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UNCERTAINTY IN STOCK ASSESSMENTS, SPATIAL DISTRIBUTION AND HABITAT MODELLING OF TWO SMALL PELAGIC FISH SPECIES, SARDINE (*Sardina pilchardus*) AND ANCHOVY (*Engraulis encrasicolus*), IN THE MEDITERRANEAN FROM LATE AUTUMN SPANISH ACOUSTIC SURVEYS

Volume I of I

M. Pilar Tugores Ferrà

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Doctoral Programme of Biology

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Volume I of I

M. Pilar Tugores Ferrà

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Doctor by the Universitat de les Illes Balears

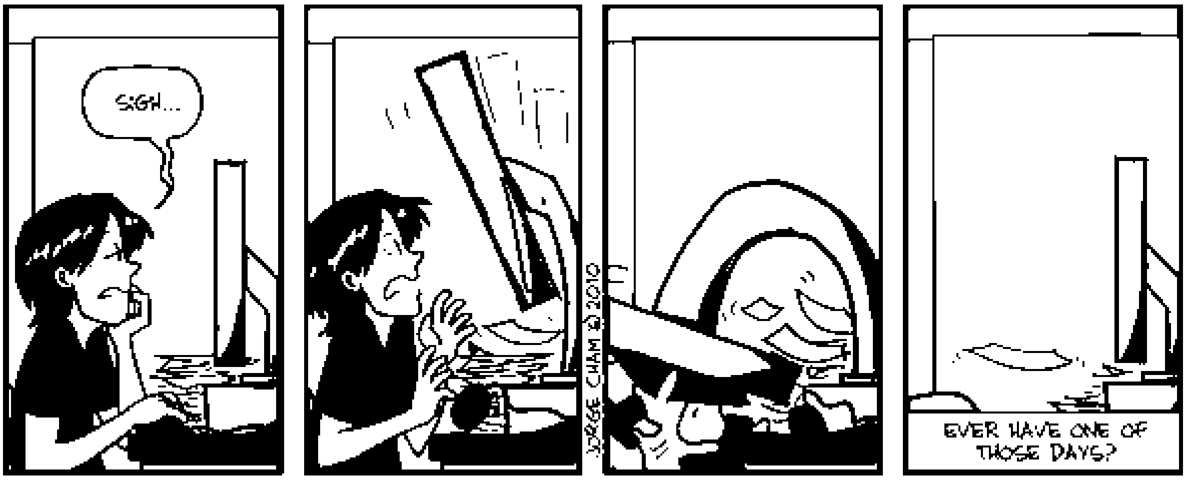
A la meva família, als meus amics, i a
tots els que d'alguna manera han fet aquest
treball posible

"We shall not cease from our exploration
And the end of all our exploring
Will be to arrive where we started
And know the place for the first time"

(T.S. Eliot)

"I almost wish I hadn't
gone down that rabbit-hole
- and yet - and yet -
it's rather curious, you know,
this sort of life!"

(Alice, in *Alice in Wonderland*,
by Lewis Carrol)



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Derived publications

Chapters 2 to 5 presented in this thesis have been partially published or submitted for publishing in the form of scientific papers. In particular,

Chapter 2 is based on the paper: “Tugores, M.P., Iglesias, M., Díaz, N., Oñate, D., Miquel, J. and Giráldez, A. 2010. Latitudinal and interannual distribution of the European anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) in the western Mediterranean, and sampling uncertainty in abundance estimates. ICES Journal of Marine Science, 67: 1574-1586”

A reduced version of **Chapter 3** has been sent for publication as: “Tugores, M.P., Iglesias, M., Oñate, D. and Miquel, J. Spatial distribution, sampling precision and survey design optimization with non-normal variables: the case of anchovy (*Engraulis encrasicolus*) recruitment in the Spanish Mediterranean waters. Progress in Oceanography. Submitted”

Chapter 4 have been partially published within a broader paper, co-authored with people from other Mediterranean countries and including data from these other countries as: “Tugores, M.P., Giannoulaki, M., Iglesias, M., Bonanno, A., Ticina, V., Leonori, I., Machias, A., Tsagarakis, K., Díaz, N., Giráldez, A., Patti, B., De Felice, A., Basilone, G., and Valavanis, V. 2011. Habitat suitability modeling for sardine *Sardina pilchardus* in a highly diverse ecosystem: the Mediterranean Sea. Marine Ecology Progress Series, 443: 181-205”

Chapter 5 have as well been partially published within a broader paper, co-authored with people from other Mediterranean countries and including data from these other countries as: “Giannoulaki, M., Iglesias, M., Tugores, M.P., Bonanno, A., Patti, B., De Felice, A., Leonori, I., Bigot, J.L., Ticina, V., Pyrounaki, M.M., Tsagarakis, K., Machias, A., Somarakis, S., Schismenou, E., Quinci, E., Basilone, G., Cuttitta, A., Campanella, F., Miquel, J., Oñate, D., Roos, D., and Valavanis, V. 2013. Characterizing the potential habitat of European anchovy *Engraulis encrasicolus* in the Mediterranean Sea, at different life stages. Fisheries Oceanography, 22 (2): 69-89”

Llist of acronyms and abreviations

AIC - Akaike's Information Criterion

ANOVA - Analysis Of Variance

AUC - Area Under the ROC

CFP – European Common Fisheries Policy

CHLA - sea surface chlorophyll concentration

CI – confidence interval

CUFES – Continuous Underway Fish Egg Sampler

CV – Coefficient of Variation

DSP – Digital Signal Processing

EDSU – Elementary Distance Sampling Unit

EU – European Union

EVA – Estimation of the VAriance

FAO – Food and Agriculture Organisation of the United States

GAMs - Generalised Additive Models

GCV - Generalized Cross Validation

GFCM - General Fisheries Commision for the Mediterranean Sea

GLOBEC - Global Ocean Ecosystem Dynamics programme

GSA - Mediterranean Geographical Subarea

I2D – intrinsic geostatistics in 2 dimensions

ICES – International Council for the Exploration of the Sea

IEO – Instituto Español de Oceanografía

MDT - maximization of the specificity-sensitivity sum

MPA – Marine Protected Area

NASC – Nautical Area Scatering Coefficient

NC – Northern Current

NS – Northern subarea (defined in Fig. 2.1)

PAR - photosynthetically active radiation

PDF – probability distribution function

PRV – prevalence

PSH	potential spawning habitat
ROC	Receiver Operating Characteristic curve
RSH	realised spawning habitat
SGMED	Study Group on Mediterranean Fisheries
SLA	sea level anomaly
SS	Southern subarea (defined in Fig. 2.1)
SSS	sea surface salinity
SST	sea surface temperature
T1D	transitive geostatistics in 1 dimension
TS	target strength
Tukey HSD	Tukey’s Honestly Significant Difference test

Contents

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Summary

Small pelagic fish are species that live in the water column and have little relationship with the sea bottom. During the day they may form schools with feeding, defence or energetic efficiency purposes and disperse during the night. The importance of small pelagic fishes within the marine ecosystem rely in the proportion of biomass they represent and the clue function they develop as intermediate links in the energy transfer between lower and upper levels of the trophic chain. Their populations are particularly sensitive to environmental fluctuations (Cole and McGlade, 1998; Lloret *et al.,* 2004) and frequently highly exploited by commercial fisheries. These may occasionally collapse the stocks affecting both the marine ecosystem and the fisheries they sustain.

In the Mediterranean, almost 50% of the total annual landings are attributable to small pelagic fishes (Lleonart and Maynou, 2003). In the Western Mediterranean Sea, sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*) are the two most important species in terms of landed biomass and commercial interest (Lleonart and Maynou, 2003). Despite their importance little is known about the spatial distribution of these stocks or about the relationship between the spatial distribution and environmental variables.

Since the '90s acoustic surveys are annually performed in the Spanish Mediterranean continental shelf in late autumn (Abad *et al.,* 1998 a,b) coinciding with anchovy's recruitment and the beginning of the spawning season for sardine (Abad and Giráldez, 1993; Giráldez and Abad, 1995). Although the main goal of these surveys is to estimate abundance and biomass of sardine and anchovy, data about the whole pelagic community has also been gathered. Furthermore, in the last decade it was detected an increasing appearance of other small and medium-sized pelagic species and the application of a multi-species approach to Mediterranean fisheries assessment was advised (Lleonart and Maynou, 2003).

The present work is structured in two sections. The first section of the work will analyse the spatial distribution (1D and 2D) of sardine and anchovy by means of geostatistical techniques, both transitive and intrinsic methods (Matheron, 1969). Special attention will be paid to the estimation of the uncertainty associated to abundance estimations and, concretely, the uncertainty caused by sampling scheme which is thought to be one of the main contributors to random error (ICES, 1998).

The second section will explore the environmental factors that drive the presence or absence of anchovy and sardine in late autumn. Satellite environmental data as sea surface temperature, salinity, chlorophyll-a, photosintethic active radiation, sea level anomalies or bottom depth will be related to the presence-absence of sardine and anchovy stocks through Generalised Additive Models (GAM) to try to depict the relationships that may be found between both (Bellido *et al.,* 2008; Giannoulaki *et al.,* 2008). The spawning area of sardine will also be studied in order to model the presence-absence of sardine eggs and try to understand the evolution of their stocks.

Resumen

Los pequeños peces pelágicos son especies que viven en la columna de agua y que tienen poca relación con el fondo marino. Durante el día forman bancos de peces con el objetivo de alimentarse, defenderse de potenciales depredadores o por motivos de eficiencia energética, dispersándose durante la noche. La importancia de los pequeños pelágicos en el ecosistema marino radica en la proporción de biomasa que representan y en la función clave que desempeñan como eslabones intermedios, transfiriendo energía entre los niveles tróficos inferiores y superiores de la cadena trófica. Sus poblaciones son particularmente sensibles a las fluctuaciones ambientales (Cole and McGlade, 1998; Lloret *et al.,* 2004) y frecuentemente se encuentran en un régimen de explotación elevado por parte de las pesquerías comerciales. Esto puede comportar de manera ocasional el colapso de sus poblaciones explotables, afectando al ecosistema marino y a las pesquerías que las mantinen.

Casi el 50% del total de la biomssa anual desembarcada en los puertos del Mediterráneo provienen de los pequeños peces pelágicos (Lleonart and Maynou, 2003). En el Mediterráneo Occidental, la sardina (*Sardina pilchardus*) y el boquerón (*Engraulis encrasicolus*) son las dos especies más importantes, tanto en términos de biomasa como capturada como por su interés comercial (Lleonart and Maynou, 2003). A pesar de su importancia, la distribución espacial de las poblaciones explotables es poco conocida así como también lo es la relación de la distribución espacial con los parámetros ambientales.

Desde principios de los años 90, se llevan a cabo campañas acústica en la plataforma continental española del Mediterráneo a finales de otoño (Abad *et al.,* 1998 a,b), coincidiendo con el reclutamiento de la anchoa y la época de puesta de la sardina (Abad and Giráldez, 1993; Giráldez and Abad, 1995). A pesar de que el principal objetivo de estas campañas es la estimación de la abundancia y de la biomas de la sardina y el boquerón, datos de la comunidad pelágica en conjunto también se recogen periódicamente. Además, a lo largo de la última década se ha detectado una aparición incremental de otras especies de pequeños y medianos pelágicos y por tanto, se aconsejó la aplicación de un enfoque multiespecífo en la evaluación de pesquerías del Mediterráneo (Lleonart and Maynou, 2003).

El presente trabajo se estructura en dos seciones. La primera sección del trabajo analizará la distribución espacial (1D y 2D) de la sardina y el boquerón por medio de técnicas geoestadísticas, tanto transitivas como intrínsecas (Matheron, 1969). Se prestará especial atención a la incertidumbre asociasda a las estimaciones de abundancia y, concretamente, a la incertidumbre asociada al diseño de muestro que se considera uno de los factores que contribuyen con mayor intensidad al error aleatorio (ICES, 1998).

La segunda sección explorará los factores ambientales que condicioinan la presencia o ausencia de sardina y boquerón a finales de otoño. Datos ambientales obtenidos de satélite, como la temperatura superficial del mar, la salinidad, clorofila, radiación fotosintéticamente activa, anomalía del nivel del mar y la profundidad del fondo marino se relacionarán con la presencia-ausencia de las poblaciones explotables de sardina y boquerón mediante modelos aditivos generalizados (GAM, del acrónimo inglés) para determinar las relaciones existentes (Bellido *et al.,* 2008; Giannoulaki *et al.,* 2008). El hábitat de la puesta de sardina será igualmente estudiada para modelar la presencia-ausencia de huevos de sardina e intentar entender la evolución de las especies explotables.

Resum

Els petits peixos pelàgics són espècies de peixos que viuen a la columna d'aigua i que tenen poca relació amb el fons marí. Durant el dia formen bancs de peixos amb l'objectiu alimentar-se, defensar-se en front potencial depredadors o per eficiència energètica, dispersant-se durant la nit. La importància dels petits pelàgics a l'ecosistema marí radica en la proporció de biomassa que representen i en la funció clau que exerceixen com esglaons intermedis, transferint energia entre les nivells inferiors i superiors de la cadena tròfica. Les seves poblacions són particularment sensibles a les fluctuacions ambientals (Cole and McGlade, 1998; Lloret *et al.,* 2004) i freqüentment es troben baix un règim d'explotació elevat per part de les pesqueres comercials. Això pot comportar de manera ocasional el col·lapse de les seves poblacions explotables, afectant a l'ecosistema marí i a les pesqueries que sostenen.

Gairebé el 50% del total de la biomassa anual desembarcada als ports del Mediterrani prové dels petits peixos pelàgics (Lleonart and Maynou, 2003). Al Mediterrani Occidental, la sardina (*Sardina pilchardus*) i l'aladroc (*Engraulis encrasicolus*) són les dues espècies més importants, tant en termes de biomassa capturada com pel seu interès comercial (Lleonart and Maynou, 2003). Malgrat la seva importància, la distribució espaial de les poblacions explotables és poca coneguda així com també ho és la relació d'aquesta distribució espaial amb variables ambientals.

D'ençà de principis dels anys 90, es duen a terme campanyes acústiques a la plataforma continental del Mediterrani espanyol a finals de la tardor (Abad *et al.,* 1998 a,b), coincidint amb el reclutament de l'aladroc i amb l'època de posta de la sardina (Abad and Giráldez, 1993; Giráldez and Abad, 1995). Tot i que el principal objectiu d'aquestes campanyes és l'estimació de l'abundància i de la biomassa de la sardina i l'aladroc, dades del conjunt de la comunitat pelágica també es recolleixen. A més a més, al llarg de la darrera dècada s'ha detectat una aparició incremental d'altres espècies de petits i mitjans pelàgics i per tant, es va aconsellar l'aplicació d'un enfoc multiespecífic a l'avaluació de les pesqueres del Mediterrani (Lleonart and Maynou, 2003).

El present treball s'estructura en dues seccions principals. La primera secció del treball analitzarà la distribució espaial (1D i 2D) de la sardina i l'aladroc per mitjà de tècniques geoestadístiques, tant transitives com intrínseques (Matheron, 1969). Es prestarà especial atenció a la incerteza associada a les estimacions d'abundància i, concretament, a la incertesa originada pel disseny de mostreig que és considerat un dels factors que contribueixen amb més intensitat a l'error aleatori (ICES, 1998).

La segona secció explorarà els factors ambientals que condicionen la presència o absència de sardina i aladroc a finals de tardor. Dades ambientals obtingudes de satèl·lit, com la temperatura superficial de la mar, la salinitat, clorofil·la, radiació fotosintèticament activa, anomalies del nivell de la mar i la profunditat del fons marí es relacionaran amb la presència-absència de les poblacions explotables de sardina i aladroc mitjançant models additius generalitzats (GAM, de l'acrònim anglès) per determinar les relacions existents (Bellido *et al.,* 2008; Giannoulaki *et al.,* 2008). L'hàbitat de la posta de la sardina serà igualment estudiada per tal de modelar la presència-absència d'ous de sardina i intentar entendre l'evolució de les seves poblacions explotables.

Chapter 1. General Introduction

Chapter 1. General Introduction

1.1 Motivation and definition of the problem

The pelagic ecosystem is the combination of physical and biological interactions that occur in the water column of seas and oceans worldwide, with little contact or dependence with the sea bottom. The pelagic ecosystem is the most productive in the oceans and represents around a 95 % of the world ocean production (Margalef, 1993). Its exploitation plays an important social and economical role, contributing to up to a 50% of the world landings of marine species (Fréon *et al.,* 2005). Altogether with aquaculture, fisheries provide direct and indirect employment to over 660–820 million people, or about 10–12 percent of the world's population (Food and Agriculture Organisation; FAO, 2012).

Within the pelagic ecosystem, small pelagic fishes play a key role in the functioning of the ecosystem as they transfer energy from plankton to the upper levels of the trophic chain (Cury *et al.,* 2000). They also sustain important fisheries worldwide making them highly valuable in economical terms as well (Cury *et al.,* 2000; Shannon *et al.,* 2000; Daskalov, 2002). Their relative low position in the food web, their reproductive strategy of producing large quantities of eggs over extended areas and spawning periods, as long as their short life span make their populations highly dependent on the success of their recruitment and to environmental variability and changes (Cole and McGlade, 1998; Lloret *et al.,* 2004).

Since the industrialisation of the 'traditional' small-scale fisheries, collapses of small pelagic fish fisheries' have often been reported, e.g. the Peruvean anchovy (*Engraulis rigens*) in the 70s or the European anchovy (*Engraulis encrasicolus*) in the Northern Spain, where the fishery was closed between 2006 and 2010. Overexploitation was pointed out as a threat for fisheries in 1945-46 for the first time in the framework of FAO (Caddy and Cochrane, 2001) and it has been an international concern for many years since then.

Marine fisheries are threatened worldwide mainly through increasing overexploitation but also by climate change which strongly interact (FAO, 2010; Brander, 2007). Fishing reduces the age, size, and the biodiversity of marine ecosystems making populations and ecosystems more vulnerable and sensitive to climate change (Brander, 2007). Climate change has effects on demography, distribution and stock structure as well as variations in the productivity, structure and composition of the ecosystems on which the species depend (Brander, 2007).

Marine researchers and managers have the challenge to develop and implement mechanisms that are able to guarantee a sustainable exploitation of marine fisheries (Pauly *et al.,* 2002) while ensuring the persistence of the populations. Actually, the European Common Fishery Policy (CFP) has as a main goal the sustainable exploitation of aquatic living resources in economic, social and environmental terms, while applying the precautionary principle and progressively implementing an ecosystem approach to fisheries management.

A successful management needs to be based on a good knowledge and understanding of the reality that is trying to deal with. In this context, one first step is to know the state of the population that is to be managed. Acoustic surveys are used worldwide as a standard method to perform annual assessments of the stocks of pelagic fish species (Simmonds and MacLennan, 2005). One important reason for this is that acoustic surveys provide high quality data to estimate abundance and biomass of small pelagic fish species at a high spatial resolution enabling as well high quality analysis of the spatial distribution of the species under study.

In the recent years ecosystem-based management has been given growing attention (e.g. García *et al.,* 2003; Pikitch *et al.,* 2004); notwithstanding single-species stock assessments remain the base for any posterior attempt to manage whole ecosystems. The uncertainty on the reliability (or precision) of single-species stock assessments has sometimes been used to excuse the implementation of fishing restrictions that can be economically painful (Pauly *et al.,* 2002). Thus, routinely estimation of the precision of single-species stock assessment is crucial to accomplish a conscious management and is of special interest in the international community since late 80s in the framework of the International Council of the Sea (ICES). Furthermore, assessing the uncertainty in the estimates can become clue to properly understand the temporal evolution of the population. Obviously, the interest in improving the accuracy and precision of those abundance and biomass estimates by reducing the associated errors cannot be ignored.

Besides abundance estimates and its associated errors, the knowledge of the spatial distribution of fish populations and the influence of environmental factors on the stock variability is as well important for conservation biology and management of any threatened species. Knowing where a species is found is crucial to design, for instance marine protected areas (MPAs) or closed areas. Acoustic surveys provide high quality spatial data of pelagic fish species that can be applied to spatial distribution modelling or, in combination with environmental data, to model the habitat of the species (e.g. Giannoulaki *et al.,* 2007; Giannoulaki *et al.,* 2011; Bellido *et al.,* 2008).

The ability to predict the effects of measures and policies for stock management is an interesting subject to be developed. Changes in the distribution of the species, in its abundance and biomass that might be driven by environmental forcing and/or climate change would ideally need to be known in order to be able to elaborate a dynamic management which potentially would facilitate to achieve the main goal of sustainability.

Modelling the habitat of a species might be useful in order to predict potential changes in the distribution of a species originated by changes in the habitat (e.g. increase/reduction, displacement) which might be driven by the climate change. Thus, above and beyond the mere stock assessment and the estimation of its precision, habitat modelling becomes more and more interesting. Potential habitat modelling (or suitability maps) can offer some insight in this topic; in spite of the limitations of any particular modelling approach. Further, gaining knowledge about the suitable habitats for a species might be useful to identify areas that could be interesting to be protected for the species, for instance by establishing MPAs.

In the Mediterranean Sea, two small fish pelagic species European sardine (*Sardina pilchardus* Walb.) and European anchovy (*Engraulis encrasicolus* L.) dominate the fisheries' catches. They represented 32-44% of the total landings in the Mediterranean between 2003 and 2009 (FAO, 2013). In the Western Mediterranean, sardine and anchovy are as well the most important species in terms of landed biomass and commercial interest (Lleonart and Maynou, 2003) being anchovy the main target species of the purse seiners in the area (Pertierra and Lleonart, 1996; Abad *et al.,* 1998a).

Beside large pelagics, sardine and anchovy are the most abundant fish species in the pelagic community. In the Spanish Mediterranean continental shelf anchovy and sardine represented between 38 and 67 % of the estimated biomass in the acoustic surveys between 2003 and 2009 (unpublished data, IEO). In the continental shelf of the Balearic basin (Northern Spanish Mediterranean waters), sardine and anchovy represented 65-92 % of the small and medium sized pelagic species community estimated in the acoustic surveys in the period 2003-2006 (Tugores *et al.*, 2010). Their stocks have been declining since the 90s, although anchovy showed a slight recover in 2001 and 2003 (Giráldez *et al.*, 2006a,b; Palomera *et al.*, 2007). In addition, there is increasing concern about the possible over-exploitation of anchovy's recruitment since an important fraction of the fishing effort relies on immature fish (Pertierra and Lleonart, 1996). Size at first maturity occurs at 12.5 and 12.7 cm for males and females respectively while the minimum landing size is 9 cm (Pertierra and Lleonart, 1996).

The present study focus the attention to the precision of the abundances estimates of these two species provided by late autumn acoustic surveys in the Spanish continental shelf, analyse the spatial structure of their stocks and relate their habitat to the environmental characteristics present in the sampled area in late autumn (mid November-mid December).

1.2 The Spanish Mediterranean waters: geomorphological and hydrographical characteristics

The study area is located in the Western Mediterranean basin and comprises the Spanish Mediterranean continental shelf along the Iberian Peninsula, between the Strait of Gibraltar and the Spanish-French border (Figure 1.1a). The continental shelf is narrow, often less than 6 nautical miles (nm, 1 nautical mile = 1852 m) between the Strait of Gibraltar and the Cape of Palos. Northwards, the continental shelf widens till the surroundings of the Ebro River, where the maximum width is reached (33 nm). In the Catalan coast, continental shelf is narrow (less than < 14 nm), indented by submarine canyons. The total area of the continental shelf is about 8,513 nm^2 (29 199 Km^2).

The circulation is dominated by the entrance of the Atlantic waters, the North Current (NC) a cyclonic along-slope front in the north-western Mediterranean and the outflow of large rivers. The NC flows along the continental shelf from northeast to southwest (Font *et al.*, 1988), carrying water from the Gulf of Lion to the Catalan coast, and eventually reaches the Alboran Sea (Millot, 1999; Font *et al.*, 1988). Strong northerly winds, typical in winter, may intensify the NC (Pinot et al. 2002). The wide continental shelf and fresh-water run-off from the Rhone and the Ebro rivers further characterise the area. In the Alboran Sea the water circulation is dominated by less saline Atlantic water entering the basin through the Strait of Gibraltar. The surface Atlantic waters, although relatively nutrient-poor, are related with mesoscale features, such as turbulent mixing, anticyclonic gyres, meanders and eddies (Estrada, 1996) generating upwelling along the narrow continental shelf and resulting in a local enrichment of nutrients and primary production in the area (Champalbert, 1997). Two anticyclonic gyres are generated in the Alboran Sea, the most western gyre is quasi permanent while the eastern one is more variable (Millot, 1999).

The photic zone, or volume of the water column where the light penetrates, is thought to be the most productive in seas and oceans and is generally between 0 and 100-200 m depth. Moreover, primary production is higher in coastal areas with riverine outflows and also in places where water circulation generates nutrient upwelling from the sea bottom to the sea surface. In Western Mediterranean, these areas of increased productivity are found in the vicinity of the main rivers, Rhône and Ebro, and in the Alboran Sea due to water masses circulation. Mean chlorophyll-a concentration can be used as a proxy to reveal the areas of higher primary production (Figure 1.1b).

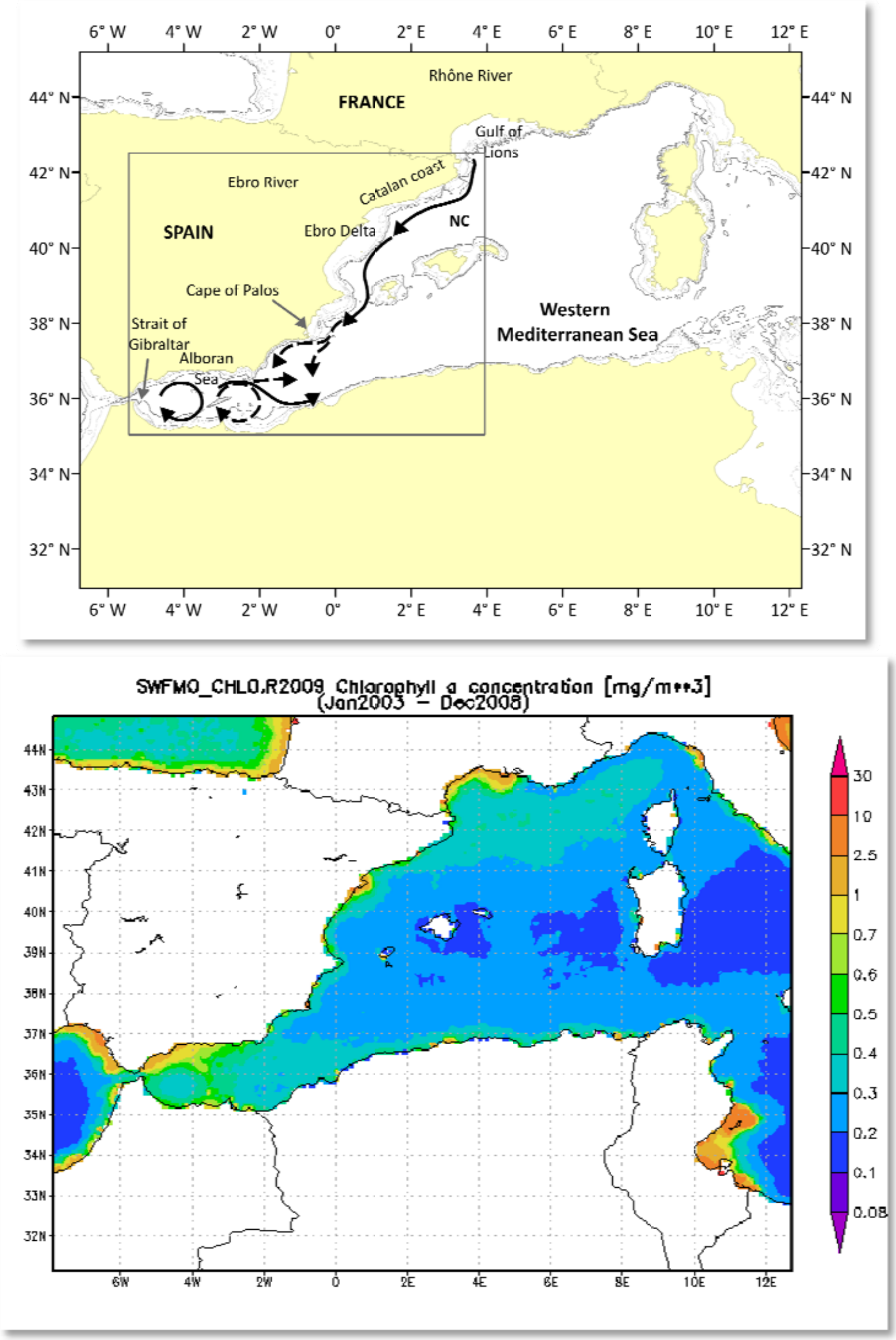


Figure 1.1. Spanish Mediterranean waters: (above) main water circulation patterns in the study area (NC: Northern current; solid lines showing the most stable circulation; dashed lines showing more variable currents) and (bottom) mean chlorophyll-a concentration (mg m^{-3}) between January 2003 and December 2008 from SeaWiFS satellite data (Acker & Leptoukh, 2007). http://reason.gsfc.nasa.gov/Giovanni)

1.3 Sardine (Sardina pilchardus Walb.) and anchovy (*Engraulis encrasicolus* L.): notes about the species ecology, biology and geographical distribution

Pelagic fishes are known to perform daily vertical migrations, usually gathering in large schools during the day and remaining disperse during the night (Fréon *et al.,* 2005). Small pelagic fishes, considering as such species with adults' length between 10 and 30 cm, are commonly foraging species of high ecological value, due to their function as bottom-up energy transferors in the trophic chain (Cury *et al.,* 2000). The biology of these species, i.e. short life-span and reproductive strategy (producing large quantities of eggs over extended areas), makes these species especially sensible to environmental changes (Bakun, 1996). Their recruitment is particularly sensible to environmental variability and changes (Cole and McGlade, 1998; Lloret *et al.,* 2004). Abrupt increases and decreases of the populations of small pelagic fishes are frequent and may affect both the fisheries they sustain and the structure and functioning of the ecosystem (Cury *et al.,* 2000; Shannon *et al.,* 2000; Daskalov, 2002), triggering the collapse of the fisheries, e.g. the Peruvean anchovy (Engraulis rigens) in the 70s or, more recently, European anchovy (Engraulis encrasicolus) in the Northern Spain, where the fishery was closed between 2006 and 2010. In the case of anchovy, their populations have been recently recognised as vulnerable to long term increase in temperature by the Global Ocean Ecosystem Dynamics programme, GLOBEC (Barange *et al.,* 2010).

