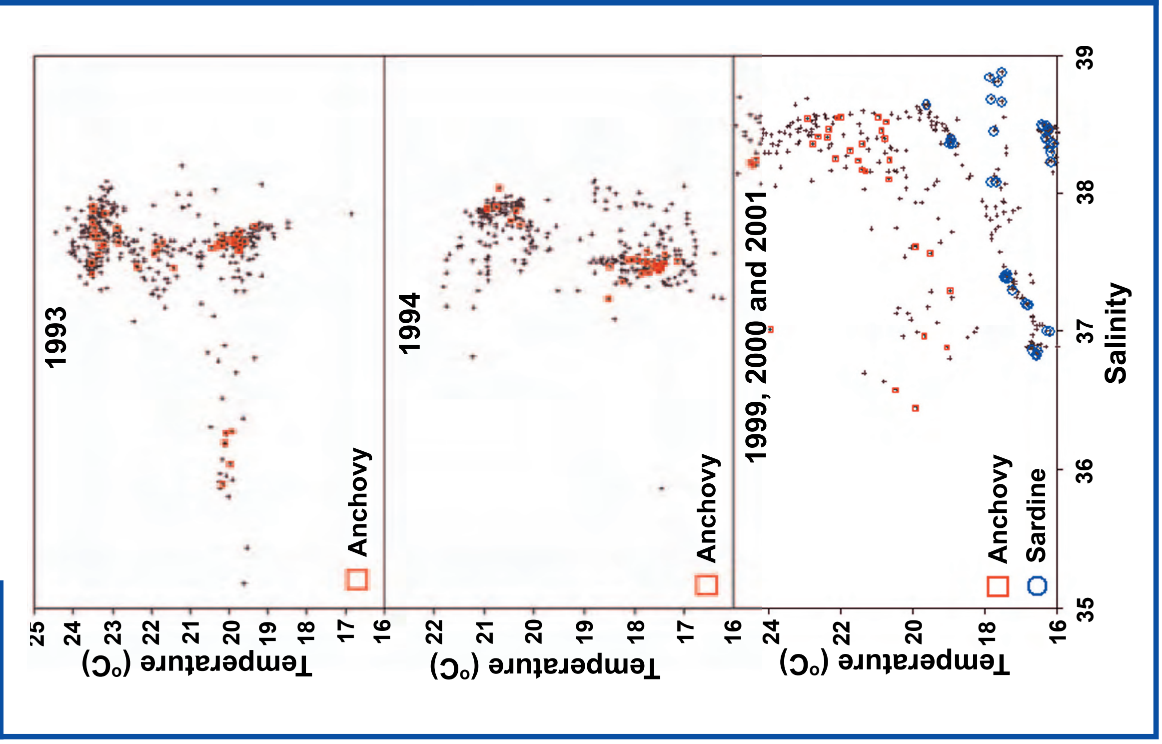

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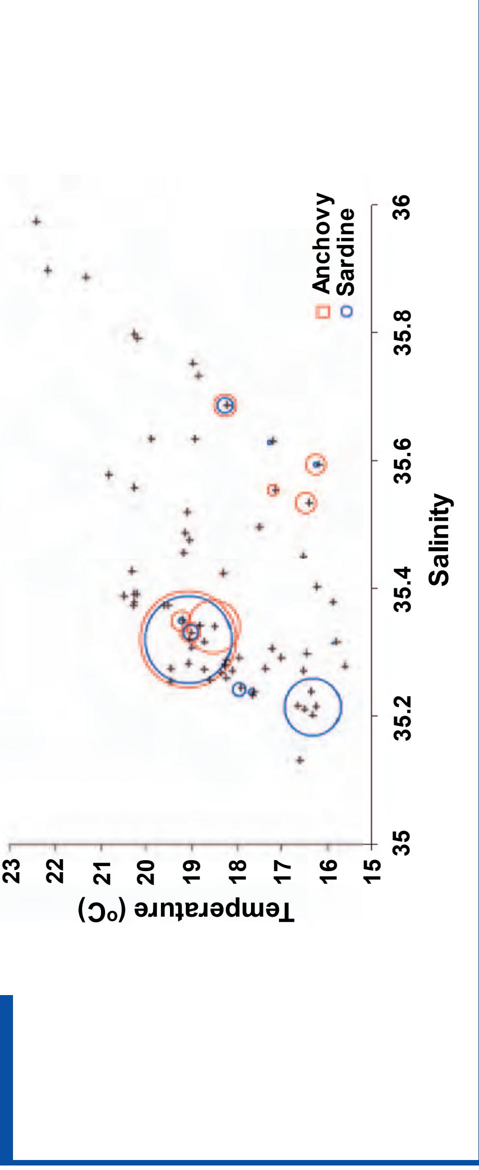

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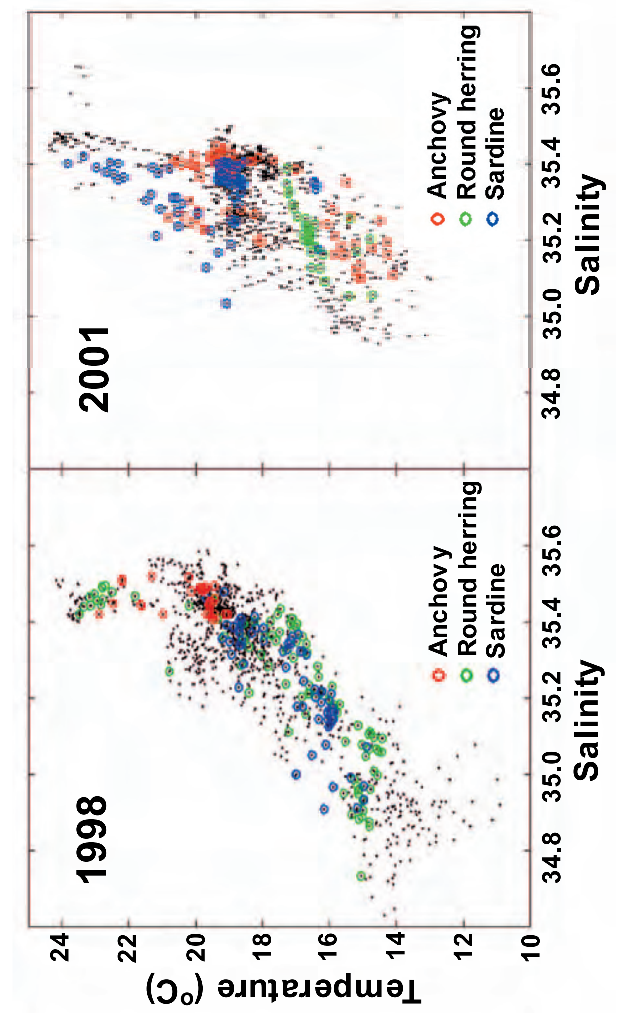

INTRODUCTION

The Small Pelagic Fish and Climate Change Programme (SPACC) is a regional programme of Global Ocean Ecosystem Dynamics (GLOBEC) International, and aims to understand and ultimately predict climate-induced changes in the productivity of small pelagic fish populations. Small pelagic fish support large fisheries in many parts of the world's oceans, and together comprise over a third of the annual global landings made by marine fisheries. In addition to their economic importance, small pelagic fish are also often ecologically important, being major zooplankton predators and the dominant prey of many piscivorous fish, marine mammal and seabird species. Small pelagic fish characteristically exhibit large fluctuations in population size that arise from high recruitment variability, this variability being considered to be primarily environmentally mediated. These fluctuations in population size vary on interannual, decadal and centennial time-scales, and synchronies in abundance of small pelagic fish populations at an ocean-basin scale suggest that this environmental forcing operates at an ocean scale. Many hypotheses have been proposed to explain these population fluctuations, one being that 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).

The SPACC Workshop to Characterize and Compare the Spawning Habitats of Small Pelagic Fishes was held to discuss and develop standardized methods for characterizing spawning habitat, and to further understanding of the linkages between fish population dynamics and ocean climate variability. The objectives of the Workshop were to characterize, in terms of environmental parameters, the spawning habitats of small pelagic fish (principally anchovy and sardine) from a variety of ecosystems using standardized analysis methods, and to use the results of these analyses to conduct inter ecosystem comparisons of anchovy and sardine spawning habitats and to infer the likely responses of these species to changes in ocean climate and also population size. Participants worked on data they had brought to the Workshop, and spawning habitat was characterized using temperature-salinity plots and single parameter quotient analysis performed on data comprising egg abundance information and concurrently-measured environmental parameters (primarily temperature and salinity) brought by participants. The application of standardized analyses follows the SPACC approach of using a common set of core measurements and analyses to infer cause-and-effect linkages between fish, zooplankton and ocean physics from comparisons of the many diverse ecosystems dominated by small pelagic fish.

The Workshop was attended by 25 participants from 12 countries, and the spawning habitats of anchovy (*Engraulis encrasicolus, E. mordax* and *E. ringens*), sardine (*Sardinops sagax* and *Sardina pilchardus*), mackerel (*Scomber australasicus* and *Trachurus symmetricus*) and round herring (*Etrumeus whiteheadi*) from the Benguela, Canary, California, and Humboldt Current systems, the Iberian Peninsula, the Bay of Biscay, the Mediterranean Sea, and eastern Australia, were examined (Fig. 1). Workshop participants considered that characterizations of spawning habitat made using the standard analyses were useful, but emphasized that comprehensive coverage (both spatial and temporal) of egg distributions and a sufficiently large range of environmental variability is required in order to fully assess spawning habitat selection. Substantial inter-annual variability in the selection of spawning habitat by small pelagic fish was observed, and whereas analyses of aggregated data were considered useful in determining average patterns, high levels of inter-annual variability indicate that data need to be interpreted within the oceanographic context observed at the time of the survey. Additionally, variation in the spawning habitat selected by different reproductive groups within the same population may also be observed. Participants cautioned that the environmental parameters chosen for analyses (principally temperature and salinity) may be proxies and may show co-variance, hence identification of the mechanisms by which fish select spawning habitat based on such analyses should be made circumspectly. Additionally, the use of other indices, particularly those related to biological productivity, may be more effective in delineating spawning habitat than physical parameters such as temperature and salinity.