Geographical and bathymetric distribution

European sardine (*Sardina pilchardus*) has a less extended geographical and bathymetric distribution than European anchovy (*Engraulis encrasicolus*). Sardine is found in the Northern hemisphere from Norway to Senegal while anchovy is found in the both hemispheres, from Iceland and Norway to South Africa. Both species are distributed in the Eastern Atlantic and the Mediterranean (Figure 1.2). In the Mediterranean they are widespread through the Western and Central Basins as well as in the Northern Aegean Sea (Figure 1.2). The bathymetric distribution of European sardine is between 25 and 100 m depth (Whitehead, 1990) whereas anchovy can be found up to 400 m depth (Schneider, 1990).

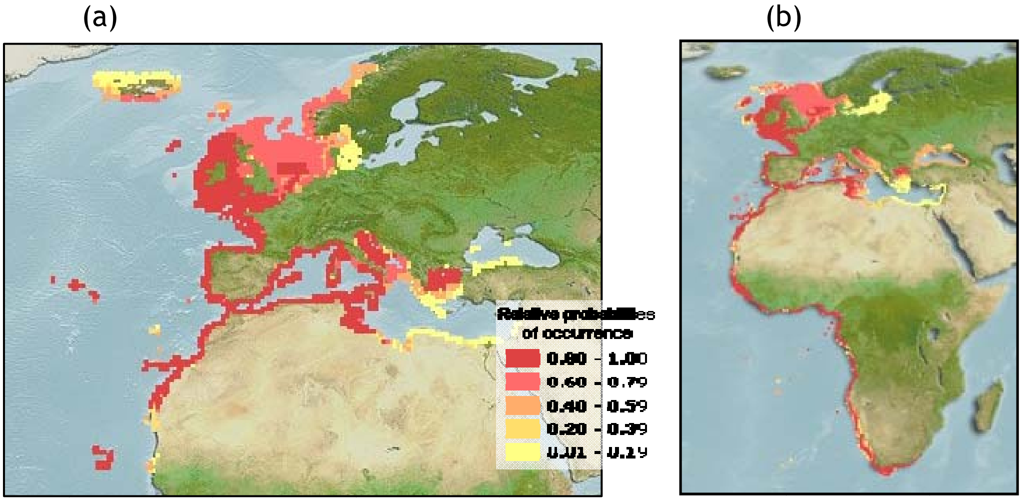


Figure 1.2. Geographical distribution of the main small pelagic fish species in the Western Mediterranean: (a) sardine, *Sardina pilchardus* and (b) anchovy, *Engraulis encrasicolus* (Modified from Fishbase; source: Whitehead *et al.,* 1988 and Whitehead, 1990).

Spawning

Sardine spawns from autumn to spring with a peak in winter, in January-February (Palomera and Olivar, 1996; Olivar *et al.,* 2001, 2003) with maximum abundance of spawners at sea surface temperatures of about 18ºC (Oliver, 1957; Olivar *et al.,* 2001). Spawning occurs mainly in inshore waters with highest concentration of sardine eggs at depths below 100 m (Olivar *et al.,* 2001, 2003). Contrarily, anchovy spawns in the warmest months (Whitehead *et al.,* 1988; Tsikliras *et al.,* 2010). In the Western Mediterranean anchovy spawns between April and October with a peak in summer, in June-August, in waters with sea surface temperature between 15º and 22ºC (Palomera, 1989, 1992; García and Palomera, 1996).

The spawning of sardine and anchovy is associated to water enrichment processes. In the Western Mediterranean, water enrichment in winter occurs at a global scale and is related to vertical mixing, which produces the recirculation of nutrients from the bottom to the euphotic zone. Vertical mixing is enhanced by winds and thus it is thought to favour sardine recruitment (Palomera *et al.,* 2007 and references therein). During summer water enrichment occurs mainly at a local scale and is related to river runoff, frontal systems and upwellings (Font *et al.,* 1987; Estrada, 1996; Arnau *et al.,* 2004). Anchovy spawning and early-life stages are closely related to these areas, especially to river outflows as anchovy spawns in the proximity of rivers, even in regions of low discharge (Palomera, 1989, 1992; García and Palomera, 1996; Olivar *et al.,* 2001). During the spawning season anchovy may eventually enter lagoons, estuaries or lakes, as it has good tolerance to low salinities (5-41ppt); contrarily, sardine larvae do not tolerate low salinities (Sabatés *et al.,* 2001).

Maturity

The length at first maturity (L_{50}) of sardine ranges from 10.9 cm to 16.8 cm (mainly age 0 groups and 1) across its distribution area. L_{50} is generally smaller in the Mediterranean Sea than in the Atlantic Ocean (Silva *et al.,* 2006 and references therein). In the Spanish Mediterranean waters, L_{50} of sardine was estimated to be 15.00 cm in the coasts of Valencia (Andreu *et al.,* 1950) and between 12.6 and 13.8 cm in the Malaga Bay, Alboran Sea (Abad and Giráldez, 1993). Regarding anchovy, L_{50} varies between 5.6 and 13.7 cm across its distribution area (Korantenk, 1993; Uriarte *el al.*, 1996). In the Western Mediterranean, it was estimated to be 12.5 and 12.7 cm for males and females respectively, while the minimum legal size in the area is 9 cm (Giráldez and Abad, 1995; Pertierra and Lleonart, 1996).

Feeding

Small pelagic fishes are planktivorous species, generally feeding on phytoplankton and/or micro- and meso-zooplankton (Freón *et al.,* 2005). European anchovy is known as a zooplanktivorous fish mostly eating copepods, but in the Black and Azov Sea it has also been found to feed sporadically on phytoplankton (Palomera *et al.,* 2007 and references therein). European sardine has a more heterogeneous diet preying on zooplankton (e.g. cladocerans or decapods) as well as phytoplankton like diatoms (Costalago and Palomera, 2014). Both small pelagic fish species are capable of switching between filter- and particulate-feeding, using particulate feeding for bigger preys. This ability, known for long for European anchovy and for sardines over the world, was only recently described for European sardine (Bode *et al.,* 2004; Garrido *et al.,* 2007, 2008; Nikolioudakis *et al.,* 2012).

In the Bay of Biscay, it has been suggested that anchovy has higher trophic plasticity than sardine, by foraging more offshore and a wider range of prey sizes (Chouvelon *et al.*, 2014, 2015). However, laboratory experiments indicate that, in opposition to anchovy, sardine can retain very small preys, i.e. nanoplankton, allowing them to reproduce under lower productivity conditions (Garrido *et al.*, 2007). Differences have been observed in the nuber of gill rakers between anchovies and sardines in the Atlantic and between sardines from the Atlantic and sardines from the Mediterranean, suggesting differences in their diets that should further be investigated (Costalago and Palomera, 2014). Nevertheless, the traditional characterization of sardine as a phytoplanktofagous fish has been put into question as long as, in terms of prey contribution to carbon intake, zooplankton seems to be more important in sardine's diet (Garrido *et al.*, 2008a; Nikoloudakis *et al.*, 2012; Costalago and Palomera, 2014).

Although in other areas, anchovy eggs are frequently found in sardine's stomach (Garrido, 2003; Bachiller, 2012; Garrido *et al.*, 2008) and although cannibalism is frequent in other areas for other species of the genus Engraulis, in the Mediterranean Sea intraguild predation and cannibalism have not been reported neither for anchovy nor for sardine or has been considered negligible (Tudela and Palomera, 1997; Fréon *et al.*, 2005; and references therein; Costalago and Palomera, 2014). In fact, almost no fish eggs are found in sardine and anchovy stomachs in the Mediterranean (Palomera *et al.*, 2007 and references therein; Bacha and Amara, 2009; Borme *et al.*, 2009; Garrido and van der Lingen, 2014 and references therein). The only exception in the 1940s and 1950s, when anchovy eggs were found in Mediterranean sardine's stomachs (Massutí and Oliver, 1948; Andreu and Rodríguez-Roda, 1951), suggesting a control role of sardine on anchovy's population (Palomera *et al.*, 2007 and references therein). A density-dependent mechanism and/or differential distribution in the water column may explain the almost absence of fish eggs sardine and anchovy stomachs in the Mediterranean (Valdés *et al.*, 1987; García and Palomera, 1996; Palomera *et al.*, 2007; Garrido and van der Lingen, 2014).

Ecological role in the ecosystem

In the Western Mediterranean the bulk of the marine biomass comes from these two small pelagic species, sardine and anchovy. As foraging species, they play an important role in transferring energy between the lower and the upper layers of the trophic chain. In the NW Mediterranean sardine plays a 'wasp-waist' flow control, affecting upper and lower levels of the trophic chain, while anchovy would display a 'bottom-up' control thus having a higher impact on the upper levels (Coll *et al.*, 2008). In the Catalan Sea adult anchovy consumed up to a 20% of the zooplankton production accessible to anchovy aggregations (Tudela and Palomera, 1997), highlighting the important role of this species in channeling energy of the pelagic food webs to higher trophic levels.

Migrations

Pelagic fishes are known to perform long migrations for spawning, feeding or wintering. In the Iberian Peninsula sardine migrates in spring from Portuguese and Cantabrian waters to Galician coast (Carrera and Porteiro, 2003). In the case of anchovy, it overwinters in the North East of the North Sea and move to the South for the rest of the year. In the Gulf of Vizcaya, anchovy move from south to north in summer (Huret *et al.*, 2007). In the Eastern Mediterranean, anchovy from the Azov Sea overwinter in the Black Sea (Borsa *et al.*, 2004).

However, migration is highly variable and might depend of the species density as well as on peculiarities of the area where the species is found. In the Western

Mediterranean large migration patterns have not been described either for sardine or for anchovy. Sardines were relatively sedentary and remain in refugee areas when they are scarce while they can be highly migratory when they are abundant, colonizing cooler waters (Lluch-Belda *et al.,* 1992). Semi-independent sub-populations of sardine seem to coexist in Western Mediterranean with small migrations between them and no significant migration along shore (Ramon and Castro, 1997). In the case of anchovy, although the seasonality of the landings might be indicative of migratory movements it could also be indicating a reduction in fleet accessibility to the stock by, e.g. a seasonal reduction of school size (Fréon, 1989), or an increase in catchability during spawning season like occurs with other pelagic species (Jorgensen *et al.,* 2004; Skaret *et al.,* 2005).

Seasonality of landings and relationships with environmental factors

In the Western Mediterranean, sardine landings peak in autumn and spring, when the population is mainly composed of 1-2 year old individuals (Lloret *et al.,* 2004) while anchovy landings peak in spring-summer (Palomera, 1992), when the population is mostly composed of 1-year old individuals (Pertierra and Lleonart, 1996). Anchovy landings are positively correlated with riverine outflows, cold winters and intense North-westerly winds, at one year lag (Martín *et al.,* 2008; Palomera *et al.,* 2007 and references therein). A positive correlation between wind and anchovy recruitment were also found in other areas of the world, e.g. South-Western Atlantic, Northern Chile and the Black Sea. In the case of sardine, wind seemed to have a positive influence on landings but not river outflows (Palomera *et al.,* 2007 and references therein).

1.4 Echointegration acoustic surveys for pelagic fish stock assessment: the case of the Spanish Mediterranean surveys

Echointegration acoustic surveys have widely been used for pelagic fish stock assessment since the late 1970s, after it was firstly proposed by Dragesund and Olsen (1965).Nowadays echointegration is the most extended method for assessing marine pelagic fish stocks worldwide (e.g. Toresen *et al.,* 1998; Dalen *et al.,* 2003). Indeed acoustic surveys are annually conducted to estimate the stocks of pelagic fishes by many international organisms of fisheries management, e.g. International Council for the Exploration of the Sea (ICES) and the General Fisheries Commission for the Mediterranean (GFCM). The reasons for this are that acoustic surveys allow direct sampling at sea, providing fishery independent estimates of the abundance of the species. Moreover, they sample a large volume of the water column and allow a wide spatial coverage in a relatively short time span.

Echointegration surveys use sound to detect organisms that are in the water column by means of an echosounder. It is a methodology that combines acoustic sampling with pelagic fishing trawls. Acoustic sampling provides an index of fish abundance while pelagic trawls provide biological information of the species as well as information of the composition of the community. The echosounder emit pulses of sound through the water, vertically from upward to the bottom, and receive the echoes generated by the organisms encountered in the sound path (Figure 1.3a). The backscattered echoes are received, amplified and graphically plotted as echograms (Figure 1.3b). However, the acquisition of high quality data was not possible till the introduction of digital signal processing into scientific echosounders by late 1980s and the establishment of standard calibration methods (Foote *et al.,* 1987).

Late autumn Spanish Mediterranean acoustic surveys: historical insight

In the Spanish Mediterranean waters acoustic surveys for pelagic fish stock assessment started to be conducted in the 1983. In 1997 these surveys were annually performed in late autumn (November-December), with the main aim of obtaining a recruitment index for European anchovy (*Engraulis encrasicolus*) and an estimation of the population of European sardine (*Sardina pilchardus*). In 1997, the surveys By that time, echograms were recorded in paper and any posterior estimate implied analysing the integram manually on a paper.

The installation in early 2000s of a scientific echosounder with digital signal processing allowed faster and more accurate processing of the data making it possible for the first time to estimate the abundance and biomass, not only of sardine and anchovy but of the accompanying small and medium sized pelagic fish species: Mediterranean horse mackerel (*Trachurus mediterraneus*), blue jack mackerel (*Trachurus picturatus*), round sardinella (*Sardinella aurita*), bogue (*Boops boops*), Atlantic mackerel (*Scomber scombrus*) and Atlantic chub mackerel (*Scomber colias*). Their commercial interest is lower and also their abundances tended, but they have also importance in the ecosystem. Further, in the late 2000s these patterns might have changed (Iglesias *et al.*, 2008). Thus, the initial objective was broadened to estimate the stock of coastal pelagic resources in an attempt to move to an ecosystem approach.

A hull-mounted split-beam SIMRAD EK500 echosounder operated from 1990 to 2005 and in 2006 it was substituted by a SIMRAD EK60 echosounder with the transducers mounted on a protruding keel (Figure 1.4). The SIMRAD EK500 echosounder operated at two frequencies, i.e. 38 and 120 kHz, while SIMRAD EK60 operated at 5 frequencies, i.e. 18, 38, 70, 120 kHz and 200 kHz, but in both cases the 38 kHz frequency was used to estimate the density and abundance of pelagic fish.

Regarding the sampling scheme, a systematic sampling design consisting of zig-zag transects was applied till 2001. In 2002 no acoustic survey was performed as long as resources were devoted to study the Prestige oil-spill in Costa da Morte (Galicia, Spain). In 2003 the sampling design was changed to a systematic sampling design consisting of parallel equidistant transects perpendicular to the bathymetry in order to have the same sampling intensity in all the bathymetric strata.

Abundance and biomass estimates of sardine and anchovy obtained from the late autumn Spanish acoustic surveys were annually submitted to the fisheries assessment groups of the General Fisheries Commission for the Mediterranean (GFCM). With the aim of standardising the different acoustic surveys performed in European Mediterranean waters and make them comparable, another acoustic survey started being performed in summer 2009 coinciding with anchovy spawning. This year was the last when late autumn acoustic surveys were performed.

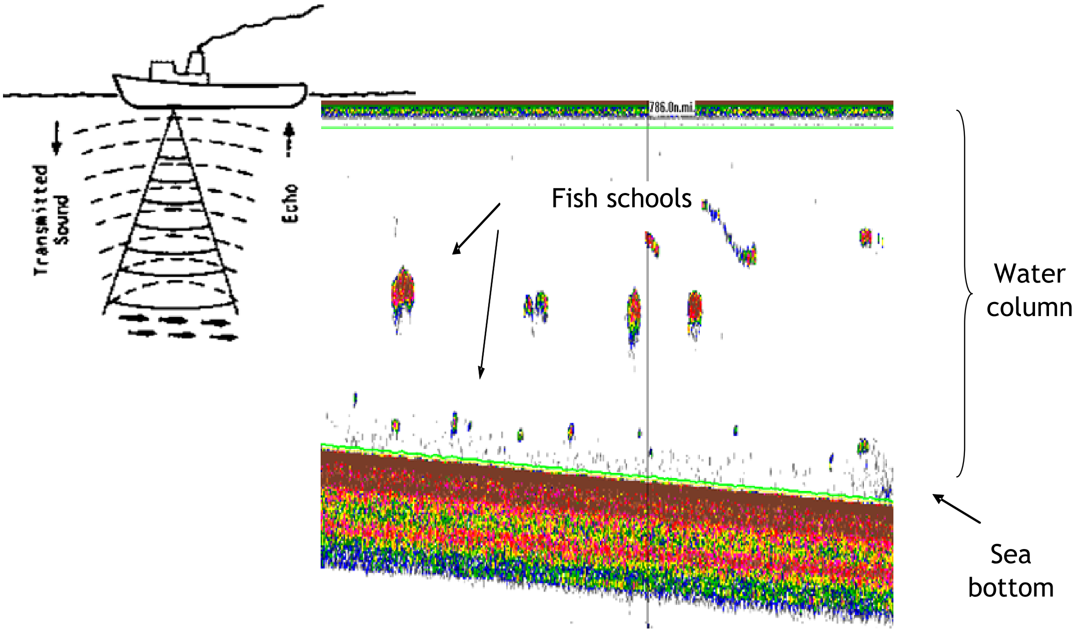


Figure 1.3. Scheme of the emission and reception of sound by an echosounder (left) (modified from FAO, 1981) and sample echogram acquired on the 3rd of December 2006 in the surroundings of the Ebro River mouth (right).

Figure 1.4. Protruding keel installed at the hull of the R/V Cornide de Saavedra in 2006 (image by Joan Miquel Batle).

Data collection

Acoustic data was collected on board the research vessel "Cornide de Saavedra", 66.7 m length (Figure 1.5a) during the end of November and beginning of December in the context of annual surveys of pelagic fish stock assessment in the Spanish Mediterranean waters (ECOMED). The surveys coincided with the recruitment period of anchovy and with the spawning season for sardine in the area (Abad and Giráldez, 1993; Giráldez and Abad, 1995). Data were continuously recorded at constant speed of 10 knots along parallel equidistant transects placed perpendicular to bathymetry (Figure 1.5B) and using a scientific split-beam echosounder, SIMRAD EK500 or EK60, working at 38 kHz (7° x 7° beam angle, 1 ms pulse length, maximum ping rate, power 2000 W). Acoustic sampling was performed from sunrise to sunset covering the entire continental shelf between 30 and 200 m depth. The echosounder was calibrated prior to each survey with a 60 mm cooper sphere, following standard techniques (Foote *et al.*, 1987). Inter-transect distance was 4 nautical miles (nm hereafter) were the continental shelf is narrow and 8 nm where the continental shelf is wide (Figure 1.5b). Transects were numbered from 1 to 128 from North to South (Figure 1.5b).

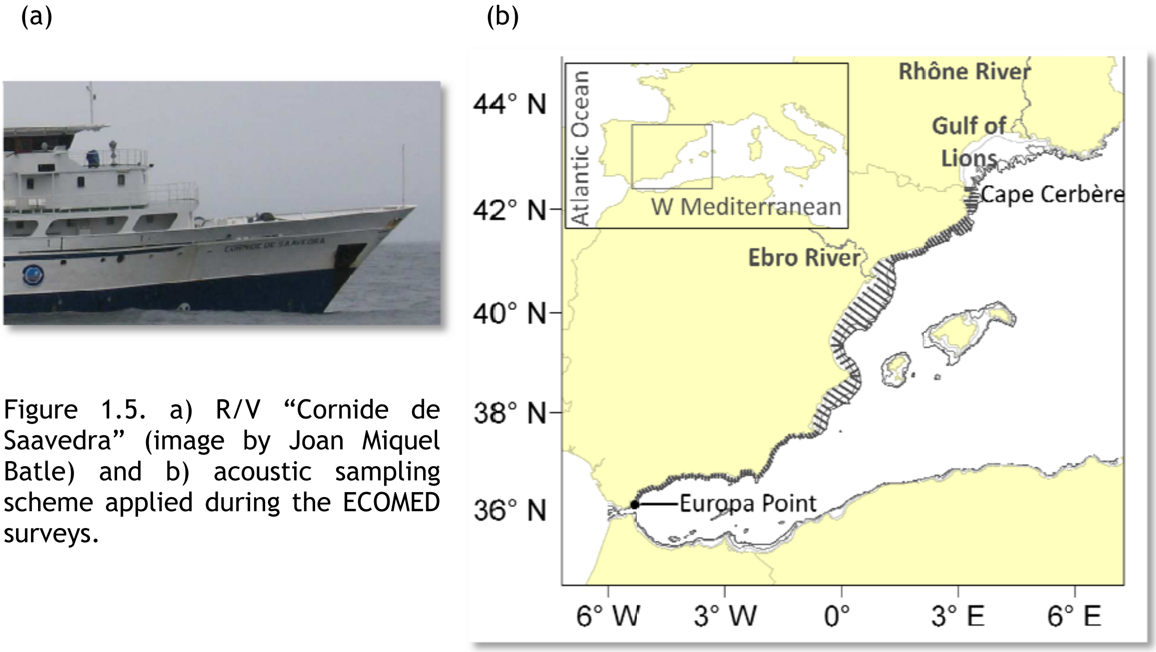


Figure 1.5. a) R/V "Cornide de Saavedra" (image by Joan Miquel Batle) and b) acoustic sampling scheme applied during the ECOMED surveys.

Mid-water pelagic fishing trawls aimed at obtaining the proportion of species present in the area were performed after sunset, between 29 and 221 m depth, at 3.5-4.5 knots (nm h^{-1}) for approximately 1 hour length. The net was 12 m vertical opening and 22 mm codend. In our study area, small pelagics are known to aggregate during the day while disaggregate and ascent through the water column during the night (Fréon *et al.*, 1996). Fish schools are not found during the night (Iglesias *et al.*, 2003) but disperse aggregations. Thus, trawls were carried out on these disperse fish aggregations and in places where, during the day, pelagic fish schools were found in concentrations high enough to be trawled and trying to cover all the areas with different types of echotraces. The number of pelagic fishing trawls made ranged between 35 and 71 in the period 2003 to 2009.

Fishes of the species found in the trawl catches were sized to the 0.5 cm total length (L_T) lower and, for the most abundant species, they were also weighted. Weight-length relationships were fitted to an exponential model using the root mean square method.

Data processing

Acoustic data were integrated at every Elementary Distance Sampling Unit (EDSU) which was set to 1 nm using the Miriax Echoview software. The amount of echo-integrated nautical miles was about 1200-1300 per year, excepting for some years when the weather conditions did not allow the coverage of the entire study area. Echoes of fish schools are considered for echointegration while other unwanted echoes are excluded, i.e. bottom, plankton layers and noise. The result of the echointegration, Nautical Area Scattering Coefficient (NASC; m^2 mn^{-2}) or s_A following MacLennan *et al.* (2002), a measure of the intensity of the echo reflected by surface unit corresponding to the pelagic community. It was divided into species using the composition of the trawl catches and applying Nakken and Domasnes method for multiple species (Nakken and Domasnes, 1975) but using backscattering cross-section by length class rather than the mean backscattering cross-section, of the form:

$$s_{A_i} = s_A \frac{w_i \sigma_{bs}}{\sum_i w_i \sigma_{bs}}$$ (Eq. 1.1)

where w_i is the proportion of the species i in the catches (in number of fishes), and σ_{bs} is the backscattering cross-section for each species and length class, instead of the mean backscattering cross-section used in Nakken and Dommasnes (1975). The backscattering cross-section per species and length class (σ_{bs}) is related to the target strength (TS) as follows:

$$\sigma_{bs} = 10^{\left(\frac{TS}{10}\right)}$$ (Eq. 1.2)

where TS is the target strength in decibels (dB) and is computed with the formula $TS=20 \log L_T + b_{20}$ (Simmonds and MacLennan, 2005) where b_{20} is empirically obtained and differs among species and L_T is the total length class. A b_{20} of -72.6 dB was used for sardine (*S. pilchardus*), anchovy (*E. encrasicolus*) and round sardinella (*S. aurita*) (Degnbol *et al.,* 1985); -68.7 dB for Atlantic chub mackerel (*Scomber colias*), Mediterranean horse mackerel (*T. mediterraneus*), horse mackerel (*Trachurus trachurus*) and blue jack mackerel (*Trachurus picturatus*) (Lillo *et al.,* 1996); -67 dB for bogue (*B. boops*) (Foote, 1980); -84.9 dB Atlantic mackerel (*Scomber scombrus*) (Edwards *et al.,* 1984) and -67.5 dB for blue whiting (*Micromesistius poutassou*) (Foote *et al.,* 1986). Thus, s_{Ai} for each species was obtained.

1.5 Structure and objectives of the present work

The present work is structured in two main sections, according to the main objectives. The first section is aimed at estimating the random error (precision) associated to the abundance estimates of anchovy and sardine in the Spanish Mediterranean waters in late autumn while analysing the structure of the spatial distribution of the populations. In particular, the error derived from the sampling design will be estimated as it is supposed to be one of the main contributors to random error (ICES, 1998). The relationship between the spatial distribution of the species and the sampling design (type and density) will allow us to estimate the precision of the abundance estimates originated by the sampling design. Data derived from acoustic surveys will serve to this purpose.

The second section will explore the relationship between the habitat of sardine and anchovy with environmental factors, as well as sardine eggs. Specifically, bottom depth and satellite environmental data will be combined with data derived from acoustic surveys. According to the modelling, the potential habitat of anchovy and sardine throughout the Mediterranean will be as well analysed.

The work will include an **Annex** containing a revision of the potential sources of error that are present in acoustic surveys and a quantitative analysis of their presence and importance in the Spanish Mediterranean acoustic surveys, especially referring to the derived sardine and anchovy abundance estimations.

Following the present chapter of General Introduction (**Chapter 1**); **Chapter 2** includes the analysis of the sample variance of abundance estimates of sardine and anchovy by means of transitive geostatistics in one dimension as well as the analysis of the one dimensional spatial distribution of these populations; **Chapter 3** is devoted to analyse the two dimensional spatial distribution of sardine and anchovy by means of intrinsic geostatistics; **Chapter 4 and 5** will include potential habitat modelling of sardine and anchovy by means of Generalised Additive Models (GAMs). Finally, **Chapter 6** will include a General Discussion and **Chapter 7** the General Conclusions.

Section I. Spatial distribution, random error and the sampling scheme

Chapter 2. Latitudinal and inter-annual distribution of European anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) and sampling uncertainty in the Western Mediterranean

Chapter 2. Latitudinal and inter-annual distribution of European anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) and sampling uncertainty in the Western Mediterranean

2.1 Introduction

Pelagic ecosystem is one of the most productive in the world as it represents about a 95% of the world ocean production (Margalef, 1993). In Western Mediterranean, small pelagic fish and concretely two species, sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*), are the two most important in terms of landed biomass and commercial interest (Lleonart and Maynou, 2003). They represented between 65 and 92 % of the biomass estimated by acoustic techniques in the Balearic Sea coastal pelagic fish community during the period 2003 to 2006 (unpublished data, Instituto Español de Oceanografía, IEO). As small pelagic fishes, they hold a key role in the energy transfer between the lower and the upper levels of the trophic chain. The sensitivity of their recruitment to environmental variability and changes (Cole and McGlade, 1998; Lloret *et al.*, 2004) along with their short life span may trigger abrupt increases and decreases of their populations which may affect both the fisheries that sustain and the structure and functioning of the ecosystem (Cury *et al.*, 2000; Shannon *et al.*, 2000; Daskalov, 2002). Landings of anchovy and sardine declined from the middle 1990s and 2005 in the continental shelf of the Balearic Sea (Giráldez *et al.*, 2006a,b; Palomera *et al.*, 2007). Moreover, there is an increasing concern about the possible over-exploitation of anchovy's recruitment since an important fraction of the fishing effort relies on immature fishes (Pertierra and Lleonart, 1996). The size at first maturity of anchovy occurs in the area at 12.5 and 12.7 cm for males and females respectively, while the minimum legal size in the area is 9 cm (Giráldez and Abad, 1995; Pertierra and Lleonart, 1996).

In Western Mediterranean anchovy spawns between April and October with a peak in summer (June-August) with sea surface temperatures between 15° and 22°C (Palomera, 1989, 1992; García and Palomera, 1996). During summer water enrichment occurs at a local scale which is mainly related to river runoff, frontal systems or upwelling of deep waters favoured by the presence of submarine canyons (Font *et al.*, 1987; Estrada, 1996; Arnau *et al.*, 2004). Anchovy spawning is associated to these areas of high hydrographic enriching processes (Palomera, 1989, 1992; García and Palomera, 1996; Olivar *et al.*, 2001). River outflows play an important role in the distribution patterns of anchovy early-life stages as anchovy spawns in the proximity of rivers even in regions of low river discharge (García and Palomera, 1996). Sardine spawns from autumn to spring with a peak in winter (January-February) (e.g. Palomera and Olivar, 1996; Olivar *et al.*, 2001, 2003) when surface temperature falls to 20°C. For sardine spawners, the maximum abundances and the higher probabilities of suitable habitat have been observed in water temperatures below 18°C (Oliver, 1957; Olivar *et al.*, 2001; Tugores *et al.*, 2011). The spawning of sardine occurs mainly in inshore waters with the highest concentration of eggs found in depths below 100 m (Olivar *et al.*, 2001, 2003; Tugores *et al.*, 2011).

Since the ‘1990s, an acoustic survey was annually performed to estimate the abundance and biomass of sardine and anchovy along the entire Spanish Mediterranean continental shelf (ECOMED surveys). The survey was carried out in late autumn and its main aim was to estimate anchovy’s recruitment as well as the abundance and biomass of sardine and of the other accompanying pelagic fish species as Mediterranean horse mackerel (*Trachurus mediterraneus*), round sardinella (*Sardinella aurita*) and bogue (*Boops boops*). Understanding the spatial distribution of small pelagic fish species, its variation in time as well as the precision of the estimates may be helpful in assessing fisheries management and would benefit other fields of knowledge. However, published information about the spatial distribution of the pelagic fish stocks present in this region is scarce (Pertierra and Castellón, 1987; Abad *et al.,* 1998 a, b; Iglesias *et al.,* 2003; Bellido *et al.,* 2008) as stated Olivar *et al.* (2003). Moreover, the need of incorporation of error estimation to stock assessment estimates is crucial in order to develop and implement sustainable management policies for the main pelagic fisheries.

A detailed analysis of the error (systematic and random) associated to echointegration acoustic surveys, and especially in multi-specific areas, is not an easy task due to the variety of sources of uncertainty in this kind of surveys, e.g. transformation of acoustic intensity into fish density, trawl sampling, species migration, bubbles of air in the surface of the water column, movement of the research vessel, hydrographical conditions or vessel avoidance (e.g., Aglen, 1994; Simmonds and MacLennan, 2005). Thus, we focus on the estimation of the overall sampling uncertainty as it is thought to be one of the main contributors to random error in acoustic surveys (International Council for the Exploration of the Sea – ICES, 1998). Transitive geostatistics in one dimension (T1D) (Matheron, 1965) enables an unbiased estimation of the sampling variance in spatially autocorrelated data, such as acoustic data, and it is applied to the cumulated abundance by transect. This method was used for the first time in fisheries acoustics in the ‘1990s and was considered suitable for monitoring total quantities of stock in regularly spaced sampling schemes (Petitgas, 1993), which are generally used in acoustic surveys. Furthermore, in our study area the morphology of the platform and the distribution of the transects makes the analysis of one dimensional data a good proxy of the latitudinal distribution of the species.

The main objective of the present study is to provide an estimation of the precision associated to abundance estimates for the two main small pelagic species in Western Mediterranean Spanish waters, anchovy and sardine derived from acoustic data. The latitudinal spatial distribution of these two species and their variation in time are also analysed. Some remarks on accuracy of the estimates are provided as well as a revision of the pros and cons of the T1D geostatistical approach. Attention is paid to the possible implications in stock assessment.

2.2 Materials and methods

Four years of acoustic data collected in the context of annual surveys of pelagic fish stocks assessment in the Spanish Mediterranean waters (ECOMED) from 2003 to 2006 was used. The study area comprises the continental shelf of the Spanish Mediterranean Sea (Figure 2.1) from south Cape Cerbère till the wetland Albufera de Valencia, with a total planar area of 4,200 nm^2 (≈ 14,406 km^2).

Morphological features of the continental shelf divide the study area into two subareas. The Northern subarea (NS), extends from south Cape Cerbère till Cape Salou and is characterised by a narrow shelf cutted by submarine canyons (planar area ~1200 nm^2). The Southern subarea (SS), which extends from Cape Salou to

Albufera de Valencia (planar area ~3,000 nm^2), has a wide continental shelf shaped by the Ebro River, which is the second most important contributing river in the Western Mediterranean (Arnau *et al.*, 2004).

The study area comprised a total of 48 transects (33 from the NS and 15 from the SS), a total of echointegrated EDSUs between 670 and 679 depending on the year and between 26 and 32 pelagic fishing trawls. Details about data collection and processing are thoroughly explained in Section 1.4.

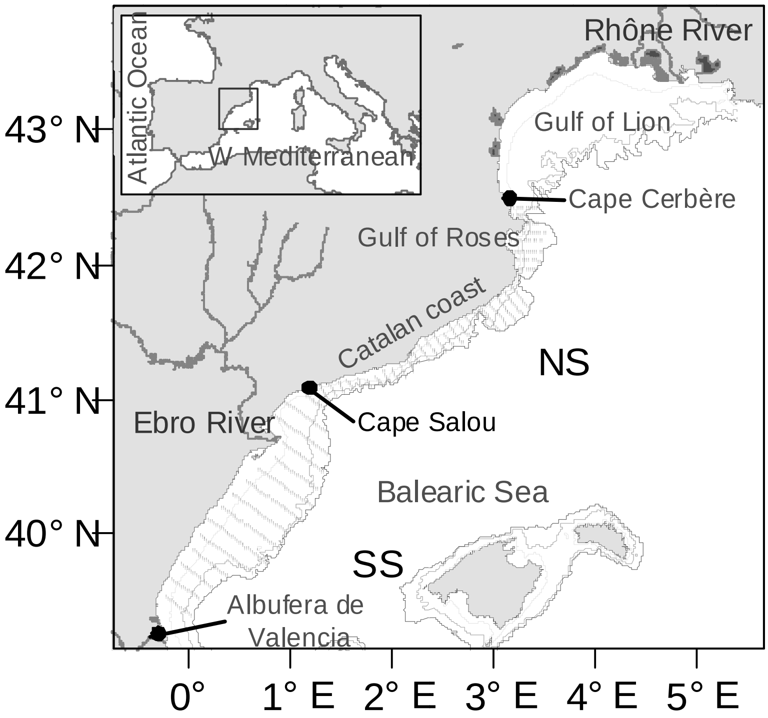


Figure 2.1. Study area, the acoustic sampling scheme and defined subareas: Northern subarea (NS) and Southern subarea (SS).

Data analysis

Abundance estimation and sampling precision

Anchovy and sardine s_A were reduced from two dimensions (2D) to one dimension (1D) by summing up the s_A in each transect for each of the four years under study (Petitgas, 1993). The total acoustic abundance (for abbreviation, abundance here after), Q, is then estimated by integration of the transect cumulates, $q(x)$:

$$Q = \int_{-\infty}^{+\infty} q(x)dx \qquad \text{(Eq. 2.1)}$$

Assuming that the variable equals to zero outside the study area, Q was approximated by a discrete sum:

$$Q^* = a\sum_{k=1}^{n} q(x_0 + h) \qquad \text{(Eq. 2.2)}$$

where a is the inter-transect distance, x_0 is the random coordinate of the first transect and h is the lag width, which is a multiple of the inter-transect distance ($h = ka$).The cumulated sums by transects were plotted and presented as bar plots.

Sampling variance (σ^2_{geo}) was estimated as the difference between the experimental transitive covariogram, $g^*(h)$, and a theoretical model (or combination of nested models) $g(h)$, to which the data was adjusted according to the formula:

$$\sigma^2_{geo} = a\sum_{k=-\infty}^{+\infty} g^*(h) - \int_{-\infty}^{+\infty} g(h)dh \qquad \text{(Eq. 2.3)}$$

The experimental transitive covariogram at a distance h proportional to the inter-transect distance is computed as:

$$g^*(h) = a\sum_{i}^{+\infty} q(x_i)\ q(x_i + ka), \qquad \text{(Eq. 2.4)}$$

where a is the inter-transect distance and *q(x)* represents the cumulated s_A by transect (Petitgas and Prampart, 1993).

For the structural analysis, we applied spherical models (sph) of the form (Petitgas and Prampart, 1993):

$$g(h) = \begin{cases} S\left(1 - 1.5\dfrac{h}{r} + 0.5\dfrac{h^3}{r^3}\right) & if\ h \le r \\ 0 & if\ h > r \end{cases} \qquad \text{(Eq. 2.5)}$$

where r is the range at which the sill (or saturation of variance) is reached, S is the sill (or value of the variance where it stabilises) and h is the distance in absolute value at every lag.

The covariograms were computed and fitted to a model by eye using the software EVA2 – Estimation of the VAriance (Petitgas and Lafont, 1997). The variance and the coefficient of variation of abundance, CV_Q, highly depend on the behaviour of the covariogram near the origin. Especially, on the presence of a significant nugget effect which will explain most of the variance and CV_Q (Thioulouse *et al.*, 1993; Bez, 2002). Thus, in order to decide if a nugget effect was necessary, models with nugget effect and without nugget effect were fitted to the experimental data. The goodness-of-fit (*gof*) was computed 1) for the overall points and 2) for the points close to the origin, using an Excel worksheet following Rivoirard *et al.*, (2000).

$$gof = \frac{\sum_h [g(h) - g^*(h)]^2}{\sum_h [g^*(h)]^2} \qquad \text{(Eq. 2.6)}$$

The closer the goodness of fit to 0 the better the fitting. Models with *gof.* ≥0.1 were rejected and an alternative model was sought till a model with *gof.* <0.1 was found. Models with nugget effect showed better *gof.* for the overall points and for the points close to the origin and are presented.

An unbiased estimator of the coefficient of variation of the assessment (CV_Q) is provided by the formula:

$$CV_Q = \frac{\sqrt{\sigma^2_{geo}}}{Q*} \qquad \text{(Eq. 2.7)}$$

Precision of an estimate is how similar different replicates would be from each other under unchanged conditions. Lower CV_Q values indicate higher precision. Note that while variance depends on the quantity assessed, the sampling intensity and the heterogeneity of the spatial distribution of the variable under study, the CV_Q only depends on sampling intensity and on the spatial distribution. Moreover, CV_Q could be used to derive confidence intervals if the transect sums are assumed to show normal probability distribution function (Rivoirard *et al.,* 2000). However, the normality assumption does not hold in our case, as suggested by Walline (2007) to occur in highly skewed data, and hence confidence intervals are not reported.

Degree of overlap and temporal stability

The Kendall tau correlation coefficient (*cor*) (Kendall, 1938) was computed, using R software (R Development Core Team, 2009), between: 1) the one dimensional spatial distributions of the two species in every year as an indicator of the degree of overlap between sardine and anchovy and 2) the one dimensional spatial distributions for each species across the different years as an indicator of the temporal stability of the spatial distributions.

Relationship between precision and estimates

In order to test a possible relationship between precision and the estimates, F-test were performed between the CV_Q (expressed in ‰) and the estimated abundance (in m^2) for each of the species and pooling together data of the two subareas (Northern and Southern subareas). We used R software (R Development Core Team, 2009).

2.3 Results

Latitudinal distribution and degree of overlap between species

In the Northern subarea, cumulated s_A per transect show that in the period 2003-2006 anchovy tended to gather in the most northern part (Figure 2.2), between 42°26'N and 41°55'N. The eight most northern transects comprised between 64 to 90% of anchovy s_A. In the four years, the maximum cumulated s_A was found in transect number 5 (Figure 2.2), which was located in the Gulf of Roses; with a maximum of 11,871 m^2 in the year 2003. In the case of sardine, the s_A encountered in the eight most northern transects was high in 2004 and 2005 (54% and 81%, respectively) while it was very low in 2003 and 2006 (<0.1 % and 2%, respectively), being the sardine more southerly located (Figure 2.2). The correlation coefficients between the spatial distribution of anchovy and sardine suggested that they were highly or moderately overlapped in 2004 and 2005 (*cor*=0.772 and 0.473 respectively; p-value<0.001), in 2003 they showed low overlap (*cor*=0.269; p-value <0.05) and in 2006 their spatial distributions showed non-significant correlation (Table 2.1).

In the Southern subarea, anchovy was mainly found in the most northern part of the area (Figure 2.3), mainly between 41º01'N and 40º17'N. The five most northern transects concentrated between 68 and 74% of the anchovy s_A. The maximum cumulated anchovy s_A per transect was usually found in transects 35-36 (Figure 2.3), right in the north of the Ebro River mouth. In the year 2006 anchovy was southwardly displaced comparing to the preceding years and the maximum anchovy and sardine s_A overlapped (Figure 2.3). The bulk of sardine was commonly located between 40º54'N and 39º56'N (transects 37 to 42) (Figure 2.3). In the Southern subarea, the spatial distribution of anchovy and sardine was positively correlated for all the years but it was only significant in the year 2004 (*cor*=0.600; p-value<0.01) (Table 2.1).

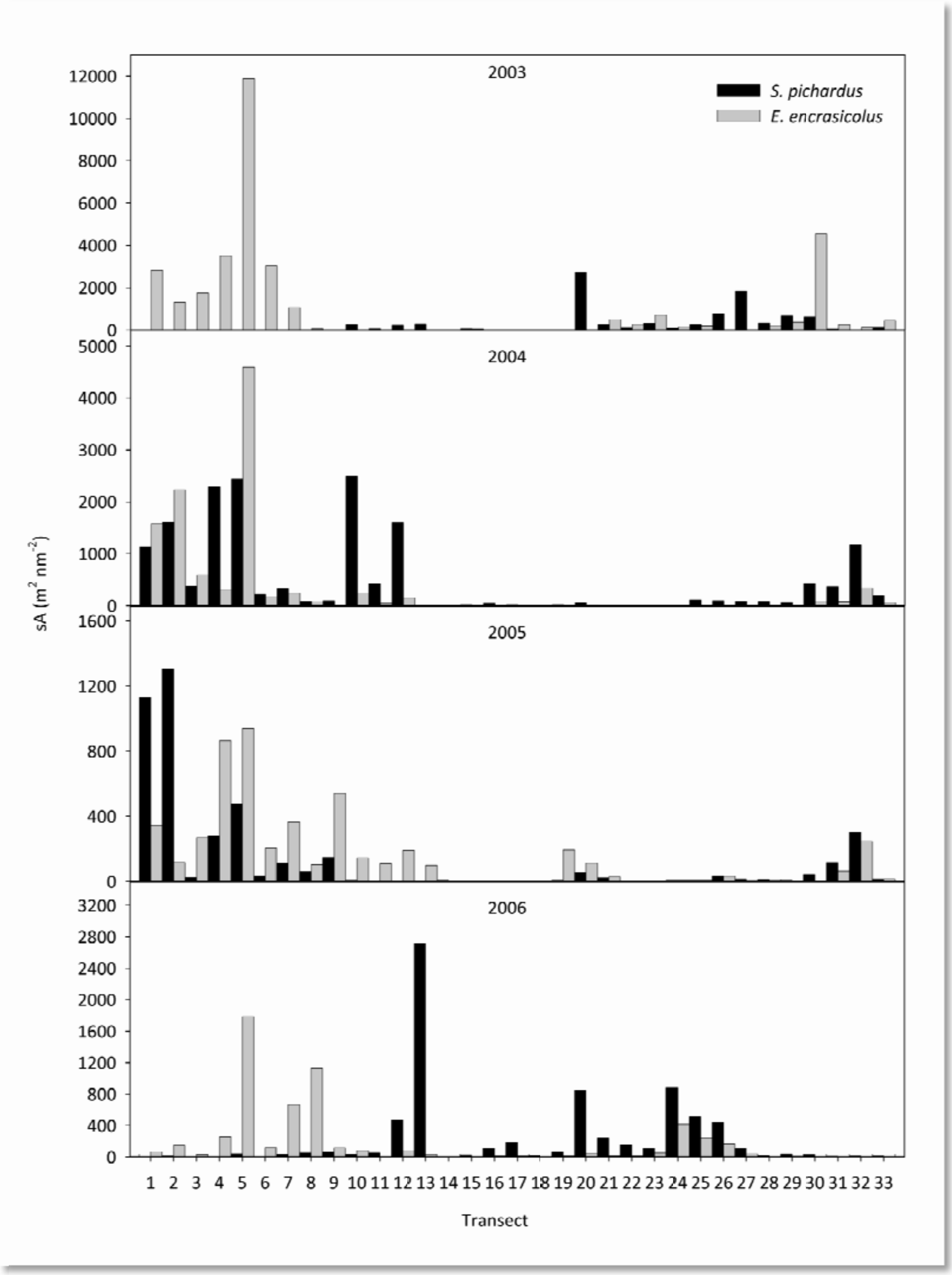


Figure 2.2. Anchovy (soft grey) and sardine (dark grey) cumulated sA (m2 nm-2) by transect in the Northern subarea.

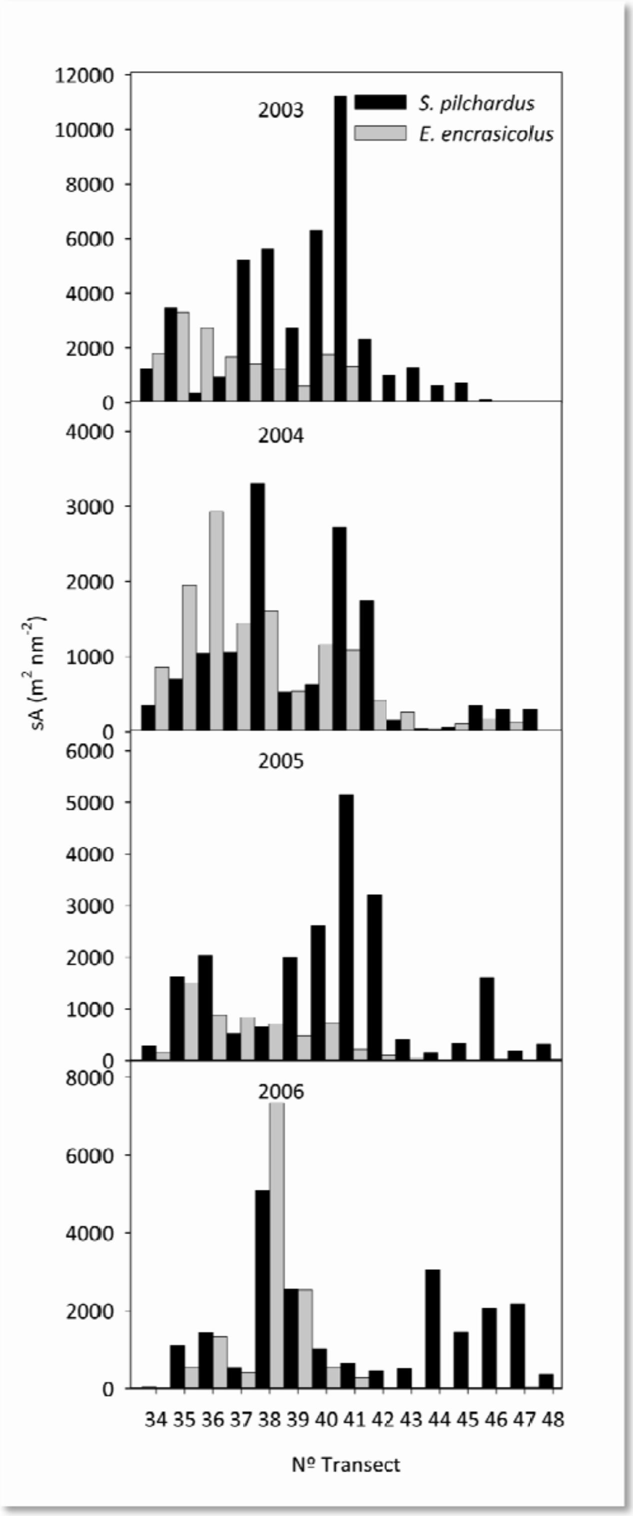


Figure 2.3. Anchovy (light grey) and sardine (dark grey) cumulated s_A (m^2 nm^{-2}) by transect in the Southern subarea.

Table 2.1. Correlation coefficient (Kendall tau) between the one dimensional spatial distributions of anchovy and sardine. NS: Northern sub-area; SS: Southern sub-area; p-values between brackets.

		Anchovy				Sardine			
		2003	2004	2005	2006	2003	2004	2005	2006
NS									
Anchovy	2003	1	0.31 (*)	0.128 (ns)	0.179 (ns)	-0.027 (ns)	-	-	-
	2004	0.31 (*)	1	0.480 (***)	0.222 (ns)	-	0.772 (***)	-	-
	2005	0.128 (ns)	0.48 (***)	1	0.341 (**)	-	-	0.473 (***)	-
	2006	0.179 (ns)	0.222 (ns)	0.341 (**)	1	-	-	-	0.269 (*)
Sardine	2003	-0.027 (ns)	-	-	-	1	-0.055 (ns)	-0.138 (ns)	0.294 (*)
	2004	-	0.772 (***)	-	-	-0.055 (ns)	1	0.439 (***)	-0.311 (*)
	2005	-	-	0.473 (***)	-	-0.138 (ns)	0.439 (***)	1	-0.318 (*)
	2006	-	-	-	0.269 (*)	0.294 (*)	-0.311 (*)	-0.318 (*)	1
SS									
Anchovy	2003	1	0.714 (***)	0.676 (***)	0.467 (*)	0.257 (ns)	-	-	-
	2004	0.714 (***)	1	0.81 (***)	0.6 (**)	-	0.6 (**)	-	-
	2005	0.676 (***)	0.81 (***)	1	0.562 (**)	-	-	0.39 (ns)	-
	2006	0.467 (*)	0.6 (**)	0.562 (**)	1	-	-	-	0.352 (ns)
Sardine	2003	0.257 (ns)	-	-	-	1	0.333 (ns)	0.429 (*)	0.029 (ns)
	2004	-	0.6 (**)	-	-	0.333 (ns)	1	0.562 (**)	-0.105 (ns)
	2005	-	-	0.39 (ns)	-	0.429 (*)	0.562 (**)	1	-0.086 (ns)
	2006	-	-	-	0.352 (ns)	0.029 (ns)	-0.105 (ns)	-0.086 (ns)	1

(ns) non significant; * < 0.05; ** < 0.01; *** < 0.001

Temporal stability of the spatial distributions

In the Northern subarea, the one dimensional anchovy spatial distributions of anchovy between years showed positive correlation coefficients for all years (*cor* between 0.128 to 0.480), but were statistically significant only for 1 year lag pairs (2003-2004, 2004-2005 and 2005-2006) (Table 2.1). In the case of sardine the spatial distribution between years showed a wider range of correlation coefficients (between -0.318 to 0.439) and was positively and significantly correlated between years 2003-2006 and 2004-2005 (*cor*=0.294 and 0.439, respectively) while it was negatively and significantly correlated for the pairs 2004-2006 and 2005-2006 (*cor*=-0.311 and -0.318, respectively) (Table 2.1).

In the Southern subarea, the one dimensional spatial distributions of anchovy were positively correlated for all time lags (*cor* between 0.562 and 0.810), with higher correlation coefficients and p-values in 1 or 2 year lag pairs than in the 3 year lag pair 2003-2006 (Table 2.1). The sardine spatial distributions generally showed smaller and non-significant correlation coefficients between years than anchovy (*cor* between -0.086 and 0.562) (Table 2.1). The one dimensional spatial distribution of sardine in 2005 was positively and significantly correlated with the spatial distribution of sardine in 2003 and in 2004 (cor=0.562 and 0.429, respectively), although the degree of correlation and significance were higher between 2004 and 2005, at one year lag (Table 2.1). These suggest that anchovy spatial distribution was more stable between years than sardine spatial distribution.

Estimates of acoustic abundance and precision

In the Northern subarea and concerning the geostatistical analysis, the nugget effect explained most of the variance both for anchovy and for sardine, ranging from 95.0% to 97.6% for anchovy and from 98.0% to 99.7% for sardine (Table 2.2). The experimental transitive covariograms and the fitted models for anchovy and sardine are shown in Figure 2.4. In the Southern subarea, the structural analyses showed that the nugget effect explained between 25.9 and 95.1% of anchovy's variance and between 92.4 and 96.8% for sardine (Table 2.2). The experimental transitive covariograms and the fitted models are shown in Figure 2.5.

Table 2.2. Summary of the structural analysis for anchovy and sardine T1D geostatistical covariogram models in Western Mediterranean Spanish waters (2003-2006). NS: Northern sub-area; SS: Southern sub-area; M: family model; sph: spherical model; nug: nugget model; r: range (nm); S: sill (x10^6); VarE: variance explained (%).