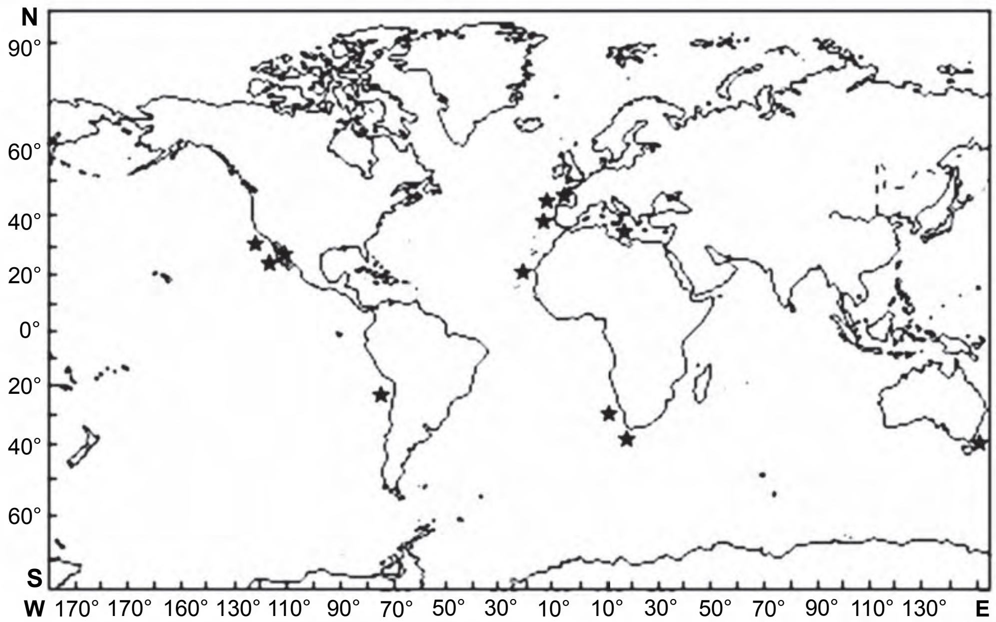

Figure 1. World map showing the locations (indicated by symbols) of small pelagic fish spawning habitat that were analysed at the Workshop.

There was insufficient time at the Workshop for extensive discussion of the methodologies used and for species and ecosystem comparisons, but some interesting points emerged. For example, whereas in some systems (*e.g.* anchovy in the Southern Benguela; anchovy and sardine in the Bay of Biscay) small pelagic fish show relatively strong selection of spawning habitat (as inferred from quotient curves), they do not in other systems (*e.g.* sardine off the Iberian Peninsula; anchovy in the Humboldt system off Chile). Environmental characteristics of spawning habitats of anchovy and sardine from the same system may show marked differences (*e.g*. the Mediterranean Sea) or they may be similar (*e.g.* the Bay of Biscay). Spawning habitat may be selected on the basis of hydrographic or biological parameters and/or spatial location, and the relative importance of these is likely to vary between ecosystems and also between species. In non-upwelling ecosystems such as the Bay of Biscay and the Mediterranean Sea, anchovy and sardine appear to select spawning habitat in geographically fixed locations that correspond to the location of river outflows.

This report provides a brief description of the standard analysis methods employed to characterize spawning habitat, and contains summaries of the results obtained at the Workshop for the various species examined.

References

Hunter J.R. and J. Alheit (Eds.). 1997. GLOBEC Small Pelagic Fishes and Climate Change Programme. Implementation Plan. GLOBEC Report No.11, 36pp.

Introduction to the Use of Temperature-Salinity Plots for Characterizing Spawning Habitat of Small, Pelagic Fish

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Introduction

Temperature-salinity plots are useful for characterizing water masses in the ocean (Sverdrup *et al*., 1942). This is usually done with water isolated from the influences of external sources, away from the ocean surface (*e.g*., heat exchange, precipitation) and edges (*e.g*., runoff). However, even near-surface, coastal water may be characterized in temperature-salinity space, as long as inference is appropriately limited. The spawning habitat of fish, in particular, may be assessed in temperature-salinity space in this manner (Checkley *et al*., 2000). This procedure is described below and examples are provided in the abstracts for the workshop, published in this volume.

Procedure

Data sets should contain observations with and without eggs of the target species of fish. Each observation (*e.g.* from a single station or sample interval) must contain, at least, values of temperature (°C, one or two decimal places), salinity (psu or ‰, two decimal places), and egg abundance (*e.g.*, eggs m^{-3}, eggs m^{-2}, eggs min^{-1}, or, if sample size is constant, eggs $sample^{-1}$). Ancillary data are useful but not necessary (*e.g.*, date, time, latitude, longitude, and chl *a* fluorescence). The type of units of egg abundance is not as important as the constancy of those units, *i.e*. that all data are comparable.

Convention is to plot salinity on the abscissa, or X axis, and temperature on the ordinate, or Y axis. This may be done by hand or with any computer software, *e.g.* Excel or Matlab. Firstly, all observations are plotted. Then, those observations containing a threshold abundance, or greater, of target eggs are plotted on the same graph, using a different and visible symbol. The threshold abundance is selected either objectively (*e.g*., the upper quartile of egg abundance) or subjectively (*e.g*., a value that causes a sufficient number of observations to be plotted to indicate spawning habitat). Finally, in some cases, mean values (arithmetic, either unweighted or weighted by egg abundance) of temperature and salinity are computed and plotted for observations with either any or threshold-or-larger abundances of eggs, to indicate central tendency.

Seawater density depends on pressure (depth), temperature, and salinity (Sverdrup *et al*., 1942; Pond and Pickard, 1983). It is useful to plot lines of constant density for seawater at the surface ($ó_t$, or sigma-t) in a temperature-salinity plot rather than a grid of temperature and salinity values. This is easily done in Matlab, *e.g.* using the m-file tsplot.m in the oceans toolbox distributed by the Woods Hole Oceanographic Institution (ftp://acoustics.whoi.edu/pub/Matlab/oceans/). Similar procedures may exist for use with Excel.

Interpretation

Inference is then made on spawning habitat from such a temperature-salinity plot. It ideally includes lines of constant density and different symbols for (a) all samples with egg abundance less than a threshold value and (b) samples for one or more types of fish eggs above threshold value(s).

An example of this for sardine (*Sardinops sagax*) and anchovy (*Engraulis mordax*) eggs sampled with the Continuous Underway Fish Egg Sampler (CUFES) off California for two years is given in Checkley *et al.* (2000). In the SPACC workshop of January 2004 in Concepción, Chile, analogous data were provided for more cruises off California, Mexico, Peru, and Chile. These are discussed, in general terms, in the extended abstract by Checkley *et al.* (2005) in the GLOBEC Spawning Habitats Meeting report (Castro *et al*., 2005).

In general, one seeks understanding from patterns in the data presented in temperature-salinity space. A premise is that patterns in spawning may be explained by patterns in water type or water mass characteristics known for the sampled regions. The latter information comes from physical oceanographic studies and literature. The challenge is to discern relationships between the biological and physical patterns.

It is important to recognize the limits of this analysis. As stated earlier, water mass characteristics are altered at the ocean surface and edges. Thus, data from near the surface (*e.g*. from CUFES at 3m depth) and shore (*e.g*. affected by rivers) must be interpreted with caution, particularly in regard to associating water masses with observed combinations of temperature and salinity. However, much can be learned from such analyses, when done with appropriate care.

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Introduction to the Use of Quotient Curves for Characterizing Spawning Habitat of Small, Pelagic Fish

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Introduction

Quotient curves provide an easy to implement tool to characterize the spawning habitat of small pelagic fishes in regard to physical and/or biological parameters. A quotient curve is a bi-variate curve, considered as an exploratory data analysis technique (Lluch-Belda *et al.*, 1991) that describes the "relation shape" between relative abundances of fish eggs and environmental variables such as temperature, salinity, depth, phytoplankton, *etc.* (*e.g.* van der Lingen *et al.*, 2001). This abstract describes how quotient curves are constructed, and illustrations of this are provided in the abstracts for the Workshop, published in this volume.

Procedure

Quotient curves are computed on simple datasets. Datasets should provide egg abundance and other biological and physical measurements collected from field sampling for all the stations sampled (single station, integrated segment). The presence or absence of eggs is equally important. Egg abundance units can be measured in m^{-3}, m^{-2}, min^{-1}, but need to constant for all the stations. These eggs abundances must be associated with one or more environmental factor such as temperature (°C), salinity (psu or ‰), *etc*. Other information can be useful at latter stages of analysis (*e.g.*, date, time, latitude, longitude…) but are not required for the quotient curves.

The units used in the dataset are of no special importance because the quotient curves are based on relative occurrences. The first step is to define a pertinent classification for the environmental variable (*e.g.* 0.5 or 1.0°C classes for temperature), and the environmental variable is then assigned a number of categories (around 30) to ensure that maximum occurrence per category does not exceed 20% of all measurements and that it remains significant for each category. Stations are then assigned to a category, from which the relative "importance" or weight of each category is computed. Spreadsheet software is used.

The same procedure is applied to egg abundance data, with each environmental category being assigned a relative egg abundance value (egg abundance within the category divided by total abundance of eggs). The final step is to compute the quotient between the relative abundance of eggs and the percentage occurrence of the category. To prevent artefact from very high egg abundances, a smoothing function (running mean of 3-5 points) is applied to the quotient curve.

Interpretation

The curves represent the relative abundances of eggs over the whole spectrum of environmental values. Since the sampling strategy is rarely balanced regarding the environmental variable, the quotient curve provides an efficient weighting procedure. Inferences are made from the curves, with quotient values greater than one (>1) of particular interest, since they express significant selection for that range of the environmental variable (positive selection), whereas quotient values less than one (<1) indicate avoidance of those environmental ranges for spawning (van der Lingen *et al*., 2001). Examples of quotient curves are given in Twatwa *et al.* (2004), where the spawning habitats of anchovy (*Engraulis encrasicolus*) and sardine (*Sardinops sagax*) in the Southern Benguela upwelling ecosystem were characterized using CalVET net data collected during annual pelagic spawner biomass surveys. Despite some overlap, the spawning habitats of these two species show significant differences.

It is important to emphasize that this approach is no substitute for in-depth statistical approaches of complex correlation which can be undertaken using GLM or GAM models. Quotient analysis provides a first step exploration of these relations using simple spreadsheet software and simple structured data. This step is a very relevant input for further elaborate approaches.

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Preliminary Data on Spawning Habitat Characterization of Blue Mackerel, *Scomber australasicus*, in South-Eastern Australia

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Surveys for eggs and larvae of blue mackerel (*Scomber australasicus*) are currently underway along shelf waters off southeastern Australia, and are designed to locate spawning areas and evaluate egg production for future application of DEPM-based biomass estimates. This large collaborative project is being funded by the Fisheries Research & Development Corporation (FRDC) with in-kind contribution from AMC. This abstract summarizes the results of four surveys completed in 2002-2004 that covered some 1,050 nm of coastline between southern Queensland and Tasmania (Table 1).

Table 1. Summary of data used in this analysis

Eastern Australian region	Year/month of sampling	Method of egg collection and number of samples	Environmental parameters
Southern Queensland to southern New South Wales (26.0° - 37.5°S)	October 2002 and 2003	Vertical tows with bongo sampler (3m long, 0.6m diameter, 300 and 500mm mesh nets); 171 samples	As above
Southern New South Wales to central-eastern Tasmania (37.5° - 41.5°S)	February 2003	As above 55 samples	As above
Central New South Wales to eastern Victoria (34.5° – 38.5°S)	February 2004	As above 55 samples	As above

Late-stage blue mackerel eggs were initially identified using characters of *S. japonicus* eggs (Fritzsche, 1978); identifications were verified using PCR-based mtDNA fragment amplification and sequencing (S. Appleyard, CSIRO Hobart). Larvae were identified using Neira *et al*., (1998). Eggs and larvae in October 2002 and 2003 (spring) were confined to the shelf area between 27.5˚S (southern Queensland) and 33.5˚S (northern New South Wales), with few occurrences past the shelf break. No eggs or larvae were found south of 33.5˚S in October 2002 or 2003, or in either of the February (summer) surveys. Mean temperatures (mean salinities) at positive egg stations in October 2002 and 2003 were 15.9–22.1˚C (35.5–36.1 psu) and 18.9–23.0˚C (35.3–35.4 psu), respectively (Plate 1). Season(s) and water temperatures when eggs and larvae have been collected match those reported for *S. australasicus* in New Zealand, i.e. spring/summer, 15.0–22.0˚C (Crossland, 1981).

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CHARACTERIZING THE SPAWNING HABITAT OF ANCHOVETA, *ENGRAULIS RINGENS*, IN NORTHERN CHILE

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Details of data used in this analysis are given in Table 1. In general, the temperature at 10m depth ranged from 13 to 17ºC, except for years with El Niño events (such as 1997) that ranged from 16 to 20.5ºC (Fig. 1). The quotient analysis has not provided a clear explanation of preferred spawning temperatures of *E. ringens*. In some years a bimodal situation is observed, but this is not consistent from year to year. In 1997 (El Niño), a preference for temperatures between 17.5 and 18.5ºC was apparent. Combined data for all years shows a bimodal quotient curve (Fig. 2), with the first peak between 15 and 17ºC and the second peak from 18.5 to 19ºC, that corresponds to the El Niño event of 1997. The T-S plot for 1996, 1997 and 2000 (Plate 2) would indicate that eggs are present in almost all combinations of temperature and salinities.

Table 1. Summary of Daily Egg Production (DEPM) surveys in northern Chile from which data were used in this analysis

Region	Species	Year/season of sampling	Method of egg collection and number of samples	Environmental parameters
Northern Chile	*Engraulis ringens*	August (winter) surveys, 1992, 1995-1997 and 1999-2002	CalVET 1992 = 542 1995 = 578 1996 = 752 1997 = 800 1999 = 598 2000 = 502 2001 = 514 2002 = 589	SST* Temperature at 10m depth, surface salinity*, salinity at 10m depth* *: Not all years

It is remarkable that during the strong El Niño event that occurred in the Eastern South Pacific during 1997 and which drastically altered the physical environment in coastal waters off northern Chile, anchoveta eggs were abundant and widely distributed, and hence did not indicate any dramatic decline in the spawning process. The quotient analysis shows a preference for higher temperatures in 1997, compared with non-El Niño years, which seems to be contradictory. The same unclear situation is shown using the T-S plots, in that eggs appear in almost all combinations of temperature and salinities. Northern Chile is known to be subject to strong interannual variability in the physical, chemical and biological environment because of the ENSO cycle, and *E. ringens* needs to be adapted to these changes. It is likely that there are oceanographic features, other than temperature or salinity, which affect the selection of suitable spawning areas for *E. ringens* from northern Chile. Interannual variability in sea level, thermocline depth, changes in surface chlorophyll-*a* patterns, and alterations in the extension and depth of the oxygen minimum zone, have been much less studied. Variability in the biological environment, such as the rates of primary production, and the presence of predators and food resources for the spawning population, also need to be considered.

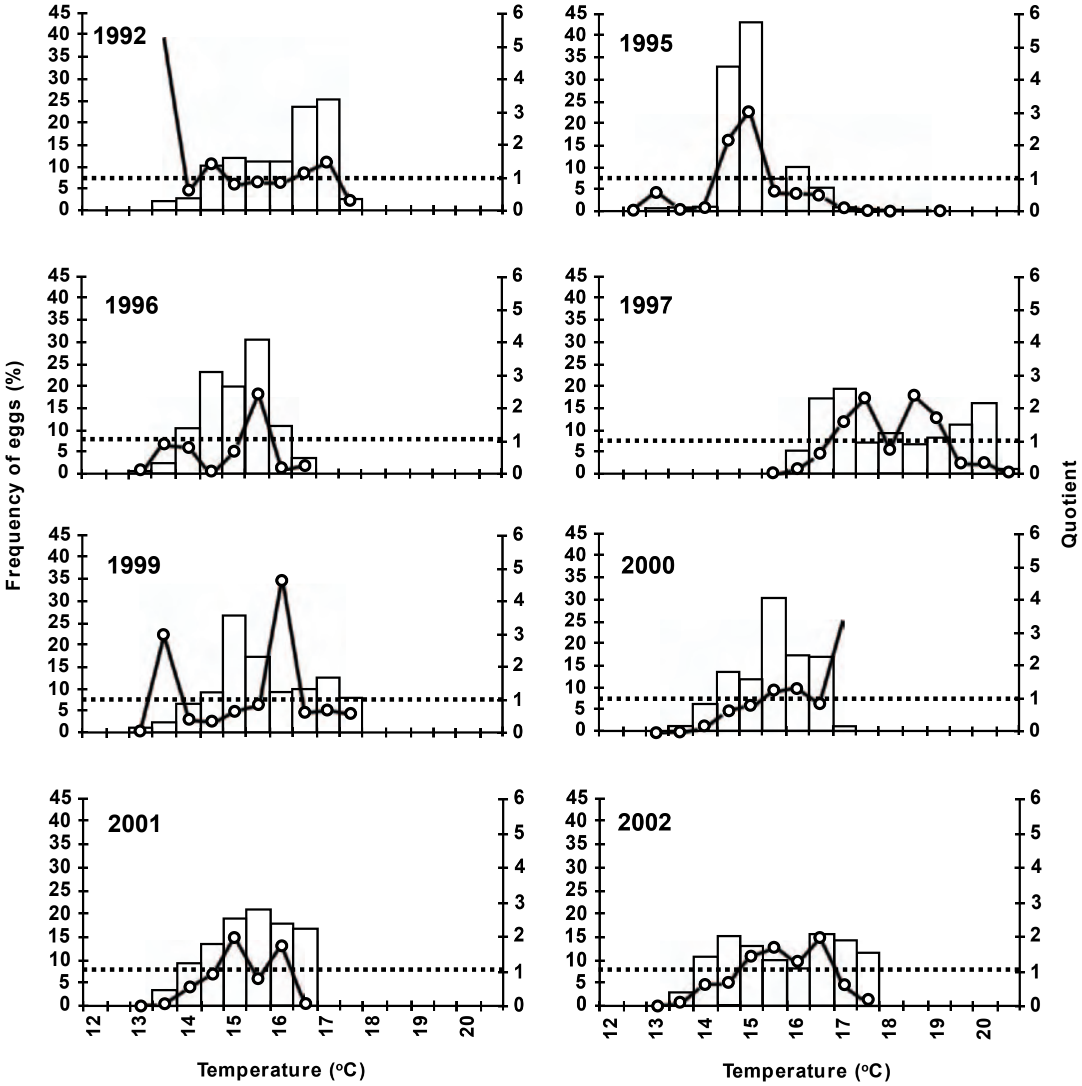

Figure 1. Frequency distribution of temperature (histograms) at 10m depth at all CalVET stations sampled, and *Engraulis ringens* egg abundance/temperature quotient (line with circles), for various years of DEPM application over the period 1992-2002.

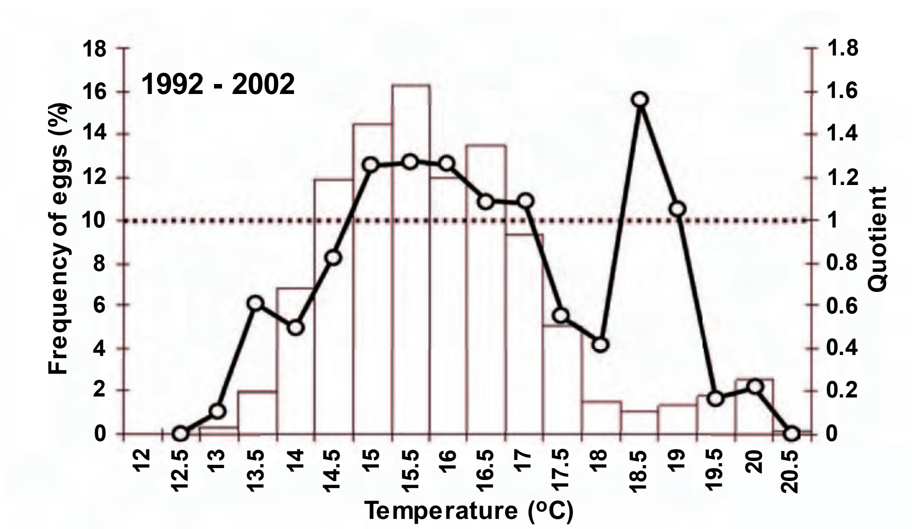

Figure 2. Frequency distribution of temperature (histograms) at 10m depth at all CalVET stations, and egg abundance/temperature quotient (line with circles) for *Engraulis ringens* using combined data for various years of DEPM surveys.

Single Parameter Quotient Analysis for Sardine and Anchovy in the Gulf of California

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Single parameter quotient analysis for egg abundance and SST was conducted using data for sardine (*Sardinops caerulea*) and northern anchovy (*Engraulis mordax*) in the Gulf of California. The study area and sampling grid are shown in Figure 1, and further sampling details are provided in Table 1.

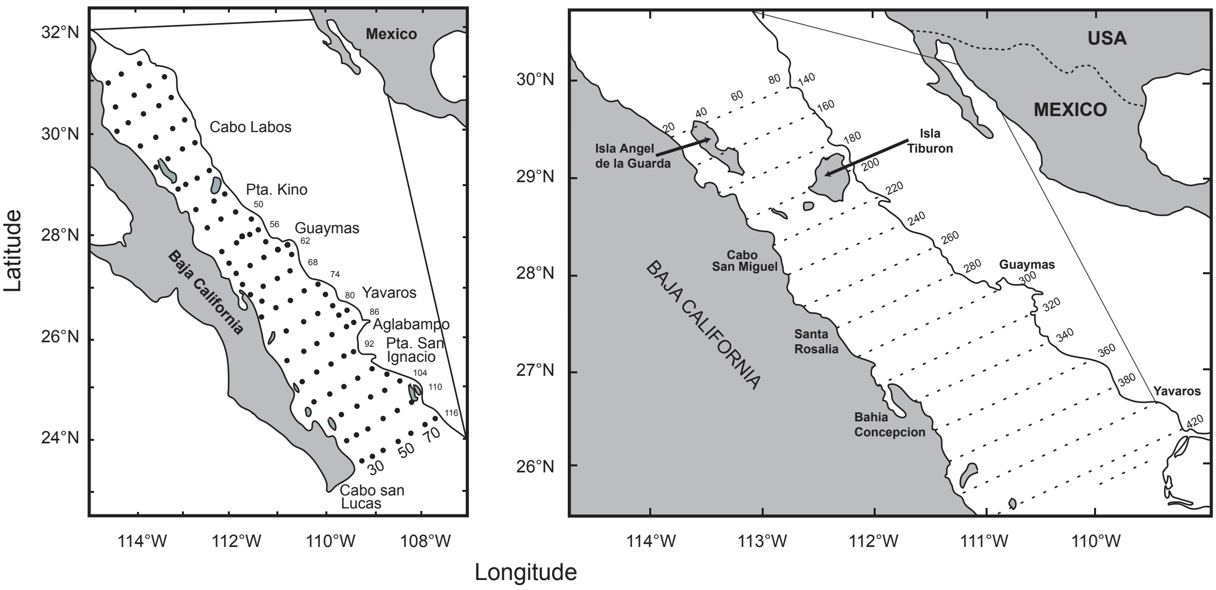

Figure 1. Study area and sampling grid for (a) Bongo (for sardine eggs) and (b) CalVET (for anchovy eggs) net hauls.