Area/ Species		2003			2004			2005			2006		
NS													
Anchovy	M	sph	sph	nug	sph	sph	nug	sph	sph	nug	sph	sph	nug
	r	-	28	-	132	28	-	132	44	-	132	28	-
	S	-	450	350	5	47.5	70.0	1.6	5.7	2.7	0.95	0.95	10.8
	VarE	-	4.4	95.6	0.1	2.4	97.6	0.4	4.6	95.0	0.1	3.4	96.9
Sardine	M	sph	sph	nug	sph	sph	nug	sph	sph	nug	sph	sph	nug
	r	132	60	-	132	48	-	-	36	-	-	84	-
	S	3.19	23.2	25.4	10.5	42.1	50.6	-	5.92	6.93	-	9.0	32.0
	VarE	1.9	0.1	98.0	0.2	1.7	98.1	-	2.3	97.7	-	0.3	99.7
SS													
Anchovy	M	sph	sph	nug	sph	sph	nug	sph	sph	nug	sph	sph	nug
	r	120	88	-	120	72	-	120	70	-	120	44	-
	S	87.2	23.19	233	40.5	124	1.44	2.18	36.0	2.51	7.8	260	230
	VarE	0.5	18.1	81.4	12.1	62.0	25.9	1.0	29.2	69.8	0.1	4.9	95.1
Sardine	M	sph	sph	nug	sph	sph	nug	sph	sph	nug	sph	sph	nug
	r	120	48	-	120	48	-	120	80	-	120	-	-
	S	443	1080	443	103	51.3	48.2	126	239	98.3	313	-	157
	VarE	3.8	3.8	92.4	3.3	4.1	92.6	2.0	5.6	92.4	3.2	-	96.8

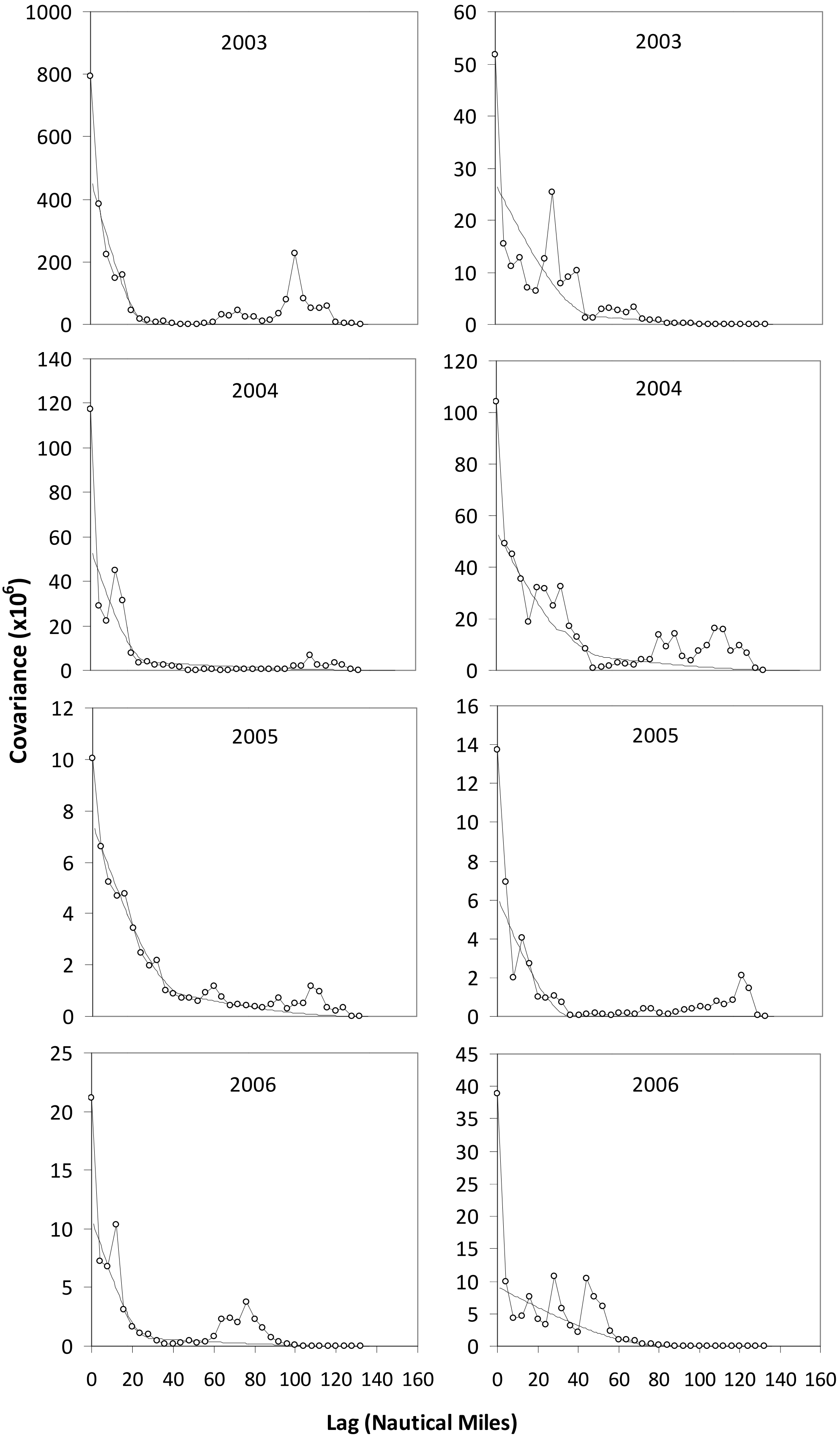


Figure 2.4. Experimental transitive covariograms (dotted line) and fitted models (solid line) for anchovy (left) and sardine (right) in the Northern subarea. Note that the y-axis scale differ for the different plots.

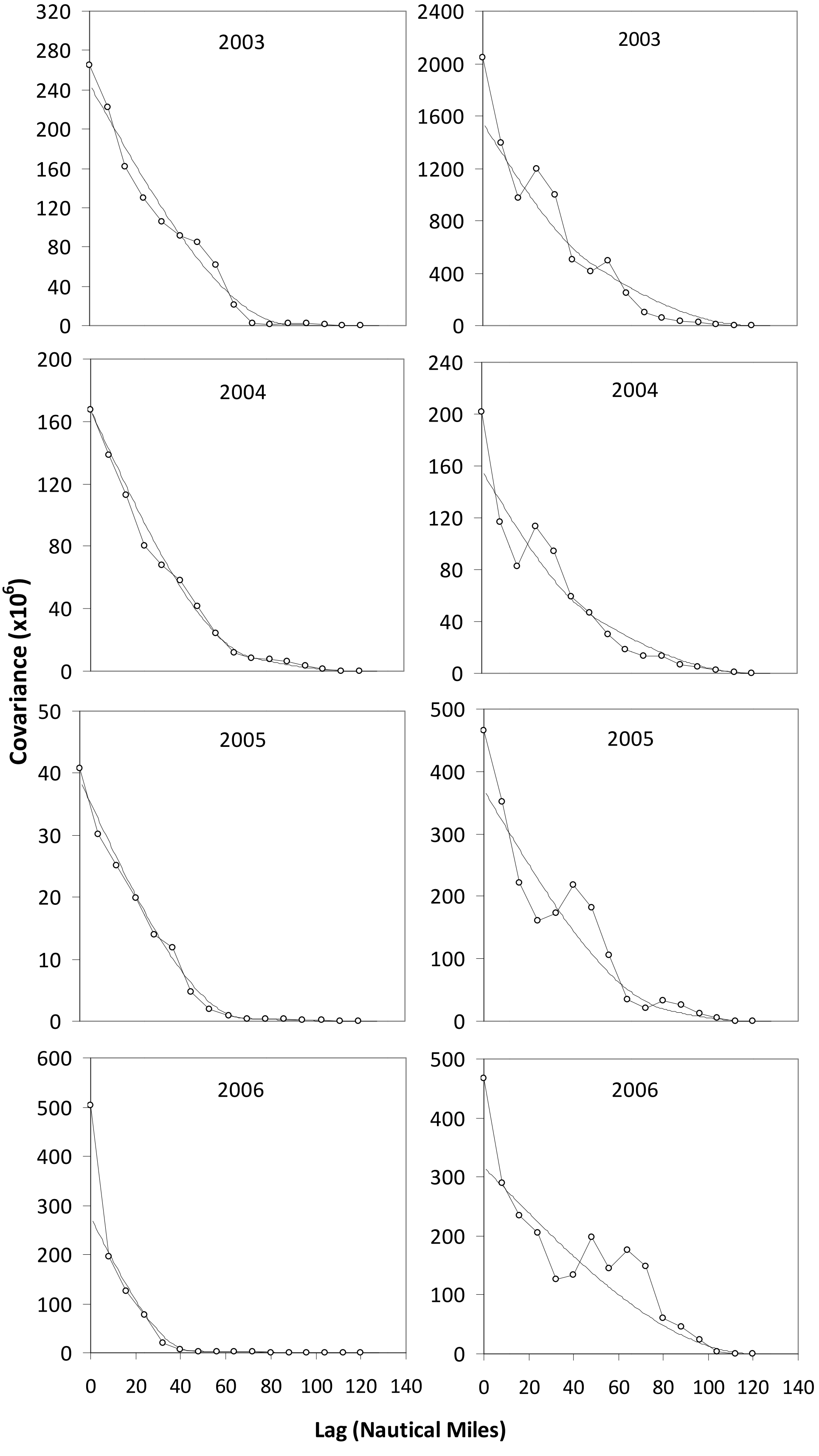


Figure 2.5. Experimental transitive covariograms (dotted line) and fitted models (solid line) for anchovy (left) and sardine (right) in the Southern subarea. Note that the y-axis scale differ for the different plots.

The estimates (*Q**) of the two species declined between 2003 and 2006 in the two subareas and in the study area as a whole (Table 2.3). In the Northern subarea the drop was considerably more intense for anchovy than for sardine, anchovy decreased from 132,660 m^2 (3.83x10^4 σ_{geo}) to 22,044 m^2 (0.67x10^4 σ_{geo}) and sardine from 36,300 m^2 (1.02x10^4 σ_{geo}) to 29,040 m^2 (1.14x10^4 σ_{geo}) (Table 2.3). On the contrary, in the Southern subarea the sardine fell more intensively than anchovy: sardine decreased from 345,600 m^2 (6.19x10^4 σ_{geo}) to 179,904 m^2 (3.60x10^4 σ_{geo}) whilst anchovy descended from 127,560 m^2 (1.53x10^4 σ_{geo}) to 104,760 m^2 (4.40x10^4 σ_{geo}) (Table 2.3). Moreover, anchovy and sardine were more abundant in the Southern subarea than in the Northern subarea, with the exception of the year 2003 when anchovy estimates were quite similar in the two subareas (Table 2.3).

Table 2.3. Acoustic abundance (Q*) in m^2, geostatistical variance (σ^2_{geo}), geostatistical standard deviation (σ_{geo}) and coefficient of variation (CV_Q) for anchovy and sardine in Western Mediterranean Spanish waters (2003-2006).

Area/	**Anchovy**				**Sardine**			
Parameter	**2003**	**2004**	**2005**	**2006**	**2003**	**2004**	**2005**	**2006**
NS								
*Q**	132,660	43,560	20,064	22,044	36,300	63,228	17,028	29,040
σ^2_{geo} (10^8)	14.64	2.87	0.11	0.45	1.04	2.06	0.28	1.29
σ_{geo} (10^4)	3.83	1.69	0.33	0.67	1.02	1.44	0.53	1.14
CV_Q (%)	28.84	38.89	16.80	30.29	28.04	22.71	31.28	39.05
SS								
*Q**	127,560	101,640	45,600	104,760	345,600	106,080	168,600	179,904
σ^2_{geo} (10^8)	2.34	0.44	0.29	19.36	38.36	4.16	8.51	12.95
σ_{geo} (10^4)	1.53	0.66	0.54	4.40	6.19	2.04	2.92	3.60
CV_Q (%)	11.99	6.56	11.76	42.00	17.92	19.24	17.30	20.01
Whole								
*Q**	260,220	145,200	65,664	126,804	345,963	169,308	185,628	208,944
σ^2_{geo} (10^8)	16.98	3.31	0.40	19.36	39.39	6.23	8.79	14.24
σ_{geo} (10^4)	4.12	1.82	0.63	4.45	6.28	2.49	2.96	3.77
CV_Q (%)	15.84	12.53	9.63	35.10	18.14	14.73	15.97	18.06

In the Northern subarea, the coefficient of variation of the estimations (CV_Q) varied from 16.80 to 38.89% for anchovy and from 22.71 to 39.05% for sardine (Table 2.3). In the Southern subarea, the CV_Q of sardine was lower and more stable than in the Northern subarea, ranging from 17.31 to 19.97% (Table 2.3) while for anchovy CV_Q was also low for the first three years (CV_Q between 6.56 and 11.99% for the period 2003 to 2005) but in the year 2006 it reached 42.00% (Table 2.3). These suggest that the precision of the estimates was generally higher in the Southern subarea for both species.

Global stock assessment and precision

Concerning the whole study area, the stock of both species declined in the period 2003-2006, in consistency to the observed trend in each subarea (Table 2.3). Anchovy dropped from 260,220 m^2 (4.12 x10^4 σ_{geo}) to 126,804 m^2 (4.45 x10^4 σ_{geo}), the minimum being found in the year 2005 (Table 2.3). In the case of sardine, the stock decreased from 345,963 m^2 (6.28 x10^4 σ_{geo}) to 208,944 m^2 (3.77 x10^4 σ_{geo}).

Relationship between precision and acoustic abundance

A significant and inverse relationship was found between the CV_Q (expressed in ‰) and acoustic abundance (in m^2 nm^{-2}) for sardine ($F_{1,6}$=5.856; P=0.052) while no relationship was found in the case of anchovy.

2.4 Discussion

Spatial segregation and preferential areas for anchovy and sardine stocks

In Western Mediterranean, the most important small pelagic species are anchovy and sardine (Lleonart and Maynou, 2003). Their one dimensional spatial distributions showed varying degree of overlap over the years in late autumn, sometimes indicating obvious segregation. In any case, the maximum cumulated s_A per transect were spatially segregated. In Southern Benguela, spatial segregation occurred between sardine (*Sardinops sagax*) and anchovy (*E. encrasicolus*) when low biomass was observed while when biomass was high, they shared the space (Barange *et al.,* 2005). This is not clearly happening in our study area most probably because of the low levels of biomass present in our area in relation to the biomass reported by Barange *et al.* (2005) as well as the difference in the primary production of the two ecosystems (Coll *et al.,* 2006). Alternatively, in the Humboldt system the range of anchovy (*Engraulis rigens/encrasicolus*) distribution was related to the size of favourable habitat, cold and productive water masses, while sardine (*Sardinops sagax*) distribution was more pervasive (Bertrand *et al.,* 2004; Swartzman *et al.,* 2008). The size of the stock had a secondarily effect. Sardine and anchovy are known to occupy different ecological niches, in terms of water masses, tolerance to abiotic factors, migrating capacities and feeding (Bertrand *et al.,* 2004; Gutiérrez *et al.,* 2007), even at larval stages (Morote *et al.,* 2010). Thus, habitat and feeding preferences may play a role in explaining the partially differing spatial distribution observed in our area. Thus, the hypothesis of a habitat-based model, in line with Bertrand *et al.,* (2004) and Swartzman *et al.,* (2008) should be investigated.

Anchovy stock in late autumn was persistently found in two preferential areas (or hot spots): in the Gulf of Roses and in the north of the Ebro River mouth. These are well known anchovy spawning sites, with high water enrichment (Palomera, 1989; Estrada, 1996; García and Palomera, 1996; Olivar *et al.,* 2001) and they have also been identified as potential concentration-retention sites (Agostini and Bakun, 2002). More specifically, the highest abundances of anchovy recruits found in the Southern subarea and in the present study showed spatial overlap with the maximum abundances of anchovy larvae reported in previous studies (Palomera, 1992; Olivar *et al.,* 2001). Furthermore, microzooplankton showed high dry weight and protein content off the Ebro River mouth but in sampling sites south the river mouth, evidencing high food availability and of high quality for anchovy early-life stages (García *et al.,* 2006). This highlights the importance of the areas of high water enrichment for early-life stages and recruitment of anchovy and suggests that anchovy would remain or survive in higher proportions in these areas since spawning and until late autumn.

In the Southern subarea, the higher amount of sardine stock was located south of the Ebro River mouth. Sabatés *et al.* (2007) suggested that anchovy was the only species in the NW Mediterranean which early-life stages are able to survive in exceptionally low salinity values (Sabatés, 1990). Therefore, since the bulk of sardine stock was found south the Ebro River mouth and sardine during its spawning season (Abad and Giráldez, 1993), it might indicate that sardine were preferentially occupying areas not too close to the Ebro River mouth where the lower salinity peaks are more likely to occur.

Stock assessment

In late autumn, the bulk of anchovy and sardine stocks were found in the Southern subarea in the period 2003-2006 (Table 2.4). In the year 2003, the anchovy stock showed a high pick in the Northern even surpassing the stock in the Southern subarea. This abrupt increase of anchovy in the Northern subarea might have been driven by larval transport from the Gulf of Lion (Arnau *et al.*, 2004; Sabatés *et al.*, 2001, 2007) which is facilitated by plums of fresh water from the Rhône River or anticyclonic eddies originated in the Gulf of Lion by barotropic and baroclinic instabilities or strong wind pulses (Flexas *et al.*, 2002; Arnau *et al.*, 2004) and may reach the Catalan coast (Arnau *et al.*, 2004; Sabatés *et al.*, 2001, 2007).

In our study area, anchovy and sardine stocks declined between 2003 and 2006, consistent with the decrease in their stocks observed in the area since the ’90 s (Giráldez *et al.*, 2006a, b; Palomera *et al.*, 2007). Small pelagic fish have suffered from intense exploitation in NW Mediterranean (Morales-Nin and Pertierra, 1990; Pertierra and Lleonart, 1996; Abad *et al.*, 1998 a,b) and the exploitation rates are higher than in other upwelling ecosystems, e.g. Benguela or Humboldt (Coll *et al.*, 2006). This could have an influence on sardine and anchovy populations, e.g. reducing their resilience or ability of recovery (Folke *et al.*, 2004). Additionally, environmental changes might have reduced the habitat suitability for two species. Northern expansion of southern species such as anchovy or sardine has been reported in the North Atlantic and in the North Sea (e.g. Beare *et al.*, 2004; Alheit, 2009) and in the Mediterranean it has been observed for other pelagic species as *Sardinella aurita* (Sabatés *et al.*, 2006). Hydroclimatic conditions have also changed in the last decades, for instance Mediterranean river runoff showed a decreasing trend since the 60’s with the exception of the rivers Po and Rhône (Ludwig *et al.*, 2009). Acoustic surveys in the Gulf of Lion showed an increasing trend in sardine biomass for the period 1993 - 2005 while anchovy biomass showed a declining trend for the same period (Palomera *et al.*, 2007). Thus, the Gulf of Lion might remain as a residual suitable area for sardine in Western Mediterranean but not for anchovy.

Precision of the estimates and some notes about accuracy

The CV_Q only depends on the sampling intensity and on the heterogeneity of the spatial distribution. If we assumed equal heterogeneity of the spatial distribution, higher CV_Q would be expected in the Southern subarea compared to the Northern subarea since sampling intensity in the Southern subarea is half the sampling intensity in the Northern subarea. However, our estimates are generally more precise (lower CV_Q) in the Southern subarea. This evidence the spatial distribution of anchovy and sardine was more homogeneous in the Southern subarea than in the Northern subarea in the studied period. The distinctive geomorphological and hydrodynamic characteristics of the two areas (e.g. extend of the continental shelf, exposure to strong winds or food availability) are likely to play an important role in explaining the differing heterogeneity. This is interesting in order to plan future surveys in the area. In order to obtain the same (or similar) precision in all the areas, a reduction of the inter-transect distance in the Northern subarea would be advisable. On the contrary, if the main interest is increasing the precision of the global estimation, an intensification of the sampling design in the areas where the estimates are higher (in the present case the Southern subarea) would reveal more efficient, as they contribute more to the global estimate and variance.

The random error associated to the global estimates presented in this study and derived from the systematic sampling scheme (9.63 – 18.14%) was considered acceptable, with the exception of anchovy 2004. Using the same geostatistical method, Norwegian herring showed a CV_Q of 12.5% (Petitgas, 1993) while a mixture of pelagic fish in Senegal was found to have a CV_Q between 4 and 15% (Samb and Petitgas, 1997). Despite sampling scheme is considered the main source of random error in acoustic surveys, it has to be taken into account that other sources of uncertainty were not considered like TS equations or trawl sampling (for a review see Simmonds and MacLennan, 2005). Moreover, the along transect variance has not been considered due to the dimensionality reduction (from two dimensions to one dimension). However, variance is expected to be much greater between transects than along transects and one dimensional and two dimensional approaches would give similar estimations of the variance of the total estimates (Petitgas, 1993). Thus it might not imply an important bias in the global precision.

In the year 2006, the anchovy estimates showed an exceptionally low precision (CV_Q=42.00%) in the Southern subarea which led us to a visual inspection of the echogram scrutinization. A possible overestimation of anchovy was detected in the transects with maximum abundances but it was impossible to verify as no fishing trawl was performed at that particular location. This might have overinflated anchovy estimates, variance and CV_Q and should be further investigated.

Despite the low amount of data available, a direct relationship seems to exist between sardine estimates and precision. This suggests that if the sardine stock further declines, the precision of the estimates would also decrease. An increase of the sampling intensity would be necessary to maintain the actual level of precision. This should be bear in mind in the planning of future surveys for assessment purposes. In the case of anchovy it could be that precision decreased with the stock but longer time series are needed to reach strong conclusions.

Regarding the accuracy of the estimates, anchovy spatial distribution analysed in the present study mainly reflects the spatial traits of the recruitment of the year. Between 81 and 94% of the anchovy captured during the surveys were mainly 0-aged individuals (unpublished data, IEO). Due to the low proportion of anchovy adults, an underestimation of adults might exist. Adult anchovy may be located far offshore in winter approaching shallower waters in spring-summer in the search of warm waters to spawn (Pertierra and Castellón, 1987). However, it cannot be inferred from our data and would need further investigation.

In the case of sardine, studies carried out in the ‘80s suggested that adults were located further off-shore in spawning migration by the season of the year our surveys were performed (Pertierra and Castellón, 1987). This would imply an underestimation of sardine stock. In the present study, the bulk of sardine overlapped in a latitudinal direction, the higher sardine eggs and larvae concentrations found in previous studies (Olivar *et al.*, 2001; Sabatés *et al.*, 2007). Although further analysis is needed, the observed spatial overlap suggest that sardine was already occupying the spawning grounds by the time of the year the surveys were performed and thus, minor underestimation is expected from this source.

Transitive geostatistics in one dimension and other statistical methods

Pelagic fish stocks are commonly estimated by means of acoustics and using parallel equidistant transects. Transitive geostatistics in one dimension (T1D) provide a useful tool to assess the precision (CV_Q) of global estimations in the case of sufficiently regular sampling schemes (Rivoirard *et al.*, 2000). T1D could also be used to derive confidence intervals if transect sums showed a normal probability distribution function (Rivoirard *et al.*, 2000). Nevertheless, T1D does not allow local estimations and thus two dimensional maps cannot be obtained. However, transitive geostatistics do not require probabilistic assumptions, and particularly stationarity hypothesis do not need to be satisfied (Matheron, 1965; Petitgas, 1993). Transitive methods work with variables that equal to zero outside the limits of a finite domain and the exact limits of the domain do not need to be known. In transitive geostatistics, the behaviour of the variable can be influenced by the geometry of the domain (e.g. decreasing near the limits of the domain).

More sophisticated methodologies such as geostatistical simulations yielded similar precision estimates for walleye pollock (*Theragra chalcogramma*) (Walline, 2007). This provides further validity to the results obtained by the T1D approach. Moreover, classical statistics that rely on random sampling overestimated the variance and the CV_Q (results not shown), thus provide biased estimations of the precision of pelagic fish stock assessment as they not take into consideration the spatial correlation observed in our data.

To sum up, our study shows that even reducing the dimensionality (from two dimensions to one dimension) our data can provide valuable information about anchovy and sardine spatial distributions in a proxy of a latitudinal direction and the inter-annual variation. The on dimensional spatial distribution of anchovy stock (mainly recruits) in late autumn is more stable through years than sardine and preferentially occupies the main spawning areas. The bulk of the two species is generally found in the vicinity of the Ebro River, being the anchovy more close to the river mouth. Transitive geostatistics in one dimension (T1D) require less statistical assumptions than the widely used intrinsic geostatistics, are suitable to estimate sampling uncertainty for global estimates and, assuming a good covariogram model choice, provide an unbiased estimation of the coefficient of variation of the overall estimates (Petitgas, 1993; Petitgas and Prampart, 1993). We have shown that T1D could be used to analyse the effects of varying abundance on the precision of the estimates. Moreover, T1D may help in detecting possible errors (or weaknesses) in the data processing. These would contribute to improve not only the precision but the accuracy of the estimations that are annually provided to stock assessment groups.

Chapter 3. Two dimensional spatial distribution of anchovy (*Engraulis encrasicolus*) in the Spanish Mediterranean waters to estimate sampling precision and optimize sampling design

Chapter 3. Two dimensional spatial distribution of anchovy (*Engraulis encrasicolus*) in Spanish Mediterranean waters to estimate sampling precision and optimise sampling design

3.1 Introduction

Marine fisheries are threatened worldwide mainly through increasing overexploitation and climate change (FAO, 2010; Brander, 2007). Marine researchers and managers have the challenge to develop and implement regulatory mechanisms that are able to assure a sustainable exploitation of marine fisheries (Pauly *et al.*, 2002). In this sense, ecosystem-based management has been given growing attention in the recent years and has been proposed as a tool to overcome the increasing declining state of fisheries and oceans. Notwithstanding single-species stock assessments remain the base of any posterior attempt to manage whole ecosystems. However, the uncertainty on the reliability (or precision) of single-species stock assessments has sometimes been used to excuse the implementation of fishing restrictions that can be economically painful (Pauly *et al.*, 2002). Thus, routinely estimation of the precision (closeness between individual estimates of a variable) of single-species stock assessment is crucial to accomplish a conscious management.

In the Mediterranean Sea, European anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) constitute an important fraction of total landings, up to one half in the period 2003-2006 (FAO Fisheries Statistical Collections). Both are small pelagic foraging species and thus highly valuable in ecological terms by transferring energy from the lower to the upper levels of the trophic chain (Cury *et al.*, 2000). The biology of European anchovy, i.e. short life-span (rarely older than 3 years) and reproductive strategy (producing large quantities of eggs over extended areas), makes this species especially sensible to environmental changes (Bakun, 1996). Anchovy populations have been recognised as vulnerable to long term increase in temperature by the Global Ocean Ecosystem Dynamics programme, GLOBEC (Barange *et al.*, 2010). In the Spanish Mediterranean Sea, annual small pelagic fish stock assessments were performed in late autumn (November-December) from the 90s till 2009 by means of acoustic surveys. In the context of global climate change and high fishing pressure, concern about the overexploitation of these anchovy stocks existed, seeing that assessments showed a declining trend between 1992 and 2006, and that high fishing effort is concentrated on the small sizes (Giráldez *et al.*, 2006 a,b; Pertierra and Lleonart, 1996).

In acoustic surveys, the sampling design usually consists of the continuous collection of data along parallel transects. Assuming that acoustic data is gathered under proper conditions, density of fish can be measured with high accuracy along the line transects. Observed variations in fish density thus would reflect biological variations, or inhomogeneity in the spatial distribution (Foote and Stefanson, 1990). The sources of uncertainty (or variance) in global abundance estimates derived from acoustic surveys are many (Aglen, 1994; Simmonds and MacLennan, 2005) but the commonly applied systematic sampling design is thought to be the greatest contributor to the global variance (ICES, 1998). For spatially autocorrelated data, like acoustic data, the variance introduced by the sampling design cannot be estimated without bias with classical statistics and requires the application of geostatistics (ICES, 1993).

Geostatistics have been widely applied for mapping (through kriging) of spatially autocorrelated data for many environmental resources. Not so widespread is its application for sampling variance estimation although in the case of acoustic surveys it is rather well documented (Guillard *et al.,* 1992; Petitgas, 1993; Williamson and Traynor, 1996; Ohshimo *et al.,* 1998; Páramo and Roa, 2003; Horne and Walline, 2005; Doray *et al.,* 2008; Gurshin *et al.,* 2013). The classical semivariogram estimator, the most frequently used tool for estimating the spatial autocorrelation, is sensitive to asymmetric probability distribution functions (pdf, here after) and also to extreme values, impinging non-robustness in the spatial structure (Guiblin *et al.,* 1995; Webster and Oliver, 2007; Kerry and Oliver, 2007a,b) and/or bias in the estimation of the spatial structure (Rufino *et al.,* 2006a). In the worst scenario, the semivariogram may appear as pure nugget effect where there is an underlying spatial autocorrelation structure (Carr *et al.,* 1985).

Positively skewed data are typically encountered in many environmental studies and in ore reserve estimation for precious metals (Srivastava and Parker, 1989). In species distribution data, and specifically in data derived from acoustic surveys, pdfs show commonly zero-inflation and a small amount of really high values together with positive skewness (Petitgas, 1993; Maravelias *et al.,* 1996; Woillez *et al.,* 2009). In such type of data, the estimation of global variance is compromised provided that unbiasedness in variance estimation is guaranteed only for normally distributed data (Isaaks and Srivastava, 1989; Rufino *et al.,* 2006a).

Non-ergodic variogram estimator, proposed for heterocedastic, skewed data and/or preferential sampling (Isaaks and Srivastava, 1988; Srivastava and Parker, 1989) performed poorer than the traditional variogram estimator (Curriero *et al.,* 2002). Robust variogram estimators like Cressie and Hawkins' estimator (Cressie and Hawkins, 1980) have been used to retrieve the spatial structure of skewed data (Doray *et al.,* 2008; Gurshin *et al.,* 2013) but for log-Gaussian data have been shown worse performance than the traditional variogram estimator (Rufino *et al.,* 2006a). However, as long as the traditional variogram estimator is the only one reproducing the total variance (Maravelias *et al.,* 1996) and one of our main goals is the variance estimation, the traditional variogram estimator will be used. Notwithstanding, kriging predictions are not particularly sensitive to the type of variogram used provided that the model fits correctly the experimental curve (Journel and Huijbregts, 1978).

Once the spatial structure of the variable of interest is known, changes in the precision of the global abundance estimates due to changes in the sampling design and/or in the sampling density can be evaluated. This can become useful for survey design optimisation, e.g. by increasing the minimum distance between samples or between transects if the precision does not fall to unacceptable levels, allowing to cover the same sampling area in a shorter amount of time without compromising the quality of the abundance estimates.

The present work is aimed at analysing the spatial structure of anchovy in the Spanish Mediterranean continental shelf from late-autumn acoustic surveys along with estimating the variance introduced by the sampling design in global abundance estimates of anchovy. Due to the asymmetry in the pdfs, the effects of data transformation and methodological options in the estimation of the spatial structure and variance are estimated. In addition, to evaluate a possible optimisation of the sampling design, the variation of the global precision to changes in the inter-transect distance is as well analysed.

3.2. Material and methods

Four years of anchovy s_A data, collected in the context of annual surveys of pelagic fish stocks assessment in the Spanish Mediterranean waters (ECOMED) from 2003 to 2006 was used. Data collection and processing is thoroughly explained in Section 1.4.

Study area

The study area comprised the water column of the continental platform of the Spanish Mediterranean Sea, from Cape Salou to the Albufera de Valencia wetland (Figure 3.1), the SS as defined in the previous chapter. The area is characterised by a continental shelf with maximum width of about 30 nautical miles (hereinafter nm), freshwater nutrient-rich inputs from the Ebro River and a cyclonic along slope current, the Northern current, transporting water from the Gulf of Lions in a northeast-southwest direction. The maximum diagonal of the rectangle containing the data is about 112.4 nm long.

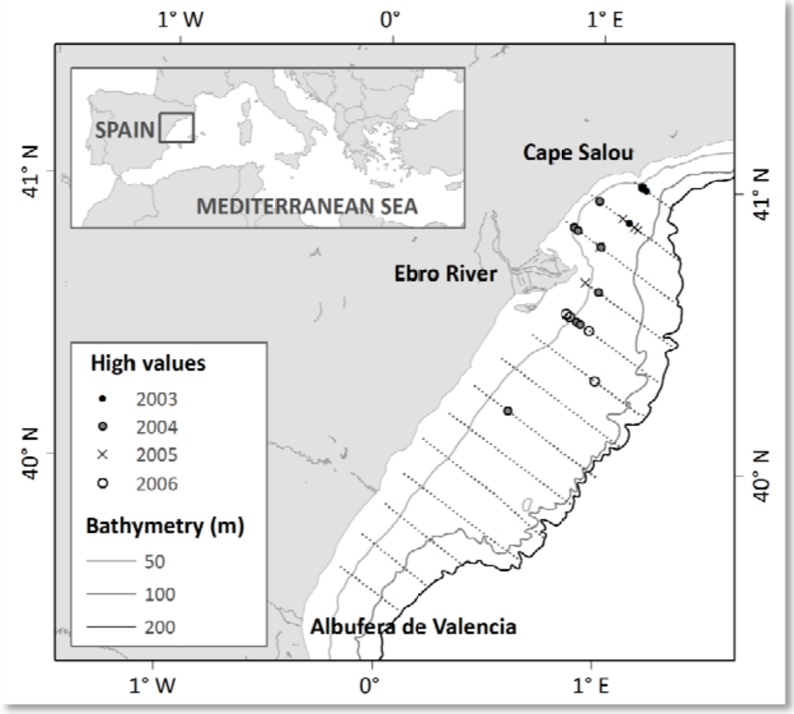


Figure 3.1. Study area, sampling scheme and location of the high anchovy density samples, removed to construct the thsA dataset for the period 2003-2006.

Data analysis

Intrinsic geostatistics in two dimensions (I2D) were applied to: A) analyse the spatial structure of anchovy density, B) produce anchovy density maps, C) estimate the global abundance of anchovy in the study area and its precision and finally, D) analyse how the precision of the global abundance estimates would change to varying sampling intensities. Additionally, the robustness of the different parameters to changing methodological options was analysed. The combination of the different methodological options applied, i.e. 5 experimental variograms, 2 model types and 4 fitting methods (Table 3.1), yielded a total of 40 estimates of the spatial structure (or fittings) per year and dataset and a total of 120 estimates of the spatial structure per year.

Table 3.1. Data transformations and methodological options used in the spatial analysis and in the analysis of the variation of global precision due to variations in sampling intensity.

		Spatial analysis			Sampling intensity
		Variogram	Fitting		
Data set	Transformation	h (nm)	Model type	Fit method	a (nm)
s_A	none	1, 3, 5, 6, 8	sph + nug, exp + nug	ols, wls_p, wls_{pd}, wls_{ps}	-
log_{sA}	log (x+1) &backtransform	1, 3, 5, 6, 8	sph + nug, exp + nug	ols, wls_p, wls_{pd}, wls_{ps}	1, 4, 12, 16, 20
th_{sA}	threshold	1, 3, 5, 6, 8	sph + nug, exp + nug	ols, wls_p, wls_{pd}, wls_{ps}	-

s_A: untransformed dataset; log_{sA}: log-transformed dataset; th_{sA}: thresholded dataset; h: lag width; sph: spherical, exp: exponential; nug: nugget; ols: ordinary least squares; wls_p: weighted least squares using the number of pairs used as weight; wls_{pd}: weighted least squares using number of pairs and inverse distance as weights; wls_{ps}: weighted least squares using number of pairs and semivariance as weights; a: inter-transect distance.

Omnidirectional experimental semivariograms were constructed using Matheron's classical variogram estimator (Matheron, 1965). The experimental semivariogram is a representation of the semivariance between pairs of sample data at evenly spaced lag distances. The analysis was performed at different spatial aggregation scales. Thus, different lag widths were used to construct the experimental variogram (Table 3.1), lag widths comprised between the EDSU (1 mile) and the inter-transect distance (a, 8 nm). Information at lower spatial scales than the EDSU would require the re-processing of the huge amount of echosounder data while the use of lag widths bigger than *a* would imply the loss of spatial information.

In the presence of spatial autocorrelation, the semivariance increases until a range after which it levels off. The value of the semivariance at the range where semivariance stops increasing is called partial sill. The search of spatial autocorrelation was limited to roughly the width of the continental shelf by establishing a cut-off distance of 1/3 of the maximum diagonal (i.e. about 37.5 nm). The nugget effect is a variogram model with a constant partial sill; it is interpreted as a discontinuity at the origin and it is thought to be related to variability at smaller scales than the smallest sampling unit and/or to measurement error.

The selection of the most appropriated models was performed after visual inspection of the experimental variograms. Automatic fitting procedures were used to fit a variogram model to the experimental variogram to ensure reproducibility and objectivity of the analysis. In particular, diverse least square methods were used (see Table 3.1). When Matheron's classical variogram estimator is applied to log-Gaussian data, least square methods are reckoned to produce more accurate estimates of the variogram than likelihood methods (Cressie, 1991; Rufino *et al.*, 2006a). The range of correlation was fitted by means of an automatic iterative procedure (Pebesma, 2004).

The analysis of basic statistics confirmed anchovy density derived from acoustic surveys showed positively skewed pdf. In the event of asymmetric pdf, data transformations and methodological options involved in the spatial analysis are known to affect the estimates of the spatial parameters, i.e. range, sill and nugget (Rufino *et al.,* 2005). Three datasets were used: i) anchovy density without transformations, s_A, and two transformed datasets, ii) log-transformed anchovy density, $\log_{sA}$ and iii) thresholded anchovy density, th_{sA}, (Table 3.1) in order to try to overcome non-normality and to avoid its effects on the spatial analysis. In addition, different methodological options were applied during the spatial analysis to provide an indicator of the robustness of the spatial analysis (Table 3.1).

The range of correlation is not directly comparable between some semivariogram models. Thus, the practical range was computed and used for comparative purposes. For a spherical model the practical range equals the range of the model while for an exponential model the practical range is defined as the range at which the sill reaches the 95% and it equals the range of correlation multiplied by 3 (Cressie, 1991; Rufino *et al.,* 2005).

For the $\log_{sA}$ dataset, the estimated spatial parameters were back-transformed to obtain estimates in the original scale without a great bias. Back-transformation was performed by means of Guiblin *et al.* (1995) algorithm of the form:

$$\gamma_Z(h) = ((\beta + \bar{z}_s)^2 + s^2)\left(1 - e^{-\alpha^2 \frac{\gamma_L(h)}{s_L^2}}\right) \qquad \text{(Eq. 3.1)}$$

Where $\gamma_Z(h)$ is the variogram of the variable Z in the original scale, $\gamma_L(h)$ the variogram in the logarithmic scale, $\overline{z_s}$ is the sample mean of the variable in the original scale, β is a constant that is added to the variable in order to avoid zero values for which the logarithm is not defined (1 in the present case), s^2 is the variance of the samples in the original scale, s_L^2, the variance of the samples in the logarithmic scale and α^2 is computed as follows:

$$\alpha^2 = \log\left(1 + \frac{s^2}{(\beta + \overline{z_s})^2}\right) \qquad \text{(Eq. 3.2)}$$

Local abundance density maps

Distribution maps of anchovy density were produced by ordinary kriging, an interpolation technique that predicts the value of a variable at unobserved locations taking into account the spatial structure through variograms (Matheron, 1965; Krige, 1951). The untransformed anchovy density was interpolated and using the different spatial structures estimated with the three datasets. A prediction grid was created within the sampled bathymetric range, i.e. 30 - 200 m depth. It was composed of 15,456 cells of about 0.19 nm^2. This cell size is smaller than one half of the minimum distance between samples to provide an optimum interpolation resolution (Hengl, 2006). As the density and abundance of any species are strictly positive variables, we forced negative kriging estimates to zero (Froidevaux, 1993). These negative kriging estimates arise when high values are surrounded by low values which are given negative weights, a masking phenomenon known as “screening effect” (Wackernagel, 1995; Armstrong, 1998).

The mean anchovy density at each grid cell, $\overline{z_E(x_i)}$, m^2 nm^{-2}, was estimated as the arithmetic average of the kriging predictions obtained by the different methodological options at each grid cell and for each data transformation. Maps of local mean of anchovy were produced using maptools and rgdal packages (Lewin-Koh *et al.,* 2011; Keitt *et al.,* 2010).

Global abundance and precision

The abundance of anchovy within the domain, Q (m^2), was estimated as the product of the mean anchovy density, $\bar{z}$ (m^2 nm^{-2}), and the area of the analysed domain, A (nm^2). The area of the domain was estimated by multiplying the number of cells in the prediction grid covering the sampled area by the area of a standard cell (2,884 nm^2). The mean density was computed with the original samples by arithmetic average ($\overline{z_s}$) and with the kriging predictions, $\bar{z}_{kri}$, (Rivoirad *et al.,* 2000), thus obtaining a global abundance of anchovy estimated by the samples (Q_s^*) and a global abundance of anchovy estimated by kriging (Q_{kri}^*).

Precision is defined as the degree to which repeated measurements show the same results under unchanged conditions and is related with random error (or variance). It is related to variance so that higher values of variance indicate lower precision and the reverse. In acoustic surveys it is generally accepted that the source of random error generating the highest amount of variance is sampling design (ICES, 1993). Thus, taking the previous assumption we used the coefficient of variation as a measure of precision of the form:

$$CV_Q = \frac{\sqrt{\sigma_{geo}^2}}{\bar{z}} \qquad \text{(Eq. 3.3)}$$

Where σ_{geo}^2 is the sampling variance estimated by means of geostatistics (Petitgas, 1993) and is computed using the previously fitted variogram models. CV_Q depends only on sampling intensity and on the spatial distribution. The process of estimating the variance through geostatistics requires dividing the area in cells and implies computer demanding calculations. Thus, bigger cells than for producing the maps were needed (cells of ~0.48 nm cell^{-1}) to reach a compromise between accurate variance estimation and computer requirements, however, still ensuring a cell size close to the optimum interpolation resolution (Hengl, 2006). The presence of inherent spatial autocorrelation in acoustic data impinged the use of geostatistics to estimate the variance without *a priori* bias.

Bias of the global abundance

The absolute bias of the global abundance anchovy was assessed as the difference between the global abundance of anchovy estimated by kriging (Q_{kri}^*) and abundance obtained with the sample mean (Q_s^*) of the form:

$$bias = \frac{(Q_{kri}^* - Q_s^*)}{Q_s^*} \qquad \text{(Eq. 3.4)}$$

Robustness of the estimates

Ideally the results obtained from the application of different methodological options or appropriate data transformation and back-transformation should be robust. This implies that the variance of the results obtained from the different methodologies when put together should be rather low and should tend to a same value. For every analysed parameter, the mean and the coefficient of variation between methodological options were estimated. The higher the *CV* is, the lower the robustness of the specific parameter.

Contrarily, the lower the *CV*, the lower is the variability between the results and, thus, the higher the robustness of the parameter to the analysed methodological options. The intensity of *CV* was graded as follows: *CV* ≤ 10 % high; *CV* between 10 and 30 % medium and *CV* >30 non-robustness. In particular, the robustness of the spatial parameters, i.e. nugget, partial sill and range, of the global abundance estimates and of the precision of the global abundance estimates were analysed.

Effects of methodological options on the estimates and sensitivity analysis

For each year, the combination of the methodological options produced a total of 120 estimates of the spatial structure, 120 kriging interpolations and 120 estimates the global precision. For each methodological option, analysis of the variance (ANOVA) was performed in order to determine if the methodological options have significant effects on the results. In the event that the ANOVA analysis yielded a significant p-value, a *post hoc* comparison test, i.e. Tukey's honestly significant difference test (Tukey HSD), to identify which level of the methodological option was producing the difference. Further, a sensitivity analysis was performed to assess the percentage of deviance explained by each methodological option in the estimated parameters by means of linear models.

Precision to varying sampling intensity

The effects of varying sampling effort on the precision of global abundance estimates was assessed by means of constructing different sampling schemes with parallel equidistant transects to changing the distance between samples (Table 3.1). Assuming that the spatial structure encountered by applying these sampling schemes would be the same as that estimated with the actual sampling design (i.e. 8 nm inter-transect distance), the precision on global abundance estimates was analysed.

All the statistical analysis was performed using the R statistical software (R Development Core Team, 2014), i.e. the skewness coefficient was computed with the package agricolae (de Mendiburu 2014), the geostatistical analysis was performed with the package gstat (Pebesma, 2004) and the estimation of the precision of the global abundance was computed by means of the package RGeostats (Renard *et al.*, 2014). Mapping was performed with the sp package (Pebesma and Bivand, 2005) in the R statistical software as well as using ArcGis 9.3.

3.3 Results

Data description

Anchovy density showed positively skewed pdf in the studied area in the four analysed years (histograms not shown). In all the datasets and years, anchovy density showed high dispersion with third quartiles smaller than the mean, high variance with high inter-annual variability (2,504 - 48,979), and high skewness coefficient (from 4 to 12), depending on the year and transformation (Table 3.2). Note that, for normal distributions the second quartile tends to equal the mean and skewness is close to zero. Sample variance and skewness were lower for the transformed datasets (both for the $\log_{sA}$ and th_{sA} datasets), than for the untransformed dataset (s_A). A clear zero inflation was evident for the three datasets (first quartiles and medians equal to 0 m^2 nm^{-2}), suggesting that data transformations reduced the dispersion of anchovy density through lowering the skewness and the variance but were unable to fully normalise the pdf (Table 3.2).

The th_{sA} dataset was constructed by removing the high values above a density threshold. The threshold was selected so that a spatial structure was observed in the semivariogram. The thresholds were 600 m^2 nm^{-2}, 400 m^2 nm^{-2}, 200 m^2 nm^{-2} and 500 m^2 nm^{-2} for the years 2003, 2004, 2005 and 2006 respectively and, in all the cases, represented a very low amount of samples (i.e. between 1 and 2%). However, these very few amount of samples removed represented a considerable proportion of the abundance of anchovy in the area, i.e. 23%, 24%, 26% and 57 % in 2003, 2004, 2005 and 2006 respectively, and a high or very high proportion of the sample variance, i.e. 66%, 69%, 77% and 96% in 2003, 2004, 2005 and 2006 respectively.

Spatial structure of anchovy distribution

Visual inspection of the experimental semivariograms showed for the s_A dataset a clear spatial autocorrelation only in the year 2006 (see grey dots, Figure 3.2). For the $\log_{sA}$ dataset, a well-defined spatial structure was observed in all the analysed years, with semivariance increasing up to a certain value and then levels-off (Figure 3.2). For the th_{sA} dataset, the autocorrelation structure was not as intense as in the $\log_{sA}$ although still present. Independently of the transformation used, the semivariance showed certain cyclic variability with periodicity of about 8-10 nm (Figure 3.2), more evident for smaller lag widths and smoothed for wider lag widths (not shown).

The automated variogram fitting failed in some years for the s_A dataset (Table 3.3). In particular, in the year 2003 only 1 out of the 40 fittings performed succeeded in retrieving a sound spatial structure (2.5% fitting success), i.e. obtained by the combination of least squares fitting method weighted to the number of pairs and to the inverse distance (wls_{pd}), a lag width of 1 mile and exponential model. This only fitted model yielded a practical range of 4 nm, a partial sill of 11,833 and no nugget effect (Table 3.3). In the year 2004, there was one experimental model for which it was not possible to obtain a spatial structure and in the year 2005, the fitting of a spatial autocorrelation structure failed in 30 out of 40 cases (25% success). Wider the lag widths (≥ 5 nm) failed more frequently to retrieve a spatial structure while the most successful were the combination of shorter lag widths (i.e. ≤ 3 nm) with more elaborated fitting methods, i.e. least squares weighted to the number of pairs and to the inverse distance (wls_{pd}) and or weighted to the number of pairs and to the semivariogram value (wls_{ps}). Furthermore, in the year 2004 two variogram fittings were excluded from the results as long as the estimated ranges were bigger than the study area.

Table 3.2. Descriptive statistics of anchovy density for each dataset and year.

Dataset	Year	n	Q_1	$\bar{z}_s$	Q_3	max	s^2	skew
s_A	2003	381	0	42.1	20.5	1,816.0	17,095.3	8.0
	2004	378	0	33.6	14.8	749.0	9,228.2	4.4
	2005	373	0	15.22	9.0	534.0	2,504.5	7.1
	2006	373	0	35.1	8.0	2,895.0	49,110.4	11.6
log$_{sA}$	2003	381	0	1.5	3.1	7.5	4.0	0.9
	2004	378	0	1.4	2.8	6.6	3.5	1.0
	2005	373	0	1.2	2.3	6.3	2.4	1.1
	2006	373	0	1.2	2.2	8.0	2.9	1.4
th$_{sA}$	2003	377	0	32.5	18.5	525.0	5,884.8	3.4
	2004	369	0	21.4	12.0	368.0	2,878.4	3.8
	2005	368	0	10.4	8.0	174.0	571.9	3.6
	2006	369	0	15.3	8.0	445.0	2,014.4	5.5

s_A: untransformed dataset; log$_{sA}$: log-transformed dataset; th$_{sA}$: thresholded dataset; *n*: number of samples; Q_1: first quartile; $\bar{z}_s$: arithmetic average of the samples; Q_3: third quartile; *max*: maximum value; s^2: sample variance; *skew*: skewness of the samples

Considering the pool of datasets, the spatial parameters were mostly non-robust with values of CV varying from 52.8 % and 91.6% for the nugget, from 61.6 % to 76.0% for the sill and from 29.8 % and 67.8% for the practical range (Table 3.3). However, analysed within each dataset (i.e. s_A, log$_{sA}$ and th$_{sA}$) the robustness of the different spatial parameters varied greatly depending on the year and dataset (Table 3.3). For the year 2003, the robustness was not computed with the s_A dataset as long as only one model was able to be fit. The nugget usually showed medium robustness for the th$_{sA}$ dataset, (*CV* from 13.9% to 22.3%), from medium to non-robust for the s_A dataset (*CV* from 15.7% to 142.4%) while it varied from high robustness to non-robustness for the log$_{sA}$ (*CV* 7.0% to 59.5%; Table 3.3). Referring to the **partial sill**, it showed high robustness for the log$_{sA}$ dataset (*CV* from 2.2% to 5.3%), medium robustness for the th$_{sA}$ dataset (*CV* between 14.6 and 20.8 %) and from medium to non-robustness for the s_A dataset (*CV* from 24.6 to 36.4%; Table 3.3). In relation to the mean estimated **practical range, its robustness** varied from medium to non-robustness for the three datasets, with *CV* ranging from 17.9 to 36.8 % for log$_{sA}$ dataset, from 25.2 to 33.7% for the th$_{sA}$ dataset and from 22.4 to 93.2 % for the s_A dataset (Table 3.3).

Table 3.3. Spatial structure of anchovy: mean estimates of the variogram parameters and associated robustness.

			nugget		sill		range	
Dataset	year	N	*mean*	*CV*	*mean*	*CV*	*mean*	*CV*
All	2003	81	2,899.9	57.8	10,374.4	61.6	31.9	29.8
	2004	117	3,448.3	52.8	4,299.0	76.0	29.3	67.8
	2005	90	815.5	77.0	1,271.4	73.1	23.1	41.3
	2006	120	15,945.7	91.6	31,706.5	72.0	32.7	57.7
s_A	2003	1	0	NA	11,833.1	NA	4.1	NA
	2004	37	5,160.0	15.7	2,839.2	30.3	34.8	93.2
	2005	10	414.9	142.4	1,628.3	36.4	3.9	34.2
	2006	40	13,490.0	78.8	45,943.9	24.6	19.9	22.4
log_{sA}	2003	40	3,578.6	59.5	16,716.9	3.4	32.0	25.3
	2004	40	3,891.7	36.4	8,664.8	4.4	28.6	31.4
	2005	40	1,463.8	12.8	2,173.0	5.3	30.1	17.9
	2006	40	33,141.0	7.0	48,254.4	2.2	52.3	36.8
th_{sA}	2003	40	2,293.7	17.3	3,995.4	14.6	32.4	30.8
	2004	40	1,421.5	13.9	1,283.4	15.8	24.8	33.7
	2005	40	267.4	22.3	280.6	19.2	20.9	25.2
	2006	40	1,205.9	15.3	921.1	20.8	25.7	34.8

s_A: untransformed dataset; log_{sA}: log-transformed dataset; th_{sA}: thresholded dataset; N: number of successfully fitted models; sill: partial sill; range: practical range.

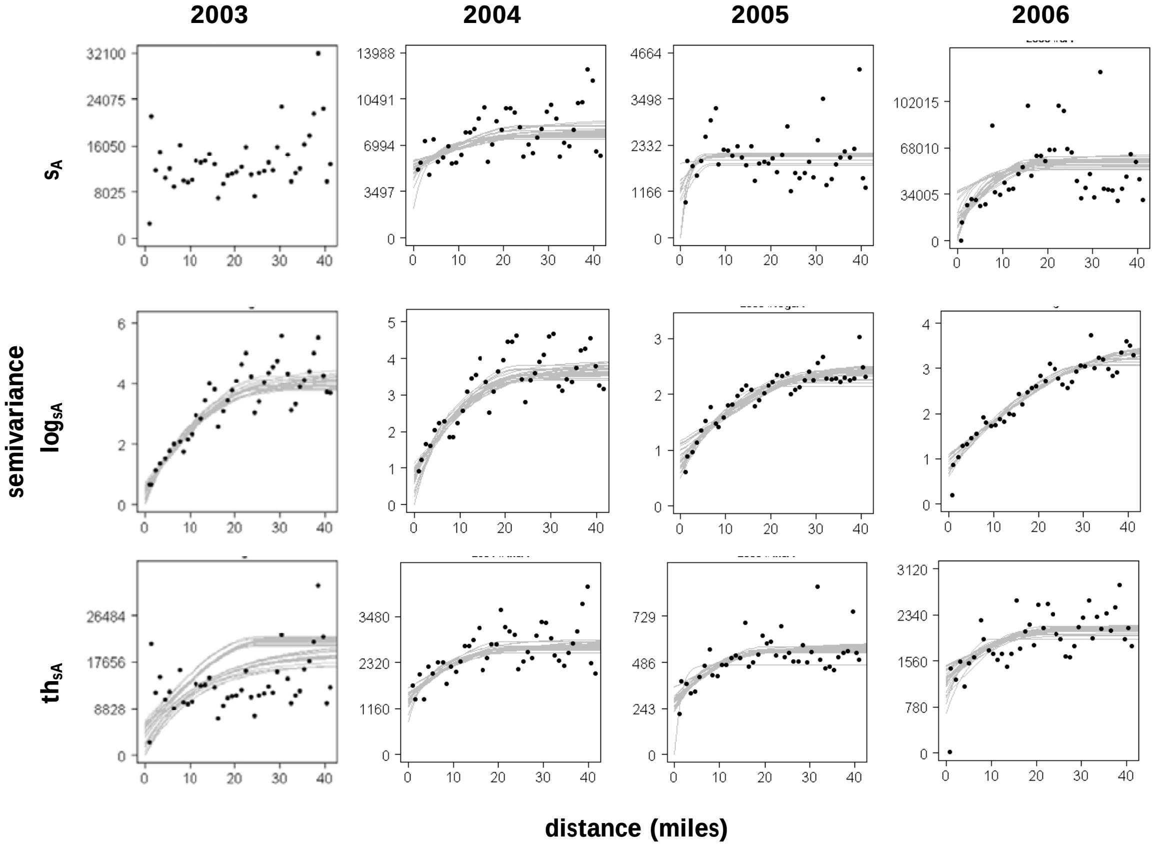


Figure 3.2. Experimental variograms (black dots) and fitted models (solid grey lines) for the anchovy density datasets. Note that every plot has different y-scales. s_A: untransformed, log_{sA}: log-transformed and th_{sA}: thresholded.

Results from ANOVA revealed that data transformation had significant effects on the three spatial parameters (Table 3.4). Sensitivity analysis showed that the percentage of deviance explained by data transformation varied widely depending on the parameter and the year, varying from 3 to 72 % of deviance explained for the practical range, from 66 to 99 % for the partial sill and from 18 to 87% for the nugget effect (Table 3.4). The type of model used had in some years a significant effect on the practical range and on the nugget effect. Specifically, the practical range estimated with a spherical model was significantly shorter than the practical range estimated with the exponential model in 2003 and 2006 while the nugget effect was significantly lower when estimated with the exponential model than the nugget estimated with the spherical model in 2003 and 2004 (Table 3.4). Regarding the lag width, it was only significant in the estimation of the practical range in 2003 and 2005, explaining in both cases about a 16 % of the deviance (Table 3.4). Finally, provided that least square methods are used, the specific type of least square method do not have significant effects on the estimated practical range, partial sill or nugget (Table 3.4).

Local abundance density maps

The mean predicted estimates of anchovy density in each grid cell, $\overline{z_E(x_i)}$, were used to produce maps of the spatial distribution of anchovy in the study area. European anchovy showed a patchy coastal distribution with preference for the areas in the surroundings of the Ebro River, generally very close to the river mouth or somewhat northwards (Figure 3.3). In the most southern area of the analysed region the density of anchovy was pretty much lower. A visual inspection of the maps reveal not great differences in local abundance density maps between data transformations the maximum difference observed in the year 2003 with the s_A dataset, where spatial distribution of anchovy seems to consist on isolated spots of density.

Table 3.4. Effects of methodological options on the estimated spatial structure parameters and sensitivity analysis: results of the analysis of variance (ANOVA), Tukey HSD tests for differences and deviance explained (%).