Results of the analysis are shown in Figure 2; northern anchovy spawn mainly between 16 and 17°C (Fig. 2a) and sardine spawn between 17 and 18°C (Fig. 2b). In order to analyse interannual variation in the selection of spawning habitat for northern anchovy, the single parameter quotient analysis was also applied for each year between 1990 and 1994. A comparison between results for anchovy obtained from data collected during the El Niño event of 1992 and the La Niña event of 1994 is shown in Figure 3.

Results obtained using this analysis are similar to those reported by Green-Ruiz and Hinojosa-Corona (1997) for northern anchovy and Hammann *et al*. (1998) for sardine: in the Gulf of California, northern anchovy spawns at lower temperatures than does sardine. Nevertheless, further analysis for sardine is necessary to include winter and summer data, and to further investigate interannual variation in spawning habitat. The influence of the 1992 El Niño event is clear, with the range of sea surface temperature in 1992 being bigger than in 1994.

Further work to assess spawning habitat selection in terms of other parameters such as depth, and an examination of the relationship between egg distribution and adult distribution, is underway.

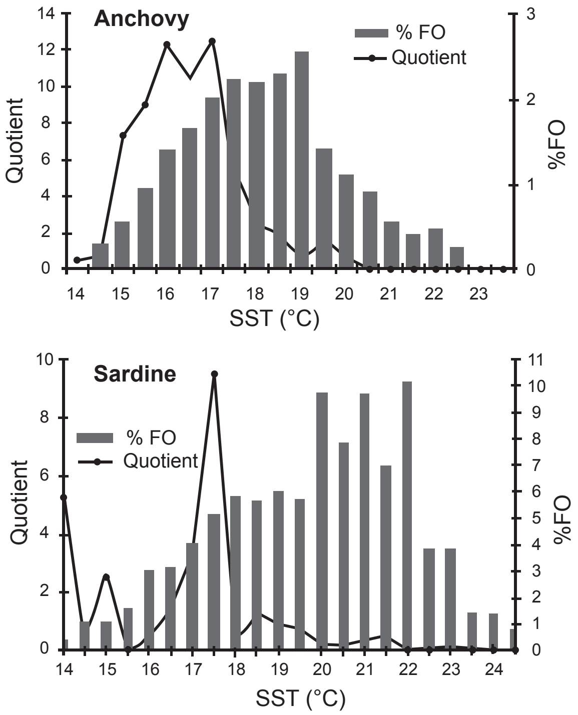

Figure 2. Quotient plots for northern anchovy (upper panel; histograms represent the frequency of occurrence of SST and symbols and lines represent the quotient curve; from data collected over the period 1990-1994) and sardine (lower panel; data collected over the period 1971-1987) from the Gulf of California.

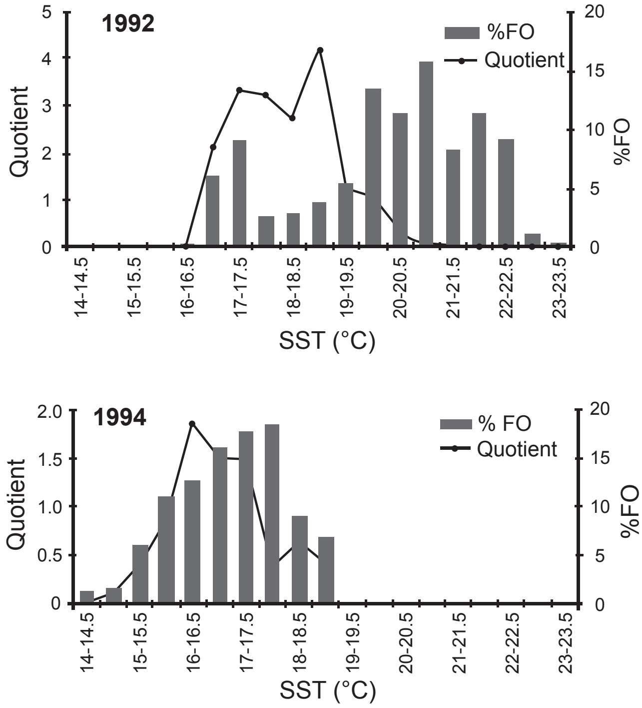

Figure 3. Quotient plots (histograms represent the frequency of occurrence of SST and symbols and lines represent the quotient curve) for northern anchovy in the Gulf of California during the 1992 El Niño event and the 1994 La Niña event.

Table 1. Summary of data used in this analysis

Region	Species	Year/season of sampling	Method of egg collection and number of samples	Environmental parameters
Gulf of California	*Engraulis mordax*	1990-1994 (winter)	CALVET; see Table 1 of Green-Ruiz and Hinojosa-Corona (1997)	SST
Gulf of California	*Sardinops caerulea*	1971-1987	BONGO; see Table 1 of Hammann *et al.*, (1998)	SST

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Acknowledgments

I thank Dr. Manuel Barange from GLOBEC International, and Secretaría de Relaciones Exteriores from México, for financial support.

Characterization of the Spawning Habitat of the Pacific Sardine *(Sardinops sagax caeruleus)* off Baja California during the Year 2000

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Beginning in January, 2000, a CUFES system was incorporated into the quarterly ocean surveys undertaken by the IMECOCAL program (Investigaciones Mexicanas de la Corriente de California, http://imecocal.cicese.mx). The IMECOCAL sampling region occupies the southern sector of the original CalCOFI grid off Baja California, Mexico, (established in the early 1950's) and extends from the U.S.-Mexico border to the southern area of the Baja California peninsula, with a maximum offshore extent of approximately 200 nautical miles. Eggs are sampled by continuous pumping through the ship's hull (*RV Francisco Ulloa*) at a depth of approximately 3 metres on transects between oceanographic stations while temperature and salinity are recorded by an onboard thermosalinograph.

Table 1. List of data included in the analyses

Region	Species	Year/season of sampling	Method of egg collection and number of samples	Environmental parameters
Southern California Current (Baja, California, Mexico)	*Sardinops sagax caeruleus*	January 2000 (winter) April 2000 (spring) July 2000 (summer) October 2000 (fall)	CUFES: 795 (January) 656 (April) 844 (July) 927 (October) 3222 (Total)	SST, surface salinity

Quarterly sampling on the IMECOCAL cruises provides information on the seasonality of egg distributions and concentrations of small pelagic fishes (Table 1). Seasonal shifts in the properties of the surface water throughout the IMECOCAL region during the year 2000 indicates that there was a significant change in the water types present in the region over the annual cycle.

Plotting egg abundances (eggs/minute of pumping) from the four cruises against surface temperatures indicates affinities to temperatures that are concentrated in four groups that lie between 11.5 and 14.2°C; 14.5 - 17.2°C; 17.5 - 21°C; and a small number of eggs between 22 and 25°C that are found in a bay in the southern extreme of the region (Fig. 1).

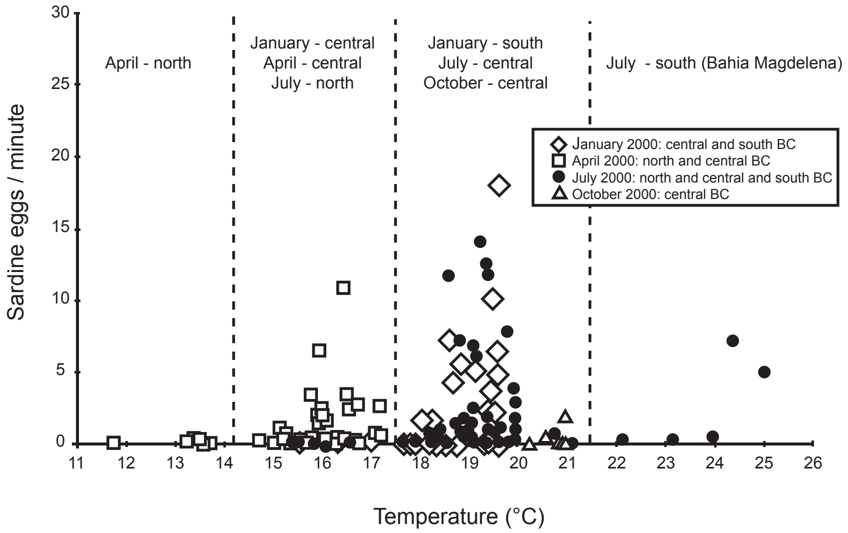

Figure 1. Sardine eggs per minute pumped by CUFES versus surface temperature from all positive stations on IMECOCAL cruises during the year 2000.

The principal locations of seasonal egg occurrences along the Baja California peninsula (north, central, south) are noted in Figure 1 to indicate the latitudinal movement of thermal habitat along the coast (seen in map distributions, not shown here). Plotting the egg occurrences in the temperature-salinity field (Plate 3) indicates that spawning occurred in two different water types (fields shown within dashed lines) that are labelled in the figure as California Current (Subarctic Water) and California Current-Transitional (mixing of Subarctic Water of CC from the north with mainly Subtropical Surface Water [warm, salty] from the west and south). The mixing relationships among water masses that form the transitional water types found in the California Current system is discussed in Durazo and Baumgartner (2002).

Figure 2 shows the results of the quotient analysis of sardine egg concentrations (eggs/minute) in relation to the distribution of temperature over the IMECOCAL region for the April 2000 cruise only. The heavy curve with solid square symbols in Figure 2 is the plot of the quotient of percent eggs/minute in relation to temperature percent frequencies over the sampling region. The heavy dashed curve with open circles indicates the percent frequencies of the temperatures throughout the region and the dashed-dot curve with solid triangles shows the % frequencies of the egg concentrations in the region.

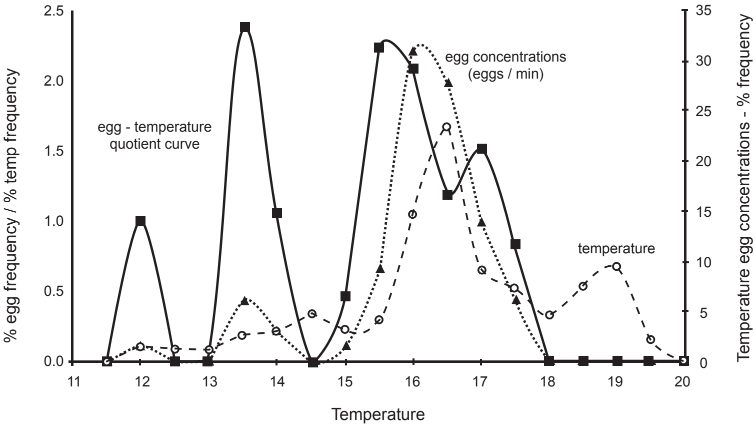

Figure 2. Normalizing sardine egg concentrations (eggs/minute pumped by CUFES) to temperature distribution observed during the IMECOCAL cruise in April 2000.

The annual cycle of sardine spawning in the IMECOCAL region can be separated into two major reproductive groups, distinguished by their association with water types, season of spawning and location of spawning (Fig. 2 and Plate 3). These differences suggest two principal thermohaline habitats in the IMECOCAL survey region that are associated with seasonal changes and geographic locality.

A “northern” group is limited to egg occurrences during January from Punta Eugenia (central Baja California) northwards, with all eggs during April associated with this group (located off northern and central Baja California), plus a small number of occurrences during July (off northern Baja California). Spawning of this northern group is confined to the Sub-arctic Water in the California Current and shows similar affinities to temperature (from quotient analysis in Fig. 2) that are found further to the north off California, USA, in the CalCOFI region. The southern part of the CalCOFI region is generally occupied by egg concentrations between 14.5 and 17°C and the northern region (north of Point Conception) by eggs at temperatures from 12 to 14.5°C. The quotient analysis (Fig. 2) shows these affinities occur with similar importance in the IMECOCAL region, but this is masked by the much more limited occurrence of 12 to 14.5°C water temperatures there.

A “southern” reproductive group consists of the January egg occurrences that located in the southern part of region, and almost all egg occurrences during July (generally located in the central area of the region), plus the eggs found in the centre (around Punta Eugenia) during October. Spawning of this southern group is limited to the California Current-Transitional Water mass formed by mixing of the Subarctic Water with Subtropical Surface Water (on western edge of California Current; warmer and more saline) and Tropical Surface Water (to the south, warmer, with similar salinities).

Reference

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TEMPERATURE-SALINITY AND QUOTIENT ANALYSES OF CUFES DATA FROM THE CALIFORNIA CURRENT REGION

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The combined use of the quotient and T-S analyses provides valuable insight into the spawning habitats, and their inter-annual variation, for the Pacific sardine and northern anchovy (Table 1). The T-S plots allow inference about the water masses sampled and their association with the eggs of these two species (Checkley *et al*., 2000). The quotient curves quantify these associations. In the springs of 2000 and 2001, anchovy spawned in warmer, saltier water than sardine, on average. The range of salinity was greatest in 2000 and sardine eggs were found broadly over this range, as manifest by both analyses. Conversely, the range of salinities encountered was smaller in 2001, as was the variance of salinity in the sardine spawning habitat (Fig. 1). The T-S plots (Plate 4) indicate that anchovy spawned primarily in water of one of two types: either upwelled (cool, high salinity) water that had warmed or North Pacific Central water. Conditions during the spring 2000 cruise included modest upwelling and strength of the California Current, and sardine spawning over a broad area, whereas spring 2001 had stronger upwelling and sardine spawning was observed in a more restricted area (http://swfsc.nmfs.noaa.gov/frd/CalCOFI/CurrentCruise/sardmaps.htm). Thus, significant inter-annual variation occurred between springs of 2000 and 2001. The use of both T-S and quotient analyses, when considered in the context of other environmental information (e.g. water mass characteristics, satellite imagery, and other, measured variables) has the potential to provide significant insight into the characteristics that define spawning habitat and its use.

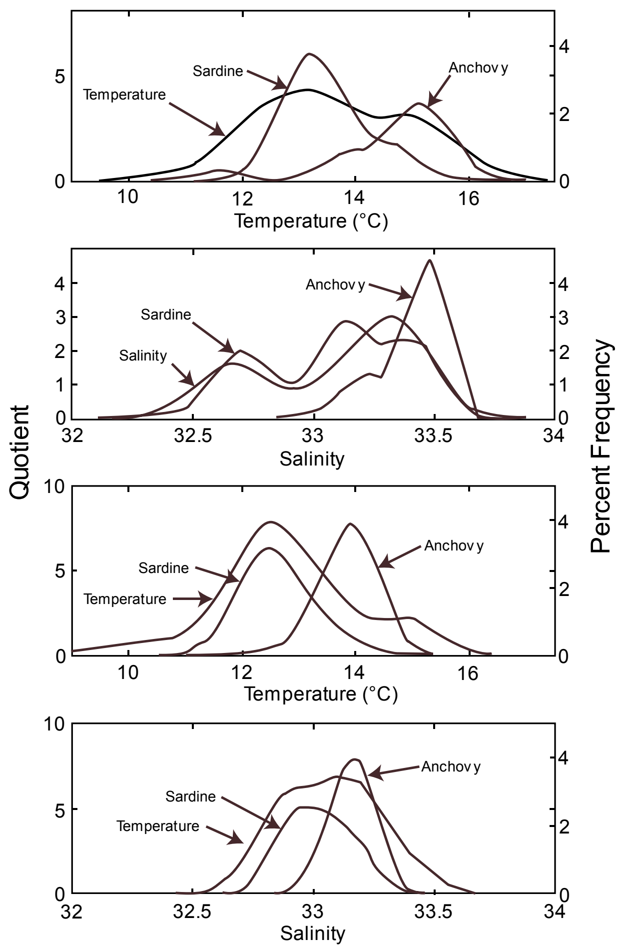

Figure 1. Quotient plots for Pacific sardine and northern anchovy using data collected during spring (April) CalCOFI cruises of 2000 (upper two panels) and 2001 (lower two panels). Bin widths were 0.1 (temperature) and 0.02 (salinity), and two-point double running means were used.

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Checkley D.M., R.C. Dotson and D.A. Griffith. 2000. Continuous, underway sampling of eggs of Pacific sardine (*Sardinops sagax*) and northern anchovy (*Engraulis mordax*) in spring 1996 and 1997 off southern and central California. Deep-Sea Research II 47:1139-1155.

Table 1. Data used in the analyses

Region	Species	Year/season of sampling	Method of egg collection and number of samples	Environmental parameters
California Current (southern sector)	*Engraulis mordax, Sardinops sagax*	2000 and 2001 spring (April)	CUFES 834 (2000) 931 (2001)	Date, time, latitude, longitude, temperature, salinity

ANCHOVY AND SARDINE SPAWNING HABITAT IN THE BAY OF BISCAY

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Details of data used for this analysis are provided in Table 1. In all analyses anchovy appear to have a preference for spawning in warmer and less saline waters than do sardine (Plate 5). However, the segregation in spawning habitat between the two species for both parameters seems to be clearer when the cruise covers large areas where no sardine or anchovy eggs are found, such as the tri-annual cruise (Fig. 1) designed to cover mackerel distribution compared to the MPDH (Método de Produción Dias de Huevas = DEPM) cruise that is designed to cover anchovy distribution.

Table 1. Details of data used in this analysis

Region	Species	Year/season of sampling	Method of egg collection and number of samples	Environmental parameters
Bay of Biscay	*Engraulis encrasicolus, Sardina pilchardus*	Tri-annual in 1998 (February - May) May-June MPDH surveys, 1999-2002.	PairoVET	SST, surface salinity, and Chl *a* for MPDH, and zooplankton for some transects.

Additionally, the results are variable from year to year, indicating no absolute preference for a range of environmental parameter values. Quotient curves using deviation from the annual average for

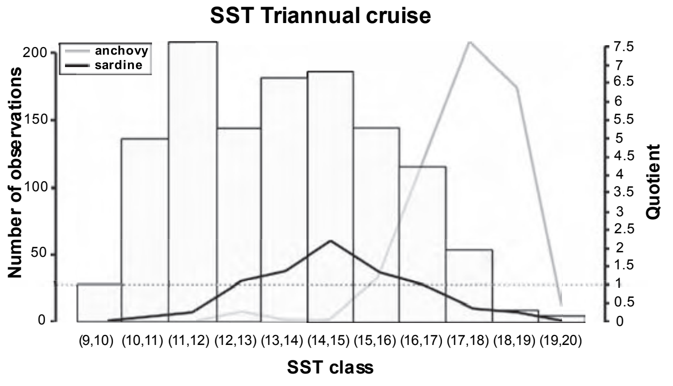

Figure 1. Distribution of SST (histograms) and egg abundance/temperature quotients for sardine (darker line) and anchovy (lighter line) eggs in the Bay of Biscay using data from the tri-annual survey.

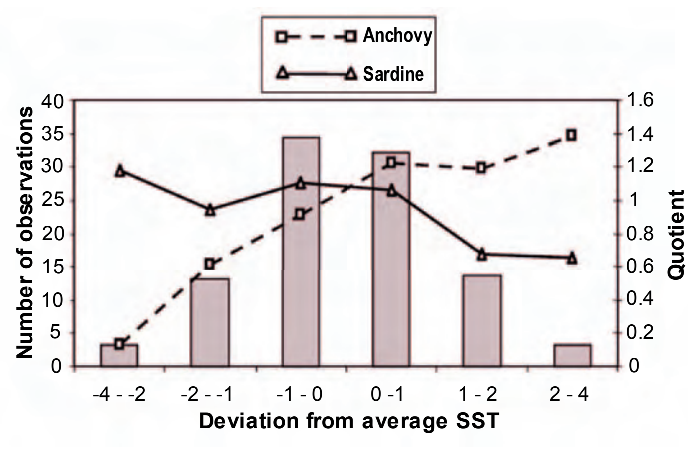

Figure 2. Distribution of SST deviation from average (histograms) and egg abundance/ temperature deviation quotients for sardine (triangles) and anchovy (squares) eggs in the Bay of Biscay using data from the MPDH survey.

temperature were also constructed, under the assumption that the species will not select spawning habitat on the basis of an absolute temperature, but the relatively cooler or warmer waters (Fig. 2). However, the variability from year to year remains. Finally for biological parameters, anchovy seems to prefer intermediate Chl *a* values, and both species differ in their zooplankton size classes preferences.

Although described as physical or biological parameters, rather than a preference for some environmental conditions, the data seem to describe the preference of anchovy for spawning in the rich waters of the Gironde plume. Those waters are less saline and warmer than surrounding waters. Secondary peaks in anchovy spawning coincide with the shelf-break, where primary production is enhanced by internal waves. Sardine spawning appears related to the shelf-break and to the plume of the Loire River farther north. In general, the spawning locations of both species in the Bay of Biscay seem to be related to geographical features that result in higher productivity (*e.g.* river plumes and the shelf-break), with sardine showing some preference for spawning in cooler waters than does anchovy.