Parameter	year	Transf.			Model			Lag width			Fit method		
		F	P	Dev. expl	F	P	Dev. expl	F	P	Dev. expl	F	P	Dev. expl
Nug	2003	8.855	$3.42x10^{-04}$*** $th_{sA}<log_{sA}$; $th_{sA}=s_A;s_A=log_{sA}$	18.30	39.82	$1.5x10^{-08}$ *** Exp<Sph	33.48	0.457	0.767 ns -	2.23	1.221	0.308 ns -	4.46
	2004	161.5	<2x10-16*** $th_{sA}<log_{sA}<s_A$	73.55	5.807	0.018 Exp<Sph	4.79	1.464	0.218 ns -	4.79	1.175	0.322 ns -	3.02
	2005	285.2	$<2x10^{-16}$*** th_{sA}, $s_A<log_{sA}$	86.78	3.23	0.076 ns -	3.70	0.648	0.630 ns -	3.13	0.214	0.886 ns -	1.00
	2006	263	$<2x10^{-16}$*** $th_{sA}< s_A<log_{sA}$	81.81	2.336	0.129 ns -	90.51	1.54	0.195 ns -	5.12	0.077	0.973 ns -	< 1%
S	2003	4872	$<2x10^{-16}$*** $th_{sA}< s_A<log_{sA}$	99.21	0.488	0.487 ns -	< 1%	0.03	0.998 ns -	< 1%	0.003	1 ns -	< 1%
	2004	113.7	$<2x10^{-16}$*** $th_{sA}<s_A<log_{sA}$	66.13	2.766	0.099 ns -	2.31	0.268	0.898 ns -	< 1%	0.285	0.836 ns -	< 1%
	2005	837.7	$<210^{-16}$*** $th_{sA}<s_A<log_{sA}$	95.07	1.104	0.296 ns -	1.30	0.196	0.940 ns -	1.00	0.041	0.989 ns -	< 1%
	2006	661.5	$<2x10^{-16}$*** $th_{sA}<s_A,log_{sA}$	91.87	0.986	0.323 ns -	< 1%	0.603	0.661 ns -	2.10	0.023	0.995 ns -	< 1%
R	2003	4.743	0.011 ns $s_A<th_{sA},log_{sA}$	10.84	43.68	$4.13x10^{-09}$ *** Sph<Exp	35.60	3.683	$8.55x10^{-03}$ * all ns	16.24	0.577	0.632 ns -	2.20
	2004	1.814	0.168 ns -	3.03	5.807	0.018 ns -	2.48	1.283	0.281 ns -	4.31	1.283	0.281 ns -	4.06
	2005	114.1	$<2x10^{-16}$*** $s_A<th_{sA}<log_{sA}$	72.39	3.735	0.057 ns -	4.07	3.999	$5.08x10^{-03}$* 1nm<6nm	15.84	1.341	0.266 ns -	4.47
	2006	76.17	$<2x10^{-16}$*** s_A, $th_{sA}<log_{sA}$	56.56	21.19	$1.06x10^{-05}$ *** Sph<Exp	15.22	0.255	0.906 ns -	< 1%	0.043	0.988 ns -	< 1%

s_A: untransformed dataset; log_{sA}: log-transformed dataset; th_{sA}: thresholded dataset; r: practical range, S: partial sill, nug: nugget effect, F: Fisher value; P: probability level; ns non-significant; * significant at P<0.05; ** significant at P<0.01; *** significant at P<0.001. Significant differences in the Tukey HSD post-hoc tests are shown under the p-value.

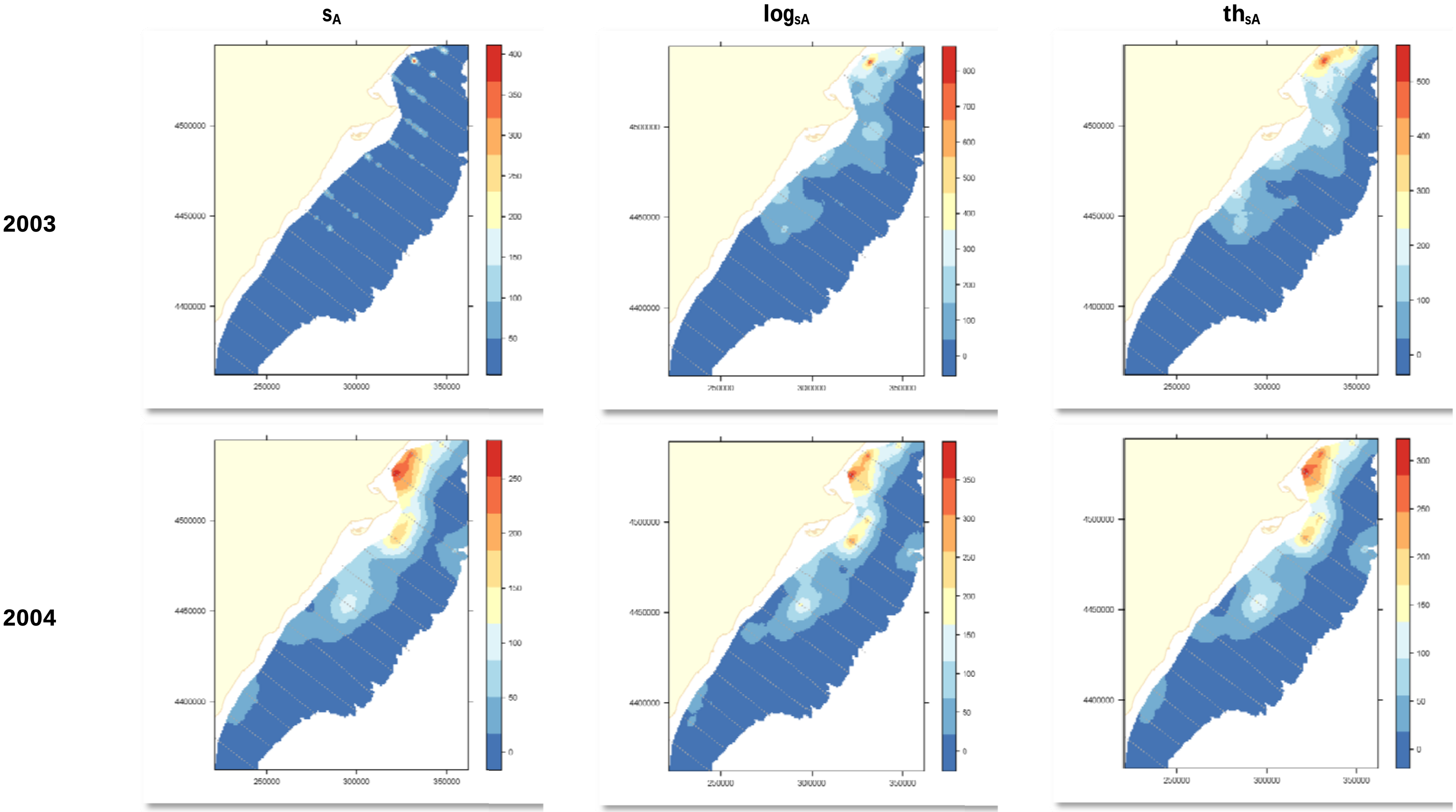


Figure 3.3. Spatial distribution of local mean anchovy density in the surroundings of the Ebro River in early winter in the period 2003-2006. Note that every plot has differing scales.

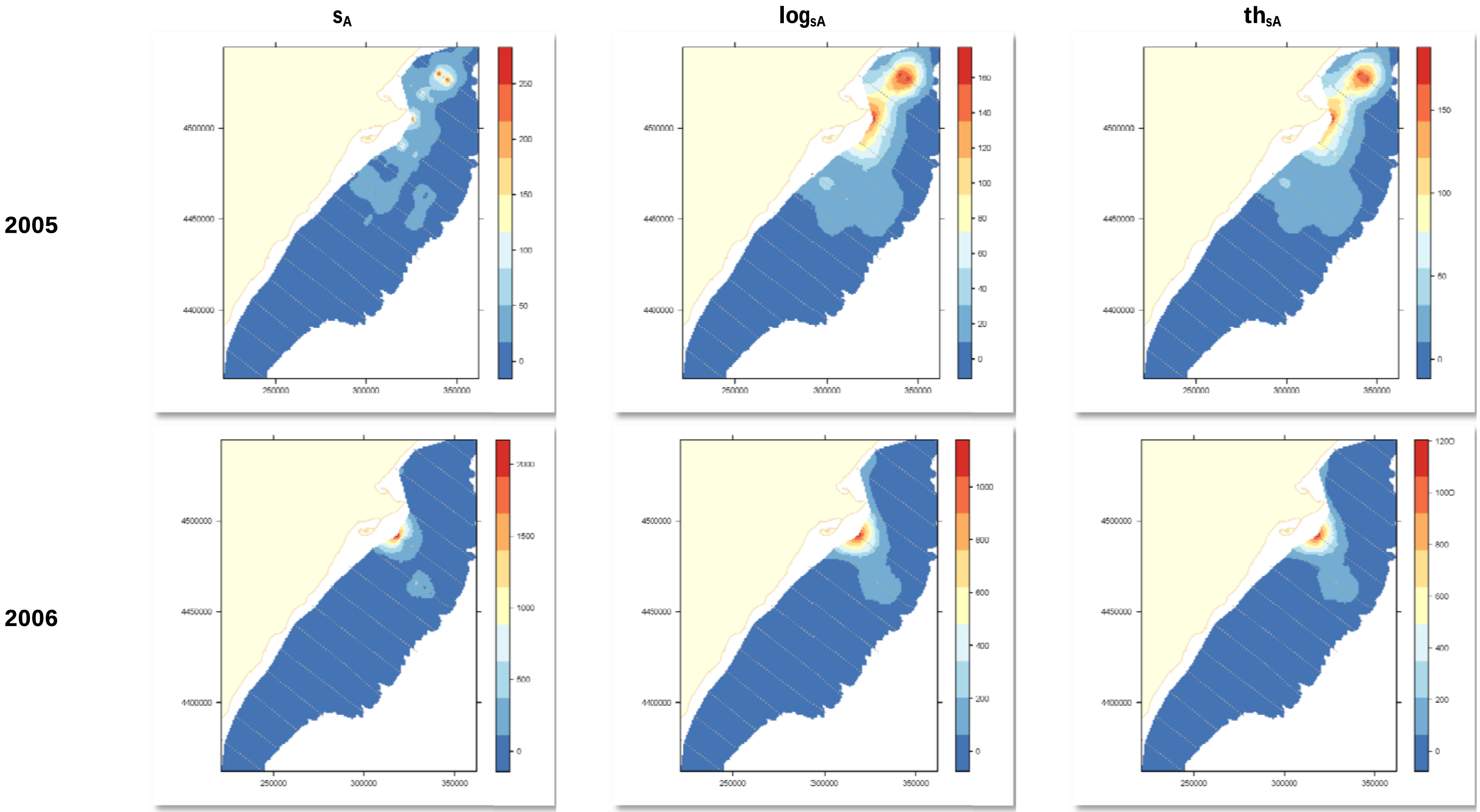


Figure 3.3 (continued). Spatial distribution of local mean anchovy density in the surroundings of the Ebro river in early winter in the period 2003-2006. Note that every plot has differing scales.

Global abundance and precision

A total of 408 kriging predictions were performed with varying amounts in the different years, depending on the amount of successful semivariogram fittings (Table 3.5). The abundance of anchovy in the analysed domain estimated by kriging (Q^*_{kri}) varied from the highest estimates in 2003 to the lowest estimates in 2005 (117,667.20 m^2 and 44,702 m^2, respectively; Table 3.5) while the other two years showed intermediate abundance values (Table 3.5). The robustness of abundance was very high both for the pooled datasets and for each dataset considered separately, with CV values always below 4% (Table 3.5).

Table 3.5. Global abundance of anchovy estimated by kriging interpolation (Q^*_{kri}), precision of the global abundance (CV_Q), robustness of the mean estimates (CV), bias of global abundance (in percentage) obtained by applying different methodological options.

			Q^*_{kri}			CV_Q	
Dataset	year	N	mean	CV	bias (%)	mean	CV
all	2003	81	113,629.60	0.8	-2.6	11.2	30.1
	2004	117	90,846.00	0.9	-2.5	12.0	29.7
	2005	90	44,702.00	0.4	0.5	12.7	40.0
	2006	120	99,209.60	2.8	-0.6	22.7	55.1
s_A	2003	1	117,667.20	NA	-1.2	13.8	NA
	2004	37	91,134.40	0.6	-2.4	13.1	7.5
	2005	10	44,702.00	0.3	0.5	16.1	5.5
	2006	40	100,074.80	3.8	-0.3	30.5	22.8
log_{sA}	2003	40	113,341.20	0.8	-2.7	13.9	16.9
	2004	40	90,269.20	1.0	-2.7	15.3	14.1
	2005	40	44,702.00	0.4	0.5	17.2	11.8
	2006	40	98,921.20	2.3	-0.7	31.6	6.9
th_{sA}	2003	40	113,629.60	0.6	-2.6	8.4	15.3
	2004	40	90,846.00	0.8	-2.5	7.6	11.8
	2005	40	44,702.00	0.5	0.5	7.3	12.1
	2006	40	98,632.80	1.5	-0.8	6.1	9.1

s_A: untransformed dataset; log_{sA}: log-transformed dataset; th_{sA}: thresholded dataset; N: number of successful fits.

The precision of the global abundance varied from around 6.1 to 31.6 %, depending on the year and on the data transformation (Table 3.5). The global precision estimated with the log_{sA} and with the s_A datasets were pretty similar while the estimation obtained with the th_{sA} was higher (Table 3.5). Regarding the robustness of the global abundance precision, it was generally non-robust when all the datasets were considered together, with values of CV ranging from 29.7 to 55.1% (Table 3.5). The robustness increased when the results were considered within each dataset, varying from highly to medium robustness for the three datasets with values between 5.5 and 22.8 % for the s_A dataset, between 6.9 and 16.9% for the log_{sA} and between 9.1 and 15.3% for the th_{sA} by dataset (Table 3.5). For the s_A dataset and in the year 2003, the robustness could not to be computed as long as merely one model was able to be fitted.

The bias varied from -2.7 to 0.5 % depending showing low departure from abundance estimated with the sample mean and it was slightly lower, in absolute value, for the s_A dataset than for the two transformed datasets (Table 3.5).

ANOVA and Tukey HSD analysis for the global abundance revealed that data transformation was significant in 2003 and 2004, but the dataset providing higher estimates was not consistent throughout the years (Table 3.6). The type of model was statistically significant for all the years, with higher estimates of abundance provide by the exponential model. The lag width was significant only in 2005, being significant only for two pairs of lag width, i.e. 1-8 and 3-1 (Table 3.6). Finally, the fit method was never significant on the global abundance estimates (Table 3.6).

Regarding the global precision, ANOVA and Tukey HSD showed that it was always affected by the data transformation used and by the model selected (Table 3.6). The global precision was always lower with the thresholded dataset and generally no differences were observed between s_A and $\log_{sA}$ besides 2004. The global precision was also lower with the spherical model than with the exponential model (Table 3.6). Conversely, it was never affected by the lag width or by the fit method applied, besides the lag width is between the EDSU and the inter-transect distance and the fit method is one least squares method. Furthermore, the variance explained by the lag width and the fit method was never high while for the transformation and the method used varied depending on the year, but in general the variance explained by data transformation was higher on the CV_Q and the variance explained by the model was higher on the case of Q^*_{kri} (Table 3.6).

Table 3.6. Effects of methodological options on the global abundance of anchovy (Q^*_{kri}) and on the precision of global abundance (CV_Q) and sensitivity analysis of both parameters: results of the analysis of variance (ANOVA), pos-hoc Tukey HSD tests for differences and deviance explained (%).

		Transf.			Model			Lag width			Fit method		
Parameter	Year	F	P	Dev. expl	F	P	Dev. expl	F	P	Dev. expl	F	P	Dev. expl
Q^*_{kri}	2003	16.05	1.45x10^{-06}*** th$_{sA}$,log$_{sA}$<s$_A$	29.16	105	3.68x10^{-16}*** Exp<Sph	57.06	0.101	0.982 ns -	< 1%	0.527	0.665 ns -	2.01
	2004	16.35	5.55x10^{-07} *** log$_{sA}$<th$_{sA}$,s$_A$	21.99	247.8	<2x10^{-16}*** Exp<Sph	67.93	0.098	0.983 ns -	< 1%	0.053	0.984 ns -	< 1%
	2005	0.289	0.750 ns -	< 1%	17.46	6.91x10^{-05}*** Exp<Sph	16.55	5.568	4.98x10^{-04}** 8nm<1nm; 3nm<1nm	20.76	1.954	0.127 ns	6.38
	2006	3.63	0.030 ns -	5.84	213.8	<2x10^{-16}*** Exp<Sph	64.43	0.636	0.638 ns -	2.16	0.073	0.974 ns -	< 1%
CV_Q	2003	87.53	<2x10^{-16}*** th$_{sA}$<s$_A$,log$_{sA}$	69.18	30.48	4.16x10^{-07}*** Sph<Exp	27.84	0.113	0.978 ns -	< 1%	0.006	0.999 ns -	< 1%
	2004	289.5	<2x10^{-16} *** th$_{sA}$<s$_A$<log$_{sA}$	83.31	17.01	6.98x10^{-05}*** Sph<Exp	12.70	0.057	0.994 ns -	< 1%	0.021	0.996 ns -	< 1%
	2005	456.9	<2x10^{-16}*** th$_{sA}$<s$_A$,log$_{sA}$	91.31	5.021	2.76x10^{-02}* Sph<Exp	5.40	0.225	0.924 ns -	1.05	0.059	0.981 ns -	< 1%
	2006	465.5	<2x10^{-16}*** th$_{sA}$<s$_A$,log$_{sA}$	88.84	7.498	7.14x10^{-03}* Sph<Exp	5.97	0.024	0.999 ns -	< 1%	0.001	1.000 ns -	< 1%

s$_A$: untransformed dataset; log$_{sA}$: log-transformed dataset; th$_{sA}$: thresholded dataset, F: Fisher value; P: probability level; ns non-significant; * significant at P<0.05; ** significatnt at P<0.01; *** significant at P<0.001. Significant differences in the Tukey HSD post-hoc tests are shown under the p-value.

Precision to varying sampling intensity

In order to follow a precautionary approach and due to the fact that computations were time consuming, the precision of the global abundance estimates to varying sampling intensities was performed only with the $\log_{sA}$ dataset as long as it was the dataset producing lower estimates of precision. The precision of global abundance decreases with increasing inter-transect distance and was generally good (<25%) for inter-transect distances up to 12 nm (Table 3.7). Conversely, for the year 2006 an inter-transect distance of 4 nm would have been needed to assure a good precision (Table 3.7).

Table 3.7. Survey design optimization for anchovy density: mean precision (*mean*) and robustness (*CV*) of the precision of the global mean abundance estimate (CV_Q) for different inter-transect distances (*a*).

	2003		2004		2005		2006	
a (nm)	mean	CV	mean	CV	mean	CV	mean	CV
1	5.8	6.44	6	7.79	6.7	3.66	13.9	8.24
4	7.2	7.52	8.5	7.64	10.0	4.87	20.3	4.53
12	22.7	21.23	23.6	16.45	24.9	17.14	47.5	14.02
16	31.1	19.05	29.8	19.59	32.3	16.92	61.0	17.92
20	39.1	23.52	38.7	18.08	40.7	18.87	81.9	15.49

3.4 Discussion

The present work aimed at analysing the spatial structure, the global abundance and precision of European anchovy in the Spanish Mediterranean continental shelf from late-autumn acoustic surveys in the period 2002 to 2006. The optimisation of the sampling design was evaluated through analysing the global precision at different inter-transect distances. To fulfil these goals, intrinsic geostatistics in two dimensions (I2D) were applied. However, the skewed pdf typical of anchovy density compromise the unbiasedness and the robustness of the estimations. Thus, the robustness of the estimations to changing several methodological options was as well analysed. In particular, the effects of, i) data transformation (log-transformation and thresholding of high values), ii) different lag-widths in experimental variogram construction, iii) the type of variogram model and iv) the fitting method used for variogram fitting were explored.

The logarithmic transformation smoothes the effects of high values and inflates the differences among low values (Guiblin *et al.*, 1995) but was unable to fully normalise anchovy density nor was the thresholding of high values. Regarding the th_{sA} dataset, the variance removed by dropping the high values artificially increased the precision of the global abundance, as this high values are recognised to be part of the population. Thus, whenever the main aim is estimating the precision of the global abundance, the use of the th_{sA} dataset should be disregarded.

The spatial distribution of anchovy showed clear autocorrelation with transformed datasets, observed at visual inspection of experimental variograms and in the 100% fitting success. This suggests that the spatial autocorrelation was masked in the original dataset by the high values (Carr *et al.*, 1985; Cressie, 1991;

Maravelias *et al.,* 1996). The fact that in the year with highest skeweness (i.e. 2006) no fitting failures occurred, suggest that, besides non-normality (Kerry and Oliver, 2007a), the location of the high values within the domain (Kerry and Oliver, 2007b) might have played a key role in this year. Furthermore, the amount of samples needed to obtain good-shaped variograms for hugely skewed data could be higher than the 100-150 samples recommended for normal data (Webster and Oliver, 1992), and even higher than the 300 used in our analysis but this issue has never been addressed. A high nugget effect may have further contributed to increase the number of samples required (Rufino *et al.,* 2006a). Notwithstanding, the application of log-transformation to not strictly log-normal data did not produce neither unrealistic results of the spatial structure nor less consistent to changing methodological options than removing outliers, in contrast with previous works (Webster and Oliver, 2001; Rufino *et al.,* 2005).

Given that the length of fish schools is around 20 m (e.g. Iglesias *et al.,* 2003; D'Elia *et al.,* 2009) and that the minimum distance between samples (EDSU) is 1 mile, the analysed spatial autocorrelation will account for clusters of fish schools (Giannoulaki *et al.,* 2006). In our area, anchovy density showed a practical range generally above 20 nm, which is a bit higher to estimates obtained for the same species in Greek waters (Giannoulaki *et al.,* 2006). The $\log_{sA}$ dataset provided the higher estimates of practical range while the s_A dataset provided the lowest, in opposition to Rufino *et al.,* (2005). This could be related to the degree of skewness and to the particular sampling design. Nevertheless, for log-Gaussian data overestimation of the range was observed when least squares fitting methods are used with the classical variogram estimator (Rufino *et al.,* 2006a). Thus, in the present work, with data far more skewed than log-Gaussian, the possible overestimation of the range by the $\log_{sA}$ dataset and its intensity would be assessed with a simulation study which was outside the scope of the present work.

Concerning the variance parameters, i.e. sill, nugget and total sill (sill+nugget), the highest estimates were obtained with the $\log_{sA}$ dataset while the lowest estimates were for the th_{sA} dastaset. The traditional variogram estimator without any transformation *a priori* provides more accurate (i.e. less biased) estimates of the spatial structure than any transformation (Rufino *et al.,* 2005). Assuming that this is the actual situation in our analysis and as long as the $\log_{sA}$ dataset provides higher variance estimates than the s_A dataset, again the $\log_{sA}$ dataset would provide overestimated variance.

The *spatial structure* was *non-robust* to data transformations, the most sensible (lest robust) spatial parameter was subjected to dataset and year. By dataset, the spatial structure was generally less robust for the s_A dataset (non-robust) than for the transformed datasets (medium to high robustness). The range was the least robust parameter for the th_{sA}, in line with Rufino *et al.* (2006b). For the s_A and the $\log_{sA}$ datasets, the least robust parameter was either the nugget or the range. Thus, determining which parameter would be more sensible and needs more attention in the fitting procedure is *a priori* difficult and would require an extensive simulation study with wide range of data types and spatial configurations.

Between the tested methodological options, data transformation generally had significant effects on the spatial parameters, the model type was occasionally significant on the practical range and on the nugget effect, the lag width was significant only on the practical range in some years and the fit method never had significant effects on the spatial parameters. *A priori* selected methodological options, i.e. the use of only two types of models (spherical and exponential), only one family of automatic fitting methods (least squares methods and avoiding likelihood methods) and lag widths between the EDSU and the inter-transect distance, may have reduced the effects that these sort of methodological options would have had on the results. However, the methodological options were selected so that nonsensical results were not incorporated in the analysis, e.g. likelihood fitting methods produced unreasonable results, similar to previous studies that were working positively skewed data (Cressie, 1991; Rufino *et al.,* 2006a) and were excluded.

The spatial structure was subsequently used to produce *annual maps* of anchovy density for the first time in the study area. The spatial distribution of anchovy was pretty patchy, with wide areas of very low density neighbouring small areas with pretty high densities. The highest densities of anchovy were commonly located in the vicinity of the Ebro river mouth, in depths shallower than 100 m, in an area of about 48 nm^2 (<2% of the study area). This area is a well known anchovy spawning region (García and Palomera, 1996; Abad *et al.,* 1998). By the time of the year the survey is conducted, i.e. late autumn-early winter, recruits constitute the bulk of anchovy population in the area (IEO unpublished data; Abad *et al.,* 1998). The high values encountered in the vicinity of the Ebro River are thought to be related to the presence of small recruits' schools. Assuming that, like mackerel or herring, anchovy prefer gathering in schools of individuals of similar length (Pitcher *et al.,* 1985) and that the distance between neighbouring individuals depends on fish length, a school of smaller fish would exhibit higher density than a school of bigger individuals (Iglesias *et al.,* 2003). The protection of this small area (~48 nm^2) by means of a MPA or a temporal closure would have potential significantly positive effects on the anchovy population in the area.

On a following step, the spatial structure was used to estimate the *abundance of anchovy* estimates in the whole study area given the present sampling design. Abundance of anchovy suffers a reduction from 117,667 m^2 to 44,702 m^2 in three years growing up to 100,074.80 m^2 in 2006. Abundance estimates were robust to all tested methodological options. This is in accordance to background knowledge, as kriging estimates are considered almost unaffected by methodological options when the variogram fits adequately the sample data (Cressie, 1991). ANOVA analysis revealed that anchovy abundance was sometimes significantly affected by the model type or data transformation and it was seldom significantly affected by the fitting method and by the lag width. These seem to be opposed to the analysis of the robustness but, in fact, it suggests that, despite being statistically significant, the amount of variance introduced by methodological options on global abundance was acceptable in terms of stock assessment. As already stated when discussing the results of ANOVA on the spatial structure, the methodological options selected *a priori* may have reduced the observed effects on the results.

The *precision of global abundance estimates* was usually below 17%, indicative of adequate suitability of the actual sampling design to estimating the global abundance of anchovy in the area. Only in 2006, the year with the highest skewness the precision is compromised. These results are in accordance with the previous work that applied a simpler statistical method, i.e. transitive geostatistics in one dimension (T1D), to the same data (Tugores *et al.,* 2010). This suggests that T1D although more simple are more easily available and provide good enough results. The precision in 2006 remained good for the th_{sA} suggesting that the survey design in 2006 was well suited for a small fraction of the anchovy population as long as the high values removed constitute a significant amount of the population in the area (although being a small amount of samples). Furthermore, the log_{sA}

dataset produced worse estimates of global precision (i.e. higher *CV*) than the s_A dataset or the th_{sA} dataset, consistent with the higher variance estimated by the log_{sA} dataset. Hence, although log_{sA} could overestimate the variance and the *CV* (thus underestating the precision) the real precision would be better than the one estimated by the log_{sA} while ensuring the retrieval of a sound spatial structure.

The *global precision* was *not robust to data transformation* but showed high or medium robustness within datasets. Kriging variance is robust to the variogram fitting for the spherical model unless understatement of the nugget effect (Brooker, 1986). Up the authors' knowledge, the robustness of the precision of global abundance to changing methodological options has never been addressed. Data transformation and model type had significant effects on the estimate precision while lag width and fit method did not. As expected by the lower estimates of total sill, the precision was higher (lower *CV*) for the th_{sA} dataset.

In the years with lower skewness (although high), i.e. 2004 and 2005, the global abundance and precision were lower for the s_A dataset than for the other datasets, suggesting that ordinary kriging produced more robust estimates than the log_{sA} or the th_{sA} for highly skewed data (skewness ≤ 7). For the higher values of skewness the retrieval of a spatial structure with the s_A dataset was highly compromised or becomes non-robust for the s_A and the log_{sA} datasets. The bias of the global abundance, however, is always slightly lower for the s_A dataset than for the other two datasets. Our findings support that the traditional variogram estimator without any transformation *a priori* provides more accurate (i.e. less biased) estimates of the spatial structure than any transformation (Rufino *et al.*, 2005), as long as the global abundance estimates obtained with the untransformed dataset (s_A) showed the lowest bias. Further, results suggest that, whenever possible the use of the s_A dataset provide more robust results as well.

The bias observed in anchovy abundance estimates was generally negative (i.e. global abundance from kriging higher than the estimated by the samples), in opposition to a previous study with moderately skewed distributions (Roth, 1998). However, the bias in absolute value was never high provided that the interpolation was performed on the untransformed dataset. Interpolation on the transformed datasets was not included in the present work due to high negative bias in global abundance estimations. The abundance of anchovy estimated by means of the s_A dataset was slightly higher and less biased than the estimates of the log_{sA} dataset. This could be explained by the fact that when used with skewed datasets, ordinary kriging when performed with the spatial structure estimated with the sA datataset (no transformation) produce more accurate estimates of the high values while when the ordinary kriging is performed with the spatial structure estimated with the log_{sA} dataset (logarithmic transformation) was more effectively reproducing the low or medium values. This in the line with what Kishné *et al.* (2003) observed for log-normal kriging (i.e. kriging in the logarithmic scale). Thus, the log_{sA} dataset would tend to underestimate the high values that have a huge influence of the overall mean thus producing lower estimates than the s_A dataset, and even smaller than the sample mean.

Finally, the effects of the application of *different sampling intensities* on the global precision was analysed to ascertain the possibility of sampling design optimisation, spending a smaller amount of time to survey the area while not compromising the precision of the global abundance estimates. An increase of the inter-transect distance from 8 up to 12 nm would not imply a huge decrease in precision, i.e. from about 17 % to around 22-25%, while reducing the amount of transects performed in the area (from 14 to 9) implying a reduction of about 100-

150 nm less of acoustic prospection. In 2006, however, the precision with 12 nm would be remarkably high although the additional survey time could be used to increase the sampling intensity in the area of the high values, for instance, with the incorporation of 5 additional transects at 4 nm inter-transect distance representing an increase of the precision to about 20% which is similar to that of the other years. Thus, increasing the sampling intensity in the area where the high values are encountered, i.e. the surroundings of the Ebro River and shallower than 100 m deep, would be advisable in order to increase the precision of abundance estimates in the years with highest abundances. Thus, the spatial location of the high values may provide useful information for survey design as well as about biological or ecological aspects of the stock itself.

To summarise, the I2D methods allow obtaining distribution maps of the species which is usually of interest for environmental and resources management and planning, e.g. to determine marine protection areas, which was not addressed in a previous work (Tugores *et al.*, 2010). The present work is the first time that maps of the anchovy population in the area are produced which, beside stock assessment could be of interest for other areas of knowledge, such as ecological interaction with other species. However, for non-normal data the analysis of the spatial structure to obtain estimates of global precision and survey design optimisation should be taken with care and cannot be based on a blind automatic procedure, requiring the application of expert criteria.

Accurate and precise estimates of abundance of many exploited and non-exploited species are required for the development of management strategies able to ensure the sustainability of the population. This is achieved with the present configuration of sampling design. A systematic survey design with a geostatistical variance estimator, like the one presented in this work, is considered the best strategy when the main aim is to obtain the most precise estimator of abundance although being aware that a stratified random survey with a pooled variance estimator would have provided better estimates of the variance of the abundance estimator (Simmonds and Fryer, 1996).

When analysing the spatial distribution of positively skewed data pdf by means of I2D geostatistics, not great attention need to be paid regarding the fitting method and the lag width provided that the fitting method is a least squared method and the lag width is between the EDSU and the inter-transect distance. Contrarily, great attention need to be paid to data transformation when one main goal is to estimate the sample variance and the precision of the global abundance, as data transformation generally had significant effects on the results. Working with the original untransformed dataset is preferred however for hugely skewed datasets (skewness>7) variogram fitting is hugely compromised and its estimation and fitting may become impossible. In that case and in order to try to make comparable estimates of variance for all the years, the lest worse option may be that of estimating the variance with the logarithmic transformation as long as it ensures the finding of a sound spatial structure while being sure that the variance is not understated and thus, the precision is not overestimated. The robustness of the spatial structure is difficult to be assessed a priori as long as it varied greatly depending on the analysed parameter and on the particular year.

Section II. Environmental variables and habitat

Chapter 4. Identifying the potential habitat of sardine (*Sardina pilchardus*) spawners and sardine eggs in the Mediterranean Sea

Chapter 4. Identifying the potential habitat of sardine (*Sardina pilchardus*) spawners and sardine eggs in the Mediterranean Sea

4.1 Introduction

Small pelagic fish, like sardines and anchovies, play a key ecological role in coastal ecosystems (Cury *et al.,* 2000) and, in the Mediterranean Sea, constitute the bulk of small pelagic fish catches. Many aspects of their life history (e.g. spawning, recruitment, development or population abundance and distribution) depend greatly on the environment (Bakun, 1996). In the Mediterranean, the European sardine (*Sardina pilchardus*) suffers a high degree of exploitation, often exceeding sustainability levels (Study Group on Mediterranean Fisheries, SGMED 2009, 2010), with many of the European Mediterranean sardine stocks exhibiting declining biomass trends in the period 2006-2009. Thus, the need of examining the relationship between the different aspects of their life cycle and the environmental conditions turn out to be crucial.

In the Mediterranean, sardine is fished by purse seiners mainly in spring-summer and, in the Adriatic Sea and in the French coastal waters, by mid-water pelagic trawls (Lleonart and Maynou 2003; Machias *et al.,* 2008), both relying on the spatial detection of major sardine aggregations by means of echosounders. According to FAO statistics, in the period 2000-2012 about half (40-60%) of the Mediterranean sardine landings are attributed to EU countries, the other half of the landings come from African countries (FAO, 1990-2015). For that same period, Spain was the country with higher contributions (31%) to EU sardine landings.

The present work takes advantage of acoustic surveys that were being regularly held in the Spanish Mediterranean waters in late autumn (mid November-mid December) for the monitoring of small pelagic fish stocks beyond the standard stock assessment purposes (Koslow, 2009). As European sardine is a winter spawner (Olivar *et al.,* 2001, 2003; Ganias *et al.,* 2007) the study period will reflect the spawning grounds of the fully recruited population that has been, more or less intensively, exploited through the fishing season and mainly coincides with the species' spawning season.

Habitat suitability modelling studies have flourished due to the increasing interest in assessing the effects of climate change on fisheries (e.g. Guisan and Zimmermann, 2000; Francis *et al.,* 2005; Weber and McClatchie, 2010), species' spatial distribution (Sabatés *et al.,* 2006) and species replacements (Montero-Serra *et al.,* 2015). Habitat suitability modelling relates environmental variables to the likelihood of occurrence of a species (Hirzel and Le Lay, 2008) and provides information about temporal changes in habitat suitability, which is essential for ecological studies, for monitoring the population status and for the implementation of effective fisheries management and conservation planning. The statistical modelling techniques that applied in the current work, i.e. Generalised Additive Models (GAMs), are being widely used in habitat suitability modelling in order to answer questions on temporal habitat dynamics (Osborne and Suarez-Seoane, 2007), regional variation in habitat preferences (e.g. Planque *et al.,* 2007; Bellido *et al.,* 2008; Giannoulaki *et al.,* 2008; Tugores *et al.,* 2011) or spatially predict climate change impacts (Trivedi *et al.,* 2008).

Identifying the potential habitat of a species implies determining the combination of those environmental conditions that enable the species survival (Guisan and Zimmermann, 2000; Planque *et al.,* 2007), however in the absence of biotic interactions like competition or predation (Austin, 2002). Nevertheless, at coarse resolutions, the distribution can be approximately recovered using only information about the environmental factors and ignoring the biotic interactions (Soberón, 2010). Knowing that meso-scale and large scale spatial distribution of sardine is driven by environmental forcing (e.g. Planque *et al.*, 2007; Stratoudakis *et al.,* 2006; Bernal *et al.,* 2007), the aim of the present work is to build a simple, robust and effective habitat model that describe the environmental conditions that are suitable for the presence of sardine spawners and sardine eggs in the Spanish Mediterranean and in the whole Mediterranean Sea in late autumn. We planned to identify the environmental parameters that affect the distribution and search for consistent patterns between the meso- or large scale aggregations of sardine (i.e. exceeding the size of several nautical miles) and the environment.

Within the current work, environmental data was used to model sardine spawners' and sardine eggs' habitat in order to (1) describe the environmental conditions that favour the presence of sardine spawners (and sardine eggs) in the Spanish Mediterranean waters in mid November-mid December (late autumn), (2) identify the areas with favourable environmental conditions for sardine spawners and sardine eggs throughout the Mediterranean, (3) describe the temporal variability of the suitable habitat in different areas of the Mediterranean, (4) analyse habitat suitability in terms of high probability and temporal persistence in the time series and (5) investigate the spatial overlap between the potential habitat of sardine spawners and sardine eggs in the same period. Finally, we analysed possible relationships between sardine potential habitat of sardine spawners and sardine landings in the Spanish waters and in the Mediterranean to explore their adequacy as spatial indicator, useful to identify the potential stock habitat under climate forcing (Barange *et al.,* 2009). This is of special importance for the Mediterranean basin as long as it is between the most affected regions by the ongoing warming trend (Lejeusne *et al.,* 2009).

4.2 Materials and Methods

Study area and data collection

The study area comprised the continental shelf of the Spanish Mediterranean waters (Western Mediterranean), between the Strait of Gibraltar and the Spanish-French border (see section 1.2, Figure 1.1). Sardine presence/absence data (2003-2009) derived from ECOMED acoustic surveys were used to model and evaluate the **potential spawning habitat (PSH)** of sardine, defined as the habitat occupied by sardine spawners during the spawning season. Presence/absence data was analysed at each acoustically prospected nautical mile. Acoustic data collection and processing as well as acoustic sampling scheme are thoroughly explained in the General Introduction (section 1.4). In addition, sardine egg data (2006-2009) collected during the same acoustic surveys were used to model the **realised spawning habitat (RSH)** of sardine, i.e. the habitat where eggs have been effectively released. Bottom depth and satellite environmental data were used in order to describe and predict the occurrence of sardine spawners and sardine eggs.

Eggs sampling

Simultaneously to the Spanish Mediterranean acoustic surveys, fish eggs were collected using an on board installed Continuous Underway Fish Egg Sampler (CUFES) and starting in 2006. Sampling scheme followed the same transect scheme previously mentioned for the acoustic surveys, samples taken from 5 m below the sea surface and integrated every 3 nm. Further details regarding egg sample collection and storage can be found in Tugores *et al.,* (2011). In the Western Mediterranean, the vertical distribution of sardine eggs is known to occur from the sea surface until 50 m deep, with the highest abundance (44%) in the upper 10 m of the water column (Olivar *et al.,* 2001). Thus, it is considered that the major centres of sardine spawning were adequately sampled for what refers to obtaining good presence-absence estimates of sardine eggs (Lynn, 2003). Estimates of eggs' abundance cannot be derived from this type of egg sampling alone.

Environmental data

Satellite environmental and bottom depth data were used as explanatory variables in the modelling process. Specifically, sea surface temperature (SST), sea surface chlorophyll concentration (CHLA), photosynthetically active radiation (PAR), sea surface salinity (SSS) and sea level anomaly (SLA) were downloaded from the respective databases (Table 4.1). Bottom depth was derived from a blending of depth soundings collected from ships with detailed gravity anomaly information obtained from the Geosat and ERS-1 satellite altimetry missions (Smith and Sandwell, 1997). These environmental variables are considered important either as a direct influence on the distribution of sardine spawners (or eggs) or as a proxy for causal factors (Bellido *et al.,* 2001). Topographic variables potentially summarize important surrogate predictor variables not captured by the available satellite variables. Monthly-averaged satellite data were processed to obtain the value of the environmental parameters at each sampling point (Valavanis *et al.,* 2004).

Table 4.1. Environmental satellite parameters and their characteristics.

Parameter	Units	Sensor/Model	Spatial resolution	Source
Sea surface chlorophyll-a (CHLA)	mg m^{-3}	MODISA	4 km	oceancolor.gsfc.nasa.gov
Sea Surface Temperature (SST)	°C	AVHRR	1.5km	eoweb.dlr.de:8080
Photosynthetic Active Radiation (PAR)	Einstein m^{-2} day^{-1}	SeaWiFS	9 km	oceancolor.gsfc.nasa.gov
Sea Level Anomaly (SLA)	cm	Merged Jason-1, Envisat, ERS-2, GFO, T/P	0.25° *	www.jason.oceanobs.com
Sea Surface Salinity (SSS)	psu	NOAA NCEP EMC CMB GODAS model (Behringer and Xue, 2004)	0.5° *	iridl.ldeo.columbia.edu

* interpolated to 1.5 km using ArcInfo

Model estimation

Generalized Additive Models (GAMs) were used in order to define the set of the environmental variables that describe the potential spawning habitat (PSH) and the realised spawning habitat (RSH) of sardine in the Spanish Mediterranean waters during the species spawning season. GAMs are widely used in habitat suitability modelling and spatial prediction because of their high accuracy (Franklin, 2009) and capability of modelling non-linearities by using non-parametric smoothers (Hastie and Tibshirani, 1990; Wood, 2006).

Data from the different years were pooled in order to grasp the temporal variability in the PSH and RSH of sardine, obtain more possible observed conditions and ensure potentiality (ICES 2005; Planque *et al.*, 2007; Giannoulaki *et al.*, 2008). In particular, data from 2004 to 2008 from acoustic sampling was used to model PSH of sardine whereas the modelling of the RSH implied the usage of egg distribution data from 2006 to 2008.

As response variable (y), we used the presence/absence of sardine spawners or sardine eggs and as independent variables (x covariates), we used the cube root of the bottom depth, the natural logarithm of CHLA, SST, SLA and PAR. The binomial error distribution with the logit link function was used and the natural cubic spline smoother (Hastie and Tibshirani, 1990) was applied for independent variables smoothing and GAM fitting. A final model was built by testing all variables that were considered biologically meaningful and statistically significant, starting from a simple initial model with one explanatory variable.

Each model fit was analysed regarding the level of deviance explained (0–100%; the higher the percentage, the more deviance explained), the Akaike's Information Criterion (AIC, the lower the better) and the confidence region for the fit (which should not include zero throughout the range of the predictor). The AIC reduces the collinearity problem in the independent variables (Sacau *et al.*, 2005).

The degree of smoothing was chosen based on the observed data and the Generalized Cross Validation (GCV) method suggested by Wood (2006). Following the selection of the main effects of the model, all first order interactions of the main effects were tested (Wood, 2006). The GCV method is known to over-fit, therefore and in order to simplify the interpretation of the results, the maximum degrees of freedom (measured as number of knots k) allowed to the smoothing functions were limited to the main effects at k=4 and for the first order interaction effects tested at k=20. Validation graphs (e.g. residuals versus fitted values, QQ-plots and residuals versus the original explanatory variables) were plotted in order to detect the existence of any pattern and possible model misspecification.

Spatial autocorrelation in the sampled data artificially increases the significance of the models but GAMs are not that much influenced by the effect of autocorrelation compared to other methodologies like GLMs (Segurado *et al.*, 2006). Model residuals were inspected and no spatial autocorrelation was observed at the analysed scale. Further, in order to avoid as much as possible this effect, Type I error rate was adjusted by using a conservative significance level, i.e. 1% rather than the usual 5% (Fortin and Dale, 2005).

Model validation

In a subsequent step, the final selected model was used to predict the probability of finding adequate PSH and RSH in the Spanish waters at 1x1 Km grid. The model predictive performance was tested and evaluated by means of the

Receiver Operating Characteristic curve (ROC) (Hanley and McNeil, 1982; Guisan and Zimmerman, 2000) and the AUC (Area Under the ROC) metric, a threshold-independent metric, widely used in the species' distribution modelling (Franklin, 2009; Weber and McClatchie, 2010). Moreover, the ability of the model to predict a presence given that a species actually occurs at a location, i.e. sensitivity, and the ability of the model to predict and absence when a species does not occur, i.e. specificity, were used for model evaluation (Lobo *et al.*, 2008). They were measured for two threshold criteria, the maximization of the specificity-sensitivity sum (MDT) and the prevalence values (Jiménez-Valverde *et al.*, 2008; Lobo *et al.*, 2008).

The AUC values range from 0 to 1, where a score of 1 indicates perfect discrimination and a score of 0.5 implies predictive ability that is no better than a random guess (Boyce *et al.*, 2002; Elith *et al.*, 2006). AUC values of 0.7-0.9 are considered moderate and >0.9 high model performance (Elith *et al.*, 2006; Franklin, 2009). AUC, sensitivity and specificity metrics were estimated for the years included in the models and, additionally, for data not included in the model construction, i.e. the Spanish acoustic survey in 2003 and 2009.

Annual potential habitat and habitat suitability

Selected models were used to predict the probability of encountering PSH (and RSH) of sardine for each year over a 4 km cells grid covering the entire Mediterranean basin. This implied that for PSH, although the model was fitted and validated at a finer resolution (1.5 km) it was mapped at a coarser grid (about 2.5 times coarser). The error was considered minimum since the available satellite data derived from a single optimum resolution (see Table 4.1) that minimizes the interpolation error and practically provides very similar values for the variables at any particular point in space for the two grids. This was considered a reasonable trade-off between the patterns identified by the model and the required computer power to map the resulted probabilities at the scale of the Mediterranean Sea. Thus, annual maps of the PSH and RSH during the species spawning season were produced for the entire Mediterranean for a seven-year period (2003-2009).

Habitat suitability was defined according to the mean and the variability of the PSH (and RSH). Thus, for the seven years annual potential habitat maps, the mean and the coefficient of variation (cv) were estimated at each grid cell. While the mean indicates the level of probability of occurrence of habitat over the time series, the cv indicates the temporal variability/stability of the habitat over time, so that high cv will imply variable habitat while low cv will imply more stability. Assuming that areas with higher probabilities of being an adequate habitat and lower temporal variability are more likely to contribute to the subsistence of a species, we defined habitat suitability as follows:

a) **Persistent hotspot**: high average probability (> 0.75) and low temporal variation (cv<0.50)
b) **Persistent preferred habitat**: intermediate average probability (>0.50 and <0.75) and low temporal variation (cv<0.50)
c) **Occasionally preferred habitat**: intermediate average probability (>0.50 and <0.75) and high temporal variability (cv>0.50) and
d) **Unfavourable habitat**: low average probability (<0.50).

Habitat suitability maps were produced for the entire Mediterranean basin.

Temporal synchrony among adjacent areas

For every annual potential habitat map, the mean habitat prediction was estimated at each Mediterranean Geographical Subareas (GSAs; Figure 4.2). A yearly-time series, consisting of the mean probability of finding adequate habitat of sardine spawners and sardine eggs, were then constructed for each GSA. The Pearson's correlation coefficient (Pearson, 1895) and its significance test were calculated between the time series of each GSA. Temporal synchrony among adjacent areas would imply that the mean habitat prediction in two contiguous GSAs increase and decrease concurrently in the yearly time series.

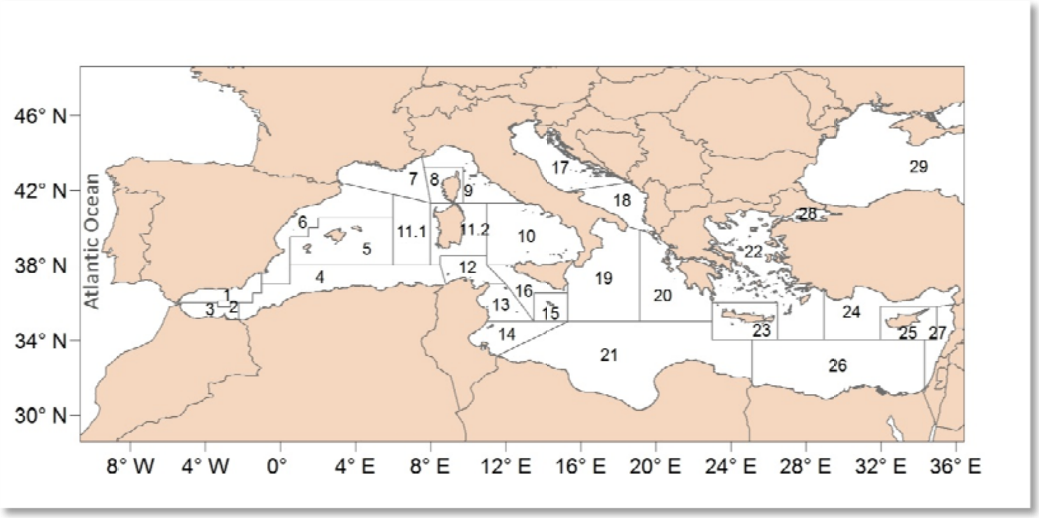


Figure 4.2. Geographical Sub-Areas (GSAs) defined by the General Fisheries Commision for the Mediterranean Sea for management purposes (Resolution GFCM/33/2009/2; GFCM, 2009) and classified by FAO subareas. In the Western Mediterranean: 1: Northern Alboran Sea; 2: Alboran Island; 3: Southern Alboran Sea; 4: Algeria; 5: Balearic Island; 6: Northern Spain; 7: Gulf of Lions; 8: Corsica Island; 9: Ligurian and North Tyrrhenian Sea; 10: South and Central Tyrrhenian Sea; 111: Sardinia (west); 112: Sardinia (east); 12: Northern Tunisia. In the Central Mediterranean: 13: Gulf of Hammamet; 14: Gulf of Gabes; 15: Malta Island; 16: South of Sicily; 17: Northern Adriatic; 18: Southern Adriatic; 19: Western Ionian; 20: Eastern Ionian Sea; 21: Southern Ionian Sea. In the Eastern Mediterranean: 22: Aegean Sea; 23: Crete Island; 24: North Levant; 25: Cyprus Island; 26: South Levant; 27: Levant. Black Sea: 28: Marmara Sea; 29: Black Sea; 30: Azov Sea.

Persistence of the habitat overlap among life-stages

The overlap between the habitat of sardine life-stages (i.e. spawners and eggs) is interesting in order to identify key areas for management purposes, as long as the protection of the overlapping areas will imply the protection of two life-stages during the species spawning season. If the habitat overlap is persistent in time, this would mean that those areas are rather stable and that do not need to be frequently re-assessed. Thus, the persistence of habitat overlap was assessed for the seven years time series (2003-2009) of predicted PSH and RSH comprising the entire Mediterranean basin.

First, habitat overlap among life stages was analysed for two habitat levels, i.e. the preferred habitat and the hotspot habitat. For every year, a binomial variable was constructed by giving a 1 when the habitat of both life stages was above a particular probability level (i.e. 0.50 for the preferred habitat and 0.75 for the hotspot habitat) and 0 otherwise. Then, the persistence was calculated as the

% of years for which a particular grid cell was rated as 1 for the two habitat overlap levels. Persistence was graded as high (> 75% of the years; 6-7 years), intermediate (>50% of the years; 4-5 years) and low (<50% of the years; 1-3 years). Maps showing the persistence of the habitat overlap between sardine spawners and eggs were produced for the whole Mediterranean Sea.

Sardine spawning habitat, fisheries landings and biological indicators

The relationship between the yearly time series of PSH and RSH in late autumn and sardine landings were analysed at the Mediterranean basin level and in the Spanish waters for the period 2003-2009. Sardine fisheries catch data were obtained from the Food and Agriculture Organisation (FAO, 1990-2015). Furthermore, somatic condition, i.e. condition factor (K_{rel}), and biomass of sardine in the Gulf of Lions from summer acoustic surveys (Van Beveren *et al.*, 2014) were retrieved in order to assess possible relationships with sardine landings and with PSH and RSH of sardine in the Spanish Mediterranean waters. The existence of relationship between both would re-enforce the idea of connexion or temporal synchrony between sardine populations (or at least their spawning) in both areas. For this, the Pearson correlation coefficient was computed and tested for its significance.

All statistical analysis, i.e. model construction, validation, annual predictions of the potential habitat and temporal correlations, was produced within the R statistical programming language (R Development Core Team, 2009). Specifically, model construction was done using the “mgcv” library, the metrics used for model validation were estimated using the “PresenceAbsence” library (Freeman and Moisen, 2008). Graphical representation of the results in the form of maps was produced by means of ArcGis 9.x program.

4.3 Results

Data description

The amount of samples in the surveys varied between 725 and 1291 for the acoustic data and between 212 and 343 for CUFES data, depending on the year (Table 4.2). Regarding sardine spawners, positive samples ranged from 31.5 to 61.5 % (Table 4.2), increasing between 2003 and 2005 and then show progressive increases and decreases in the consecutive years. The presence of sardine eggs increased from 2006 to 2007 and then showed a drastic reduction and a slight increase in 2009, although the amount of positive egg stations remained very low (Table 4.2). Regarding satellite environmental data, the years 2003 and 2004 showed wider ranges of SLA, from 2005 to 2007 the SLA range get narrower with higher minimum values and lower maximum values, increasing again the SLA range in 2008 and 2009 (Table 4.2). The lowest SLA value was observed in 2008 and the highest in 2004 while 2009 was outstanding as long as, opposed to the other years in the time series, the minimum value was positive (Table 4.2). Regarding temperature, the year 2006 was especially hot, showing the highest minimum and maximum values while 2008 showed the lowest temperatures in the time series (Table 4.2). CHLA values showed the highest minimum value in 2006 while the highest maximum values were observed in 2008 (Table 4.2).

Table 4.2. Amount of samples (N) and number of positive samples (N+) for sardine spawners and eggs.

	Acoustic	CUFES	Spawners	Eggs	SLADEC (cm)		SSTDEC (°C)		CHLADEC (mg m^{-3})	
Year	N	N	N+ (%)	N+ (%)	min	max	min	max	min	max
2003	1290	-	528 (40.9 %)	-	-5.7	10.1	13.6	17.1	0.276	4.934
2004	1292	-	578 (44.7%)	-	-5.6	14.5	13.9	17.0	0.214	1.169
2005	1271	-	782 (61.5%)	-	-1.9	4.4	13.6	16.1	0.282	3.401
2006	1029	303	623 (60.5%)	138 (45.5%)	-1.5	4.9	15.3	19.6	0.314	1.786
2007	725	212	247 (34.1%)	100 (47.2%)	-0.1	5.5	13.1	16.9	0.251	1.465
2008	1216	343	383 (31.5%)	41 (12.0%)	-9.3	14.3	12.8	15.8	0.298	6.52
2009	1005	335	363 (36.1%)	76 (22.7%)	4.6	12.3	13.5	17.8	0.230	5.28
2003-2009	7828	1193	3504 (44.8%)	355 (29.8%)	-9.3	14.5	12.8	19.6	0.214	6.52

Model estimation

The results of the final selected GAM models for sardine spawners and sardine eggs are presented in Table 4.3 and the effect of the environmental parameters on their presence is shown as plots of the best-fitting smooths, with 95% confidence intervals (Figure 4.2). Interaction effects are shown as a perspective plot without error bounds. The y-axis reflects the relative importance of each parameter of the model and for the interaction effects this is presented on the z-axis. The rug under the single variable effects plots indicates the density of points for different variable values. It should be noted that the effect of each variable is the conditional effect, i.e. the effect of this variable, given that the other variables are included in the model. Inspection of the validation graphs (not shown) indicated a distinct pattern regarding the plot of residuals versus fitted values due to the presence/absence nature of the data (no indication of a lack of fit).

The percentage of the total deviance explained by the models was 31% for the spawners' model and 43% for the eggs' model (Table 4.3). For sardine PSH, the finally selected model, constructed on pooled data from the Spanish Mediterranean waters from 2004 to 2008, included as main effects: Depth (cubic root transformed) and CHLA (log transformed) as well as the interactive effect of SLA with SST. Depth is the variable initially entered into the model that explained most of the variance (Table 4.3).

Table 4.3. *Sardina pilchardus* GAM model construction for spawners and eggs. Analysis of deviance for GAM covariates and their interactions of the final models fitted. Res.Df: residual degrees of freedom; Res.Dev.: residual deviance; Dev. Expl.: deviance explained; AIC: Aikaike Information Criterion; p-value: probability that the effects of a variable are not significant (<<0.000: p-value of all variables in the model is <<0.000).

Model	Res. Df	Res. Dev.	Dev. Expl. %	AIC	p-value
Sardine spawners					
Null model	5000.00	6926.87		6928.87	
s(Depth)	4979.64	5710.87	17.3%	5727.60	<<0.000
s(Depth)+s(CHLA)	4940.95	5444.28	20.7%	5478.39	<<0.000
s(Depth)+s(CHLA)+s(SLA)	4854.73	4963.30	26.6%	5013.83	<<0.000
s(Depth)+s(CHLA)+s(SLA)+s(SST)	4764.91	4712.16	29.1%	4780.33	<<0.000
s(Depth)+s(CHLA)+s(SLA, SST)	4766.67	4624.58	30.5%	4689.24	<<0.000
Total variation % explained			30.5%		
Sardine eggs					
Null model	834.00	1041.99			
s(SST)	770.71	793.11	17.5%	811.70	<<0.000
s(SST)+s(CHLA)	765.39	694.84	27.7%	724.06	<<0.000
s(SST)+s(CHLA)+s(SLA)	742.75	607.74	35.5%	644.25	<<0.000
s(SST)+s(CHLA)+s(SLA)+s(Depth)	740.13	574.37	39.1%	616.12	<<0.000
s(CHLA, SST)+s(SLA)+s(Depth)	729.13	537.56	43.0%	601.30	<<0.000
Total variation % explained			43.0%		

The average December values of the satellite environmental data included in the final models ranged between 0.214 to 6.52 mg m-3 for the CHLA, from 6 to 19.6 °C for the SST and from -9.3 to 14.5 cm for SLA (Table 4.2). However, plots of the best fitting smooths (Figure 4.2) indicate a higher probability of sardine presence in waters with bottom depth less than 90 m and CHLA concentrations greater than 0.45 mg m^{-3}. Nevertheless, for CHLA concentrations above 2.23 mg m^{-3} the positive effects of CHLA on the presence of sardine spawners starts reverting. Further, higher probability of finding sardine spawners was observed at two different combinations of SST and SLA (Figure 4.2), i.e. low temperatures (14-17°C SST) and slightly negative or zero SLA values (-5 to 0 cm SLA) and in higher temperatures (16-18.5°C SST) and slightly positive SLA values (1 to 5 cm SLA), within the available values.