The results also show that the analysis depends, in part, on the surveyed area. Therefore, an accurate definition of the environmental factors limiting spawning area requires the surveys to be extended to areas where neither sardine nor anchovy eggs are found.

Acknowledgements

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SPAWNING HABITAT OF IBERIAN SARDINE (*SARDINA PILCHARDUS*, W.) OFF THE NORTH SPANISH COAST

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Sardina pilchardus Walbaum is an indeterminate multiple batch spawner, with a protracted spawning season that lasts from autumn to spring (October to May). This species is found in North East Atlantic (NEA) waters and in the Mediterranean Sea and the main spawning grounds in the NEA include the Atlantic coasts of Morocco, Portugal, Spain and France. Here, a brief characterization of the spawning grounds off the north Spanish coast using two recent CUFES surveys is carried out. Table 1 summarises the years, number of stations and environmental variables used in the analysis, while Figure 1 and Plate 6 show the main results from the analysis.

Quotient analysis (Fig. 1) was carried out using temperature, salinity and depth as environmental and geographic covariates, the latter transformed to logarithm scale. Quotients of sardine egg density (eggs / m^3) are smoothed using a running median. For the 2001 survey, the salinity range

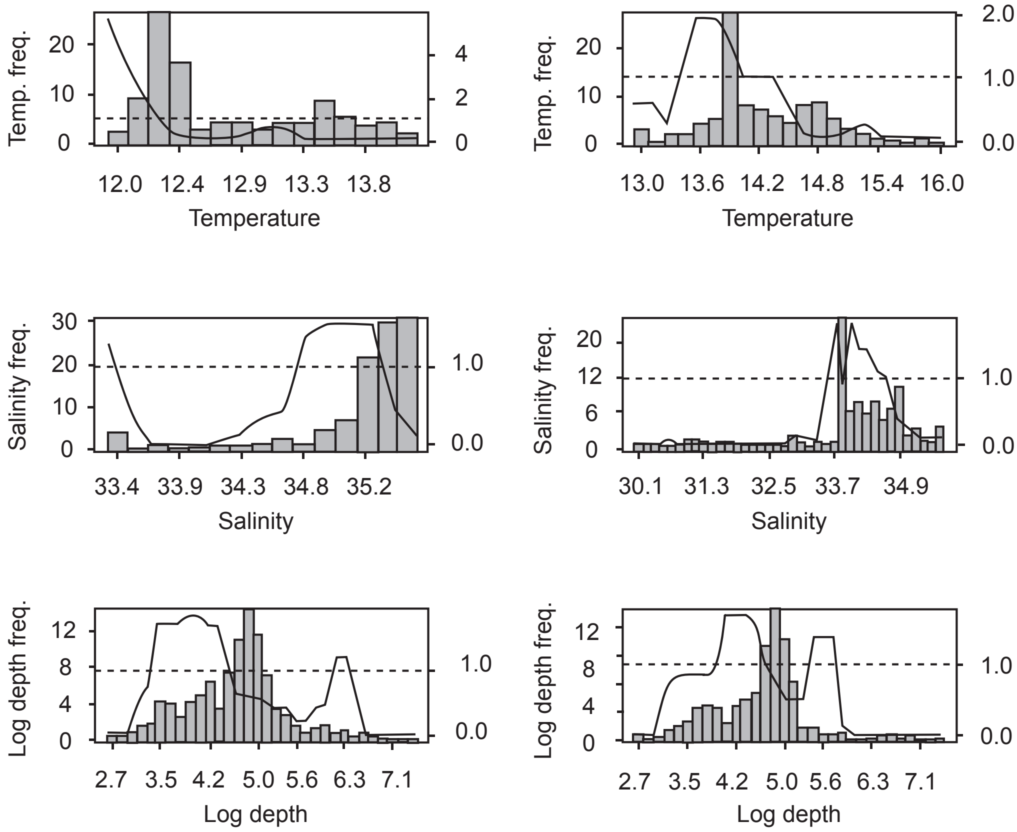

Figure 1. Quotient analysis of *S. pilchardus* egg density (eggs /m^3) in relation to temperature (top) salinity (middle) and logarithm of the bottom depth (bottom) off the north Spanish coast. Left panels represent the year 2000, right panels the year 2001. The right y-axis and the line represent quotient values, the left y-axis and histograms represent the frequency distribution values for each class of environmental variable examined, and the class values are given on the x-axis. The horizontal dashed line indicates a quotient value of 1.

used in the quotient analysis ([30 – 36]) is a subset of the one observed in the survey ([23 – 36]), excluding around 10% of the stations, and 5% of the positive stations, most of them off the northern Portuguese coast. Results from the quotient analysis show different environmental characteristics, and no clear preference for a fixed salinity or temperature range, between years. Temperature preferences are in the lower part of the range of survey temperatures in both years, while salinity follows the salinity range observed for the 2001 survey, but quotient values are higher in the lower part of the salinity range for the 2000 survey. As for depth, most of the positive stations and the classes with quotients larger than one are on the shelf (Log (Depth) < 5.3) but there is a second peak in the quotient related to a few positive stations in deeper waters, associated with a deep cannon located in the inner Bay of Biscay (Cap Breton Cannon).

The T-S plots (Plate 6) indicate quite different situations in 2000 and 2001. In 2000, most stations are located along a density isoline and only stations with lower salinity, associated with river inflows, depart from this isoline. Most of these low salinity stations show a sardine egg presence, which corresponds also with the hydrographical conditions of the northern Spanish coast, where river inflows affect only coastal areas. Stations with larger abundance of eggs are aggregated near the lower salinity and lower temperature values of the 27 pycnocline. In 2001, T-S pairs are more scattered and do not follow any pycnocline. The low salinities in 2001 are associated with large river discharges off the north Portuguese coast during this year. In both T-S plots, higher temperatures are associated with the Portuguese coast, due to spring SST warming. Following this first implementation of quotient analysis and T-S plots to study Spanish sardine, both methods are regarded as interesting tools to analyse the characteristics of the spawning areas in this area, but due to the large interannual and small scale spatial variability, longer time series and of broader coverage are desirable to perform a more complete analysis.

Table 1. Summary of data used in the analysis

Region	Species	Year/season of sampling	Method of egg collection and number of samples	Environmental parameters
North Spanish coast	*Sardina pilchardus*	March-April, 2000, 2001	CUFES 332 (2000) 360 (2001)	SST, surface salinity, bottom depth

Characterization of the Iberian Sardine (*Sardina pilchardus*) Spawning Habitat with Respect to Temperature and Salinity

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Sardine egg densities and environmental data (temperature, salinity), resulting from CUFES (Continuous Underway Fish Egg Sampler) surveying during two campaigns, in 2000 and 2002, were used to describe the spawning habitat of *Sardina pilchardus* off Portugal (Table 1). Single parameter quotient analysis (van der Lingen *et al*., 2001), and temperature-salinity plots using densities for total eggs, and for eggs per stage of development, were employed to examine spawning habitat. Eggs were grouped into ages (Days: 1 to 4) according to development stage (I to XI) and local temperature using the equation of Miranda *et al*., (1990).

Table 1. Summary of information analysed

Region	Species	Year/season of sampling	Method of egg collection and number of samples	Environmental parameters
South and Western Iberia (Portugal)	*Sardina pilchardus* (eggs staged in 11 stages)	March - April 2000; and March - April 2002 (late winter - early spring)	CUFES 810 (2000) 831 (2002)	Temperature, salinity

Temperature, measured at 3m depth, ranged from 13.5 to 17°C and from 13 to 18°C, during the 2000 and 2002 surveys, respectively, indicating some degree of inter-annual variability in water temperature. Egg percentage/temperature percentage transformations presented in Figures 1 and 2 show preferred temperature spawning ranges between 15.5 and 16.5°C for the 2000 survey, and between 15.5 and 17.5°C during the 2002 campaign, with clear peaks at the higher temperatures. The quotient analysis performed for eggs separated into the four ages and total eggs revealed that the latter reflected well the temperatures at which the younger eggs (ages 1 and 2 days), near to spawning, were found. Peaks at lower temperatures observed for Day 3 and 4 eggs resulted, in large part, from a higher contribution of individuals with slower development, in particular during 2000, since at higher temperatures hatching occurred on the second day. It is important to point out that the egg spatial distribution during the two surveys analysed here, carried out towards the end of the spawning season, showed higher egg abundances in the southern and south-western regions where sea water temperatures are usually higher. Differences in water temperature associated with geographical location may require stratification of the information to be analysed.

Temperature-salinity plots presented in Plate 7 revealed that *S. pilchardus* in Portuguese waters is eurythermic and euryhaline, with spawning occurring over the whole range of temperatures and salinities sampled. Higher egg abundances were found in temperatures ranging from 15 to 17°C and salinities from 35.75 to 36.5 psu (typical water salinity for the region); the range of salinities encountered at surveying being dependent on the contributions of water of continental origin, from the Azores current, and from the Gulf of Cadiz. The T-S diagrams constructed for total eggs provide a representative characterization of the distribution of eggs of all ages with respect to temperature and salinity.

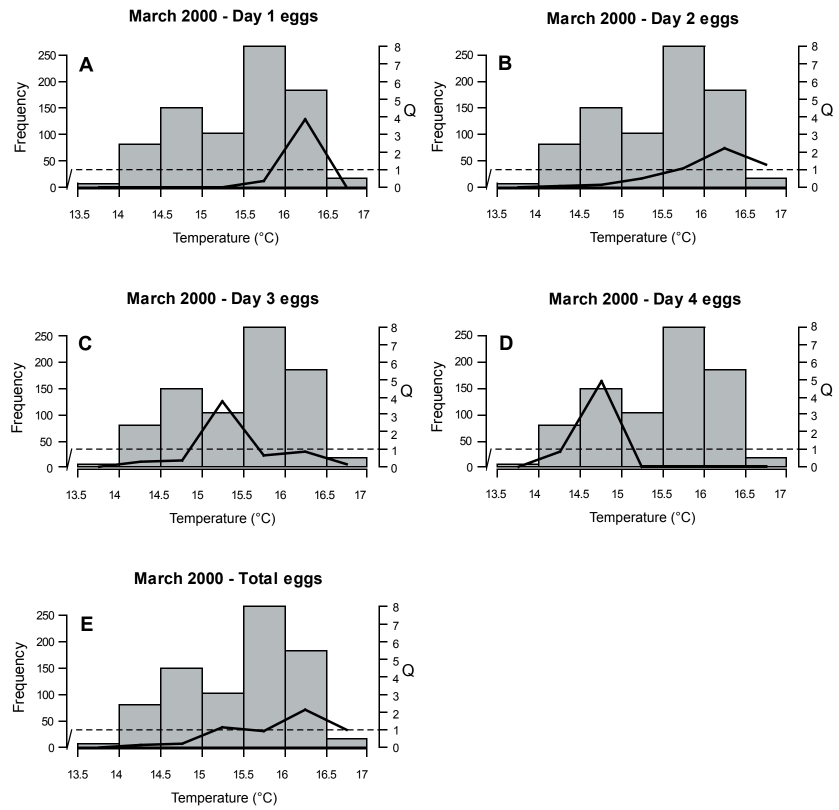

Figure 1. March-April 2000 survey. Frequency distribution of temperature sampled (histograms) and % egg density/% temperature quotient (Q; line) for Age 1 eggs (A), Age 2 eggs (B), Age 3 eggs (C), Age 4 eggs (D), and Total eggs (E).

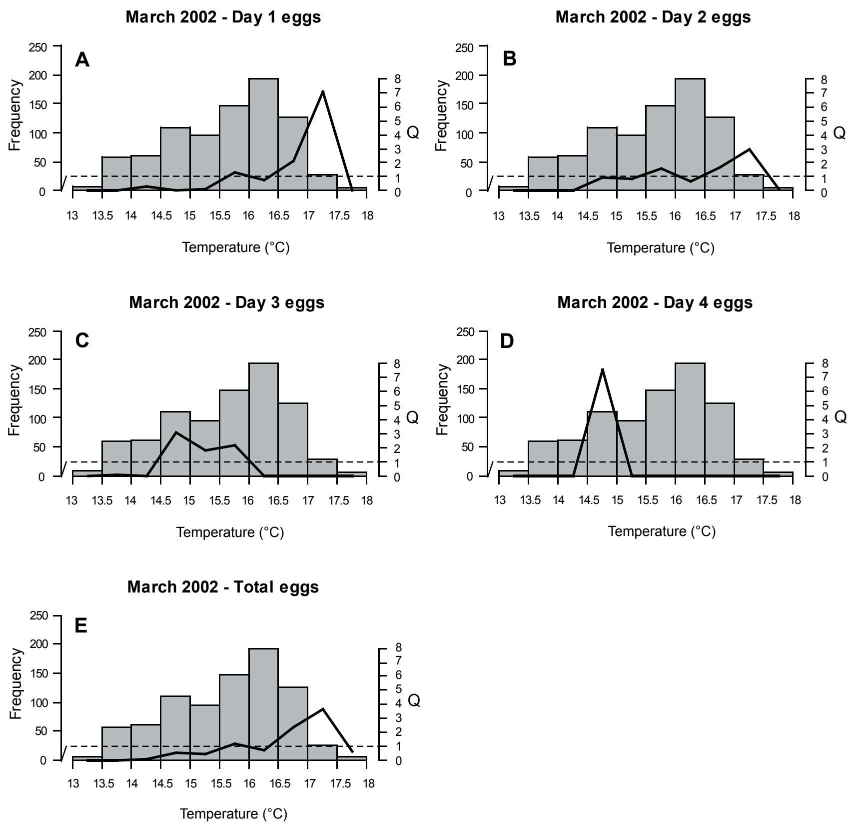

Figure 2. March-April 2002 survey. Frequency distribution of temperature sampled (histograms) and % egg density/% temperature quotient (Q; line) for Age 1 eggs (A), Age 2 eggs (B), Age 3 eggs (C), Age 4 eggs (D), and Total eggs (E).

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CHARACTERISTICS OF SPAWNING HABITAT OF *SARDINA PILCHARDUS* OFF THE SOUTH MOROCCAN ATLANTIC COAST (21-26°30´N)

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Details of sampling for sardine eggs off Morocco are provided in Table 1. The distribution of sardine eggs reveals that winter is the maximum spawning season, whereas spring and summer are secondary spawning seasons. The sardine spawning ground with maximum egg abundance is located north of Dakhla (24°N), this area being characterized by a large, flat, and not very deep continental shelf. This zone could constitute a favourable place for retention of larvae and for their development (Roy, 1991; Ettahiri *et al.,* 2003).

Table 1. Details of data used in this analysis.

Region	Species	Year/season of sampling	Method of egg collection and number of samples	Environmental parameters
Moroccan Atlantic coast 21°N - 26°N	*Sardina pilchardus*	1994 (winter and summer) 1995 (winter and summer) 1996 (summer) 1997 (winter and summer) 1998 (spring and summer) 1999 (spring and summer)	Bongo net (20cm diameter and 417µm mesh)	SST, surface salinity

The maximum of eggs is observed at temperatures between 16 and 18°C in winter, 16-17°C in spring and 17-20°C in summer (Plate 8). For salinity, the maximum spawning of Moroccan sardine is observed over a salinity range of 35.8-36.7 psu in winter, 36.1-36.7 psu in spring and 36.2-36.5 psu in summer (Plate 8).

The maximum of SST frequencies is observed at 17 and 18.5°C in winter, 16-17 and 18°C in spring, and 18 and 19°C in summer (Fig. 1A). The quotient analysis shows peaks in the quotient curve at 16, 17 and 19.5°C in winter, at 15.5 and 18.5°C in spring, and at 18, 19-19.5 and 22°C in summer (Fig. 1B). In summer, the last peak (22°C) corresponds to only one station that had a high egg density. The analysis of the frequencies of SST observations shows the existence of two peaks per seasons: a principal one and a secondary one. However, the quotient analysis shows that the maximal densities present only one major peak per season (15.5°C in spring, 17°C in winter, and 22°C in summer), and that, with the exception of summer, these peaks coincide with the principal peak established by the frequency analysis of SST.

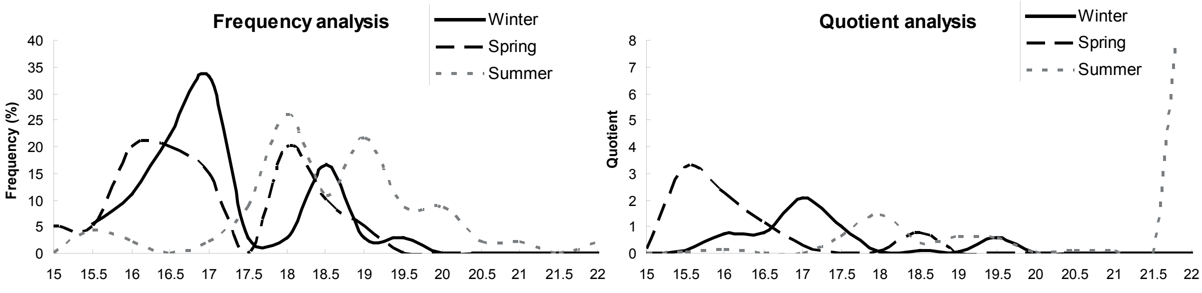

Figure 1. Seasonal frequency distribution curves of SST (A); and seasonal quotient curves for sardine eggs and SST (B).

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CHARACTERIZING SPAWNING HABITATS OF SMALL PELAGIC FISHES IN THE MEDITERRANEAN

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Available data that could be useful for the characterization and comparison of small pelagic fishes' spawning habitats in the Mediterranean Sea have generally been very limited. This is due to the fact that Daily Egg Production Method (DEPM) surveys of different stocks have not been conducted on a routine basis. In general, there are one or two applications for specific Mediterranean regions. In the Concepción Workshop data have been analyzed from both the eastern and western Mediterranean. Specifically, data from three anchovy surveys in the western Mediterranean and one anchovy as well as one sardine survey in the eastern Mediterranean have been used (Table 1).

Table 1. Mediterranean Sea data summary

Region	Species	Year / season of sampling	Method of egg collection and number of samples	Environmental parameters
NW Mediterranean, Catalan Sea and Gulf of Lions	*Engraulis encrasicolus*	June-July (summer) surveys, 1993-1994	Vertical tows (CalVET 0.150mm mesh) 430 (1993) 334 (1994)	SST (5m) SSS (5m)
NW Mediterranean, Ligurian and Tyrrhenian Sea	*Engraulis encrasicolus*	July (summer) survey, 1993	Vertical tows (CalVET 0.150mm mesh) 172 (1993)	SST (5m) SSS (5m)
NE Mediterranean, Central Aegean and Ionian Seas	*Engraulis encrasicolus*	June (summer) survey, 1999	Vertical tows (WP2, 0.200mm mesh) 164 (1999	SST (5m) SSS (5m
NE Mediterranean, Central Aegean and Ionian Seas	*Sardina pilchardus*	December - February (winter) surveys, 2000-2001	Vertical tows (WP2, 0.200mm mesh) 153 (2000 - Aegean) 129 (2001 - Ionian)	SST (5m) SSS (5m)

The single parameter quotient analysis was applied for each survey separately. The parameter examined was sea surface temperature. The results (temperature selection) differed depending on the temperature regime of the particular survey. In other words, inter-annual and regional differences in water temperature were reflected in the quotient curves. The analysis of pooled data for anchovy (all available data from the western and eastern Mediterranean) is shown in Figure 1. We believe that if many surveys from different years and areas had been included in the analysis, a selection for the temperature range of 17-23°C would probably have been found (as illustrated for the South African anchovy; see van der Lingen this volume).

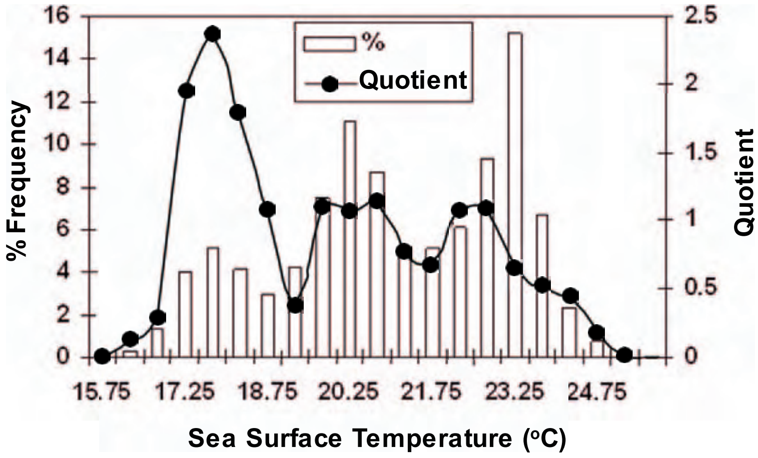

Figure 1. Frequency distribution (histograms) of sea surface temperature (at 5m) at all plankton stations sampled, and anchovy egg abundance/sea surface temperature quotient (filled circles and line) from all Mediterranean anchovy egg surveys (see Table 1). Different modes in both the SST frequency distribution and quotient curve reflect the different temperature regimes of individual surveys.

Examples of T-S plots are given in Plate 9. Neither anchovy nor sardine seemed to select specific water masses. We believe that pelagic fish spawning in the Mediterranean Sea is most likely related to specific geographical regions rather than particular water masses.

Finally, we must point out that data analyzed from the Mediterranean Sea were quite limited. Both the single parameter quotient analysis and T-S plots would be very useful if applied to longer time series of yearly egg surveys for different Mediterranean anchovy and sardine stocks.

CHARACTERIZING THE SPAWNING HABITAT OF SARDINE (*SARDINOPS SAGAX*) AND ANCHOVY (*ENGRAULIS ENCRASICOLUS*) IN THE NORTHERN BENGUELA

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During the last ten years, annual BENEFIT ichthyoplankton surveys have been conducted in the northern Benguela with the R/V *Dr. Fridtjof Nansen* (Table 1). Due to the low stock sizes of both anchovy and sardine and the timing of the surveys, relatively small numbers of eggs have been sampled in most years. However, during the last two surveys (February 2003 and January 2004), the number of sampled eggs of both species has increased. In 2003, the spatial coverage was limited, but in 2004 the coast was covered from 15°50´S to 24°30´S and eggs were found throughout the area. Therefore, only the results from 2004 are included in this report.

SST during the survey ranged between 15.7 and 23.3°C. Eggs of both species were found in waters with SST ranging from 16 to 19.5°C. In the quotient analysis, there were two peaks for both species, one at 16-16.5°C and one at 19-19.5°C (Fig. 1). However, the anchovy peak at the lower temperature range was below one and was therefore not considered as positive selection. Positive selection for anchovy was between 18.5 and 19.5°C, while positive selection for sardine was at 16-16.5°C and at 19-19.5°C. The results are in accordance with what has been found in the southern Benguela (van der Lingen *et al*., 2001) where anchovy spawn in warmer waters than sardine and the sardine quotient curve is bimodal.

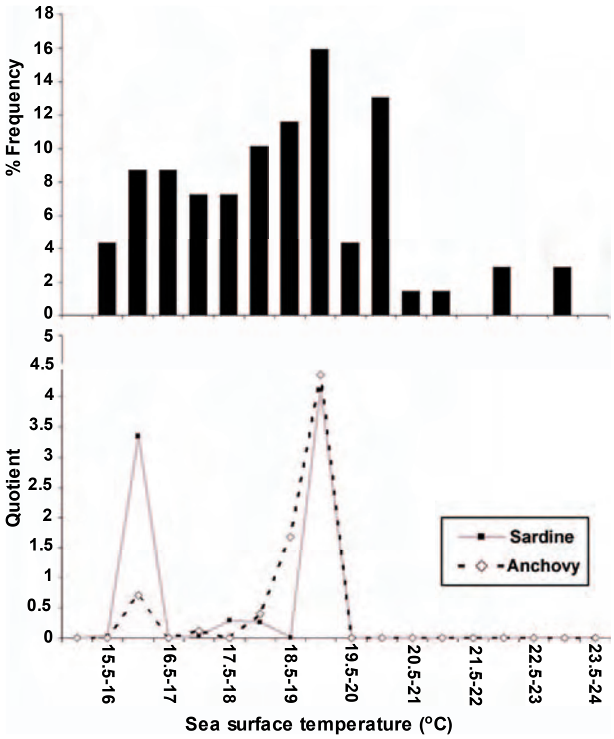

Figure 1. Frequency distribution of sea surface temperature (histograms; upper panel) and quotient (lower panel) for sardine (solid line) and anchovy (broken line) during the survey in January 2004.

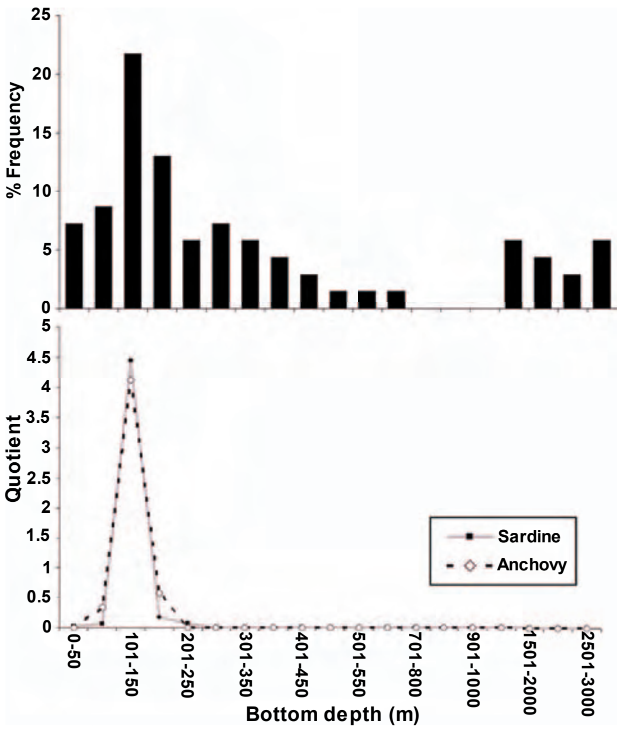

Figure 2. Frequency distribution of bottom depth (histograms; upper panel) and quotient (lower panel) for sardine (solid line) and anchovy (broken line) during the survey in January 2004.

Bottom depths during the survey ranged from 39m to more than 3000m. By using the single quotient approach to characterize spawning according to bottom depth, there was a strong selection by both species (Fig. 2) to spawn between 100 and 150m. The occurrence of fronts between cold upwelled water and warm oceanic water is closely related to bottom depth (shelf break), and it is possible that bottom depth is a proxy for fronts and that the strong observed selection is more related to fronts than bottom depth *per se*.

The temperature-salinity plot (Plate 10) shows that salinity ranged from 35.13 to 36.07. The warm, saline, Angolan water, which was encountered on the northernmost stations, is shown at the upper right part of the figure. South of this, the temperature gradient was more pronounced cross-shelf than alongshore. Eggs of both species are found in the front between the relatively cold coastal water and the warm oceanic water/warm and saline Angolan water.

The results presented here are based on limited data from only one survey, and should therefore be interpreted with caution. Even so, the results are in accordance with what has been shown in other areas; that sardine tends to spawn in colder water than anchovy. Also, there was a strong selection for bottom depth for both species, which could be related to fronts between the cold upwelled water and warm oceanic water. This could indicate that fronts with temperature gradients could be important spawning areas for both species, and this should be addressed further. It would be interesting to compare the results presented here with the more extensive data from the SWAPELS surveys that were conducted in the region during the late 1970's and early 1980's.

Table 1. List of data included in the analyses

Region	Species	Year/season of sampling	Method of egg collection and number of samples	Environmental parameters
Northern Benguela	*Sardinops sagax* and *Engraulis encrasicolus*	January 2004	Multinet 72 samples	SST, surface salinity, bottom depth

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CHARACTERIZING SPAWNING HABITAT OF ANCHOVY (*ENGRAULIS ENCRASICOLUS*), REDEYE ROUND HERRING (*ETRUMEUS WHITEHEADI*), AND SARDINE (*SARDINOPS SAGAX*) FROM CUFES SAMPLING IN THE SOUTHERN BENGUELA

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Data from CUFES samples collected during hydroacoustic surveys to estimate pelagic fish biomass in 1998 and 2001 are presented here (Table 1), since these years represent contrasting patterns of fish biomass (anchovy biomass was low in 1998 and high in 2001) and the location of intense spawning (sardine spawned primarily off the west coast in 1998 and off the south coast in 2001).

Table 1. Specifics of data used in the analyses

Region	Species	Year/season of sampling	Method of egg collection and number of samples	Environmental parameters
Southern Benguela (30-37°E and 16-27°S)	*Engraulis encrasicolus*, *Etrumeus whiteheadi* and *Sardinops sagax*	November (summer) pelagic spawner biomass surveys; 1998 and 2001	CUFES (3m in 1998 and 6m in 2001; 500µm concentrator): 1467 (1998) 1617 (2001)	SST, salinity, water depth

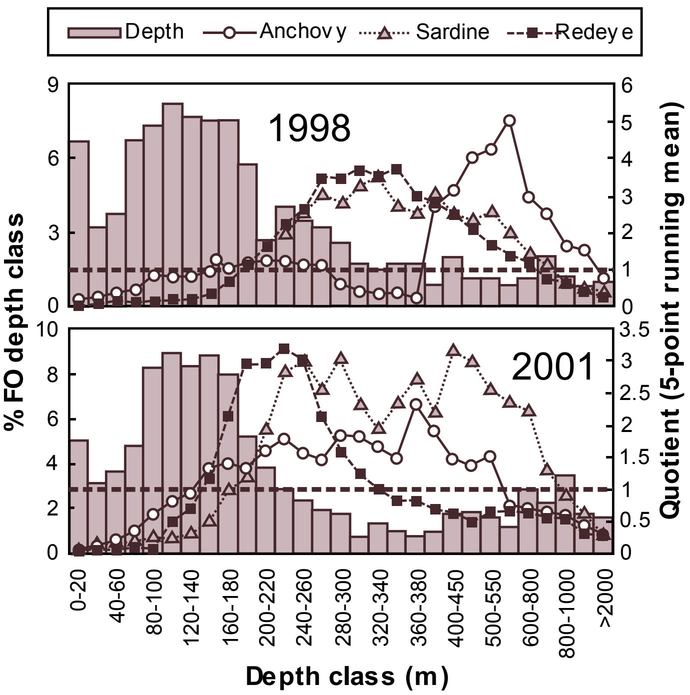

Figure 1. Frequency distribution of depth class (histograms) and egg abundance/depth quotients (symbols and lines) for anchovy, round herring and sardine in 1998 and 2001.

Quotient analysis indicated that all three species selected (*i.e.* quotient values >1) to spawn over and offshore off the shelf-edge (200m) in 1998 (Fig. 1), with anchovy showing a narrow depth range for spawning, and spawning in deeper waters, compared to the other two species. In 2001, sardine selected a narrower depth range for spawning. T-S plots show both interspecific and interannual differences (Plate 11). In 1998, anchovy spawned in warm, saline waters; sardine in waters of intermediate temperature and salinity; and round herring over a broad T-S range. In 2001, sardine spawned in waters of high temperature and intermediate salinity; anchovy spawned over a broad T-S range but mainly in waters of intermediate temperature and high salinity; and round herring spawned over a fairly restricted range of low temperature, low salinity water.

Results obtained demonstrate that quotient curves and T-S plots permit the differentiation of spawning habitat by small pelagic species in the southern Benguela; that substantial interannual variability in spawning habitat selection can occur (*e.g.* the marked shift in T-S characteristics of sardine spawning habitat between 1998 and 2001); and that biomass levels appear to affect spawning habitat characteristics (*e.g.* the broadening of the T-S range within which anchovy eggs were found in 2001 compared to 1998). Results also corroborate previous findings on spawning habitat selection by anchovy and sardine based on CalVET net samples, which indicated significant differences in spawning habitat selection by anchovy and sardine in terms of SST and salinity (Twatwa *et al*., 2004).

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GLOBEC Report No.22

Report of the SPACC Meeting on Small Pelagic Fish Spawning Habitat Dynamics and the Daily Egg Production Method (DEPM)

(14-16 January 2004, Concepción, Chile)

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