For sardine RSH, the final selected GAM model, based on pooled data from the Spanish Mediterranean waters from 2006 to 2008, included as main effects: Depth (cubic root transformed) and SLA as well as the interactive effect of CHLA (log transformed) with SST. SST is the variable that was initially entered into the model explaining the higher proportion of the total variation (Table 4.3). Plots of the best fitting smooths (Figure 4.2) indicate a higher probability of finding sardine eggs in SLA values above -1.5 cm but below 5 cm (within the available ones) and at waters within up to 110 m depth. The interaction plot between CHLA and SST also indicates higher probability of finding sardine eggs present at SST values of 14 to 17 °C when co-existing with CHLA values within 1 to 2.7 mg m^{-3} (Figure 4.2), within the available ones.

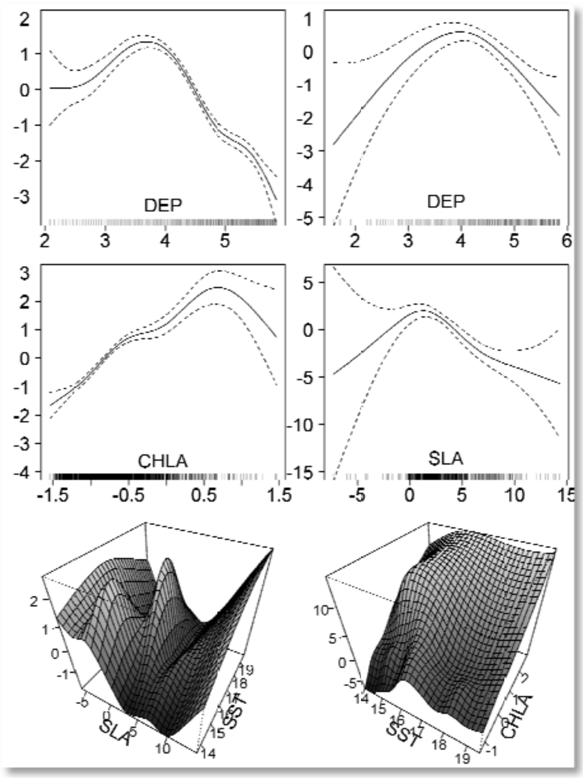


Figure 4.2. Coefficients and interaction plots of the Generalized Additive Models (GAMs) for sardine (*S. pilchardus*) PSH (left) and RSH (right). Black lines indicate the value of GAMs coefficient, dotted lines represent the confidence intervals at p = 0.05.

Model validation

The selected model for sardine spawners in the Spanish waters showed moderate prediction ability (0.77 - 0.88 AUC), while the eggs model showed higher performance ranging from moderate to high performance (0.82-0.93 AUC) excepting the year 2009, for which the performance was poor (Table 4.4). In a subsequent step, habitat suitability maps for the study regions and the entire Mediterranean Sea were estimated for the period 2003-2009 (Figures 4.3) where areas associated with a specific probability of suitable conditions for sardine presence are indicated.

Table 4.4. *Sardina pilchardus* spawners and eggs model evaluation: number of records (N); estimated area under the Receiver Operating Curve (AUC); se: standard error; mean values of sensitivity (s) and specificity (sp) accuracy measures for two threshold criteria: MDT (maximize the specificity-sensitivity sum) and prevalence (PRV) values.

Model	Year	N	AUC (±se)	MDTs	MDTsp	PRVs	PRVsp
Spawners	2003	1236	0.79±0.01	0.89	0.59	0.78	0.667
	2004	1130	0.81±0.01	0.74	0.76	0.75	0.75
	2005	1090	0.85±0.01	0.80	0.77	0.70	0.84
	2006	952	0.88±0.01	0.77	0.85	0.79	0.82
	2007	669	0.87±0.01	0.90	0.73	0.86	0.76
	2008	998	0.77±0.01	0.78	0.65	0.84	0.56
	2009	1005	0.82±0.01	0.87	0.66	0.78	0.74
Eggs	2006	280	0.82±0.02	0.97	0.54	0.78	0.65
	2007	186	0.83±0.03	0.80	0.71	0.80	0.71
	2008	294	0.93±0.04	0.83	0.98	0.87	0.85
	2009	336	0.58±0.04	0.55	0.58	0.07	0.93

Annual potential habitat

The mean probability of finding adequate habitat for sardine spawners over all the Mediterranean in late autumn, varied little from year to year with exception of a big increase in 2009 (Table 4.5). The RSH showed an increase of the mean probability from the year 2003 to 2006 and then a progressive reduction till 2009 (Table 4.5). Over the whole time series, the average probability was higher and more stable (lower relative standard error, rse) for the PSH than for the RSH (0.25±13.61 rse; 0.16±21.26 rse, respectively).

At a Mediterranean scale, the observation of the annual maps of PSH revealed varying temporal patterns for the different Mediterranean areas and it seems that the huge increase in 2009 is mainly observed in the Central and Eastern Mediterranean European waters as well as in the African coasts from Algeria to Egypt (Figure 4.3). In the Western Mediterranean European waters, increase of the probability of finding adequate habitat for sardine spawners is observed for the period 2003-2005, with maximums in 2005-2006, followed by a decrease from 2007 onwards (Figure 4.3). This is particularly evident in the Spanish and French waters. In the African coasts of the Western Mediterranean, the areas from the Northern Alboran Sea to the Central Liguran Sea seem to show similar inter-annual variability, as well as the Alboran Island with the nearby coasts of Algeria and further with the Central coasts of Tunisia (Figure 4.3). In the Central and Eastern Mediterranean, the Adriatic and Northern Ionian seem to vary similarly. In the Spanish waters, Northern Alboran Sea and Balearic Islands showed lower probabilities of adequate habitat than in the rest of the Spanish mainland waters and, while in the Northern Alboran Sea the quite smooth decrease in the PSH is observed from 2006, in the Balearic Islands the decrease is much deeper and starts one or two years later (Figure 4.3).

Table 4.5. Average PSH and RSH estimated over the entire Mediterranean basin. N_{cells}: number of prediction grid cells; in brackets, relative standard error (%).

Year	N_{cells}	PSH	RSH
2003	41370	0.18 (0.68)	0.12 (1.02)
2004	40508	0.21 (0.71)	0.18 (0.83)
2005	41288	0.22 (0.67)	0.19 (0.80)
2006	41111	0.23 (0.69)	0.29 (0.63)
2007	40498	0.23 (0.65)	0.23 (0.69)
2008	35800	0.21 (0.70)	0.11 (1.25)
2009	36230	0.45 (0.46)	0.03 (2.45)

Furthermore, the PSH in the western Mediterranean islands tends to be lower than the mainland coasts (mean probability islands: 0.13; mean probability in mainland: 0.22; F-value: 4.538; Pr (>F): 0.04*) and higher inter-annual variability (although not significant), probably reflecting higher hydrographical complexity in the Islands. The temporal pattern in the Western and Central Mediterranean Islands is quite peculiar, e.g. in Sicily, the more or less stable inter-annual probability is disturbed by a huge decrease in 2006 while Malta show a maximum in 2005 followed by a decrease and, then following the general pattern of the Mediterranean Sea, an increase in 2008 and 2009 (Figure 4.3). Further, Corsica and Sardinia have similar temporal evolution, with a maximum probability of finding adequate habitat in 2007, while the Balearic Islands show a somehow increased probability between 2005 and 2008, with no clear peak, and the minimum probability in 2009 (Figure 4.3).

High probability of RSH was estimated for many Mediterranean areas for most of the years, besides in Malta, Crete and Cyprus in which the predicted RSH was always below 0.25 (Figure 4.4). In the Libian coasts and in most of the southern Turkish coasts probabilities above 0.25 were only predicted in the years 2006 and 2007 (Figure 4.4).In the Aegean Sea, high RSH (>0.75) was identified inside the gulfs, with the highest estimates observed in 2007. In Sicily, the southern coast generally showed wider area of high probability of RSH. Referring to the RSH, the highest probability that was found in the year 2006 seem to be a effect derived from the increased probability in the Adriatic Sea, in the mainland coasts of the Western Mediterranean Sea and from the Tunisian coasts (Figure 4.4). The extremely low mean prediction in 2009 is observed in all the Mediterranean areas.

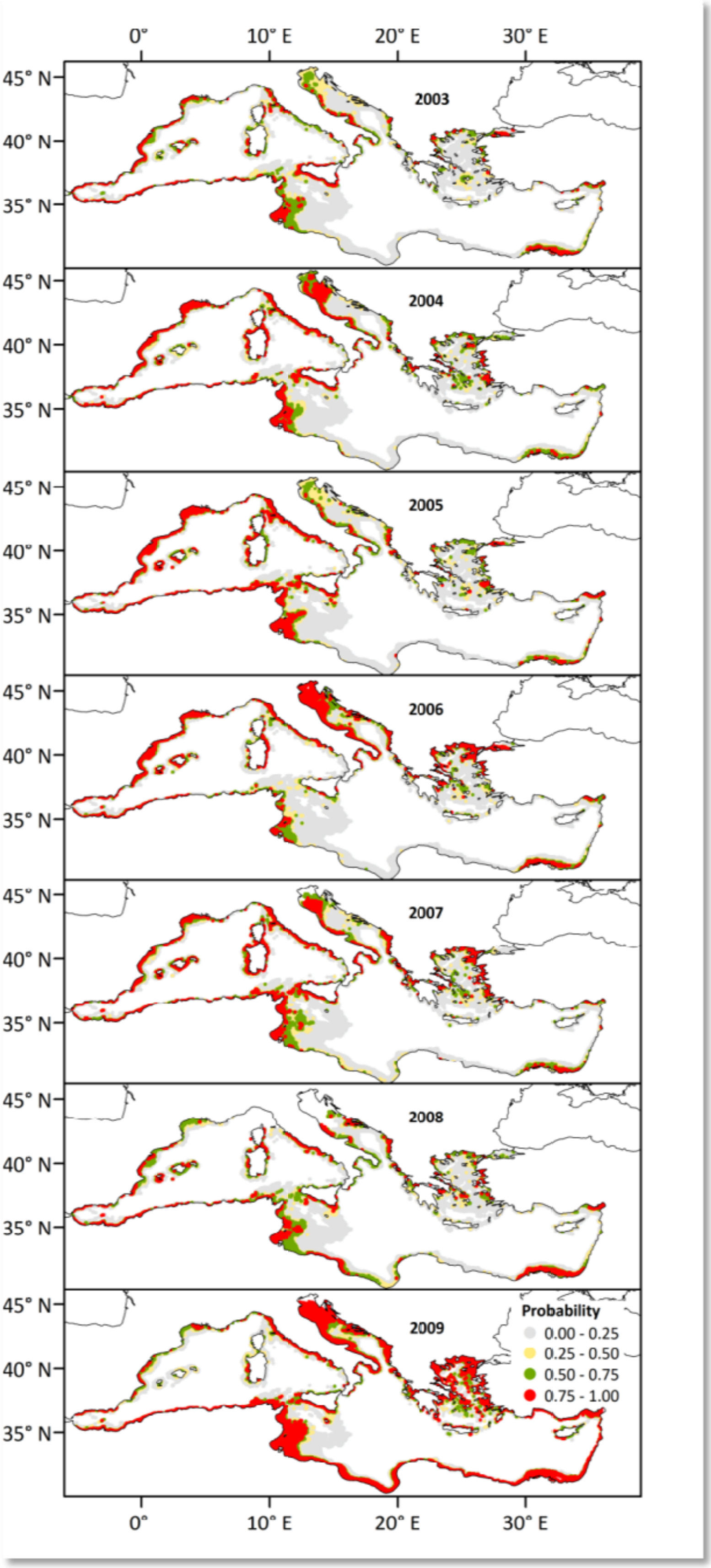


Figure 4.3. Annual maps of potential spawning habitat (PSH) for sardine (*S. pilchardus*) in the Mediterranean Sea in late autumn 2003 to 2009, indicating the probability of occurrence of adequate habitat.

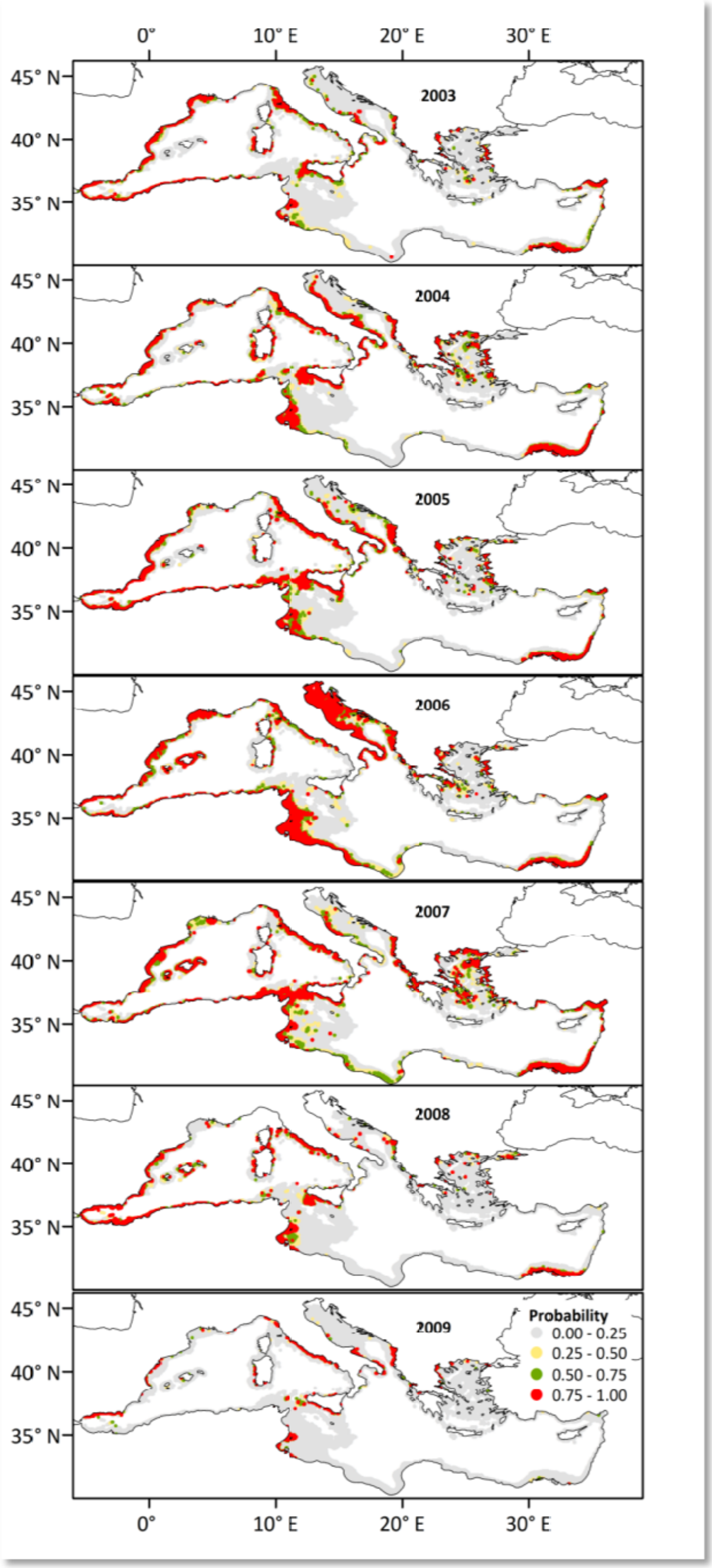


Figure 4.4. Annual maps of realised spawning habitat (RSH) of sardine (*S. pilchardus*) in the Mediterranean Sea in late autumn 2003 to 2009, indicating the probability of occurrence of adequate habitat.

Habitat suitability

In late autumn, habitat suitability maps of sardine PSH revealed the existence of persistent hotspot habitat (high mean and low cv) throughout the Mediterranean Sea (Figure 4.5). Specifically, it was observed in most of the Spanish coast, in the Gulf of Lions, in the Central Ligurian Sea, in the Southern Sicily and in some spots of Corsica and Sardinia (Figure 4.5). In the Adriatic Sea, persistent hotspot habitat was observed in the North and West coast; in the Ionian Sea, small rather isolated areas of persistent hotspot habitat were identified in both the Italian and Greek coasts and inside the gulfs of the Aegean Sea (Figure 4.5). In Sicily, persistent hotspot habitat was detected in the Southern coasts under the influence of the Sicilian Channel currents (Figure 4.5). Further, persistent hotspot habitat is found along most of the Northern African coast (besides Lybia) and in the South-East of Turkey, i.e. in the Bay of Iskenderun (Figure 4.5). Persistent-preferred habitat (intermediate probability and low variability) are predicted in wide areas of the Gulf of Gabes and in North Adriatic Sea, while occasionally-preferred habitat occupies a very small throughout the Mediterranean (Figure 4.5). The persistent hotspot habitat was almost consistently associated with the run-off of large rivers, i.e. Ebro and Rhone Rivers in the Western Mediterranean, the Po River in the north-western Adriatic Sea and the Nile Delta region, as well as with upwelling areas such as the Alboran Sea and the southern coasts of Sicily (Figure 4.5).

Habitat suitability maps of RSH indicated persistent hotspot habitat in the Spanish of Alboran Sea, from Cape of Palos to Ebro River, in spots of the Catalan coast and Gulf of Lions, along the Central Ligurian Sea, in the Italian coast of the Adriatic and in the South East of Adriatic, inside the Gulfs of the Aegean, North Egypt in the Gulf of Gabes and along the Moroccan and Algerian coasts (Figure 4.5).

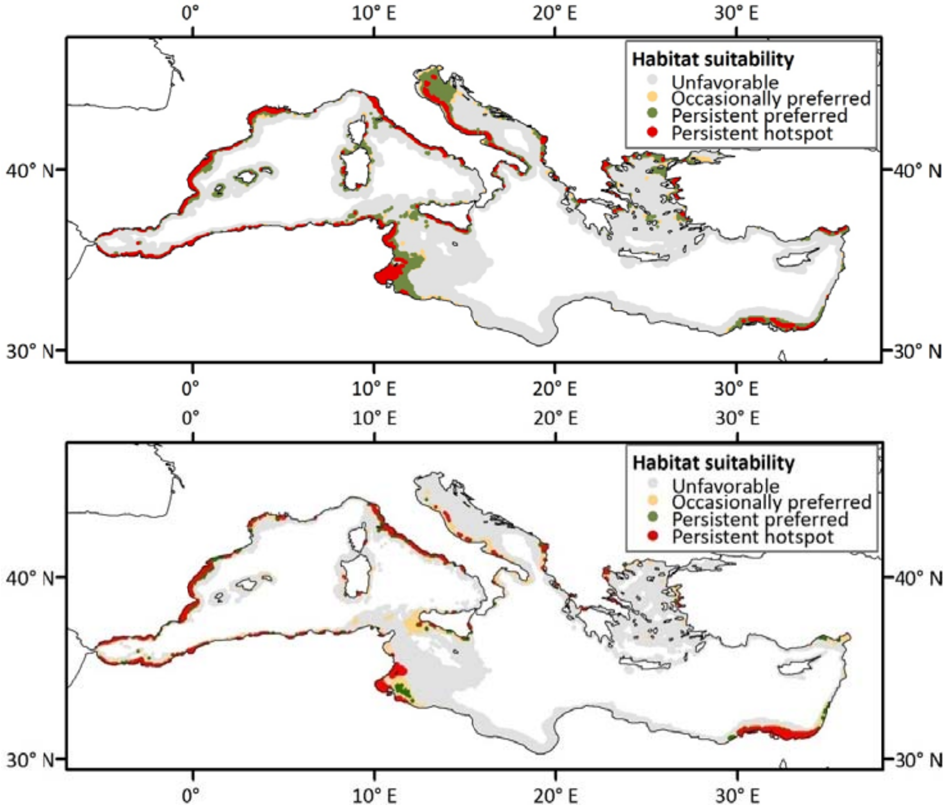


Figure 4.5. Sardine (*Sardina pilchardus*) habitat suitability maps for the potential spawning habitat (top) and for the realised spawning habitat in the Mediterranean in late autumn for the period 2003-2009.

Temporal synchrony among adjacent areas

In the Western Mediterranean, the correlation of sardine PSH time series among adjacent GSAs was positive significant between the GSA 2 and 4, 6 and 7, 7 and 9, 8 and 11 and 4 and 12 (Table 4.6; Figure 4.6). There is also a significant temporal synchrony between GSAs 10 and 16 and 12 and 13. In the Central Mediterranean, significant temporal synchrony was observed between GSAs 13 and 14, 14 and 21 and in the European coasts, between 17 and 18. There is also synchrony between GSAs 21 in the Central Mediterranean and the GSA 26 in the Eastern Mediterranean Sea (Table 4.6; Figure 4.6). In the Eastern Mediterranean, the PSH of sardine in all GSAs were positively and significantly related among adjacent areas (Table 4.6; Figure 4.6).

Regarding the RSH of sardine, positive significant correlation was seen among the time series of GSA 3 and 4 in the Western Mediterranean (Table 4.6; Figure 4.6), between GSA 10 in Western Mediterranean and GSA 16 in the Central Mediterranean, between GSAs 13 and 14 and 14 and 21 in the Central Mediterranean, between GSA 20 in the Central Mediterranean and GSA 22 in the Eastern Mediterranean and between GSA 21 in the Central Mediterranean and GSA 23 in the Eastern Mediterranean as well as between GSAs 22 and 23 and 26 and 27 in the Eastern Mediterranean (Table 4.6; Figure 4.6).

Further, in the GSAs where both the PSH and the RSH are temporally correlated it is highly likely that spawning is synchronous. This is the case of the Northern coasts of Africa in the Central Mediterranean till the Lebanon coasts, i.e. from GSA 13 to GSA 27, and of the Aegean (GSA 22) and Cretan waters (GSA 23, Figure 4.6).

Table 4.6. Temporal synchronies in PSH and RSH the time-series between adjacent areas. Only positive significant relationships are shown. cor: Pearson's correlation coefficient; p-value between brackets. W: Western Mediterranean basin; C: Central Mediterranean basin, E: Eastern Mediterranean basin.

	PSH		RSH	
	GSAs	cor	GSAs	cor
W	2-4	0.85 (0.02)	3-4	0.84 (0.02)
	6-7	0.85 (0.02)		
	7-9	0.81 (0.03)		
	8-11.2	0.92 (<0.00)		
	4-12	0.94 (<0.00)		
W-C	12-13	0.87 (0.01)	10-16	0.78 (0.04)
C	13-14	0.90 (0.01)	13-14	0.91 (<0.01)
	14-21	0.86 (0.01)	14-21	0.83 (0.02)
	17-18	0.78 (0.04)		-
C-E	21-26	0.97 (<0.00)	20-22	0.92 (<0.00)
			21-23	0.91 (<0.00)
E	22-23	0.92 (<0.00)	22-23	0.81 (0.03)
	23-26	0.94 (<0.00)	26-27	0.95 (<0.00)
	24-25	0.96 (<0.00)		
	24-26	0.97 (<0.00)		
	25-26	0.97 (<0.00)		
	25-27	0.98 (<0.00)		
	26-27	0.97 (<0.00)		

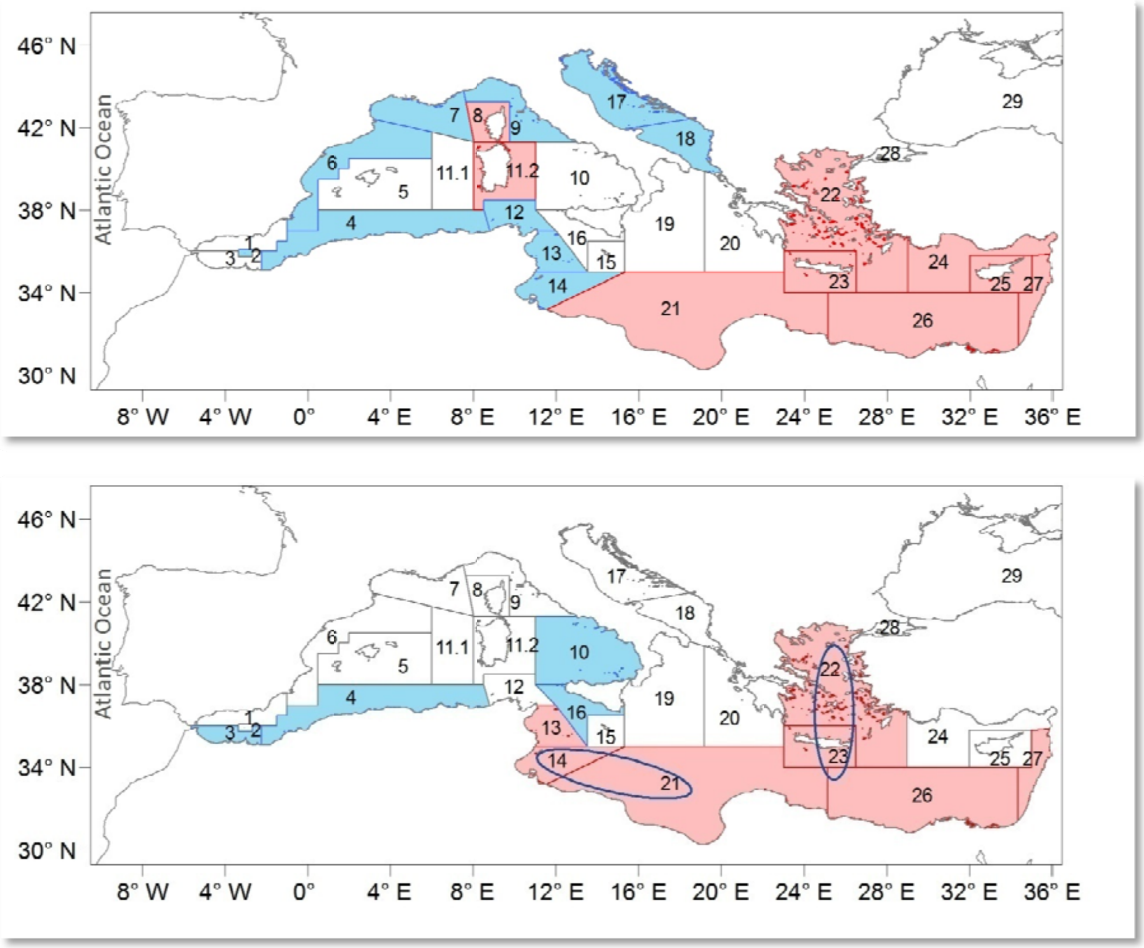


Figure 4.6. Temporal synchrony between the time series of the potential habitat in adjacent GSAs, for sardine spawners (top) and sardine eggs (bottom). In red: GSAs with high correlation coefficient (>0.90) and high significant (p-value<0.001); in blue: middle correlation coefficient (>0.80 and < 0.90) and low significance (p-value<0.05). Blue ovals indicate intermediate correlation as well.

Persistence of the habitat overlap among life-stages

The overlap between the preferred habitat of sardine spawners and eggs showed high persistence in most of the Spanish Mediterranean coasts, Morocco and Algeria, Ligurian and Tyrrhenian seas, South-East Adriatic, Nile River mouth, Gulf of Gabes and in some spots of Sicily, Sardinia and Aegean (Figure 4.7a). Intermediate persistence in the overlap between the preferred habitat of both life stages was observed in a wider area, further including the Gulf of Lions, the Western Adriatic and Sicily (Figure 4.7a). Low persistence was widespread throughout the Mediterranean basin, besides the Ligurian Sea and Algerian coasts (Figure 4.7a). Of the total area occupied by overlapping preferred habitat throughout the Mediterranean, around a 5% showed high persistence (>75% of the years; 6-7 years), some 16% showed intermediate persistence (50-75% of the years; 5-4 years) and around a 79% showed low persistence (<50% of the years; 1-3).

The overlap in the hotspot habitats of sardine spawners and eggs showed high persistence in quite reduced areas mainly concentrated in the Western Mediterranean and consisting of isolated spots in the Spanish waters around the Ebro River, in the Alboran Sea (Malaga and Almeria Bay), Gulf of Gabes, South Sardinia and East Sicily (Figure 4.7b). Overall, in the Mediterranean basin, the overlapping hotspot area showed generally low persistence, i.e. ~89% of the total overlapping hotspot area, ~10% showed an intermediate persistence while only 1% of the total overlapping area was highly persistent.

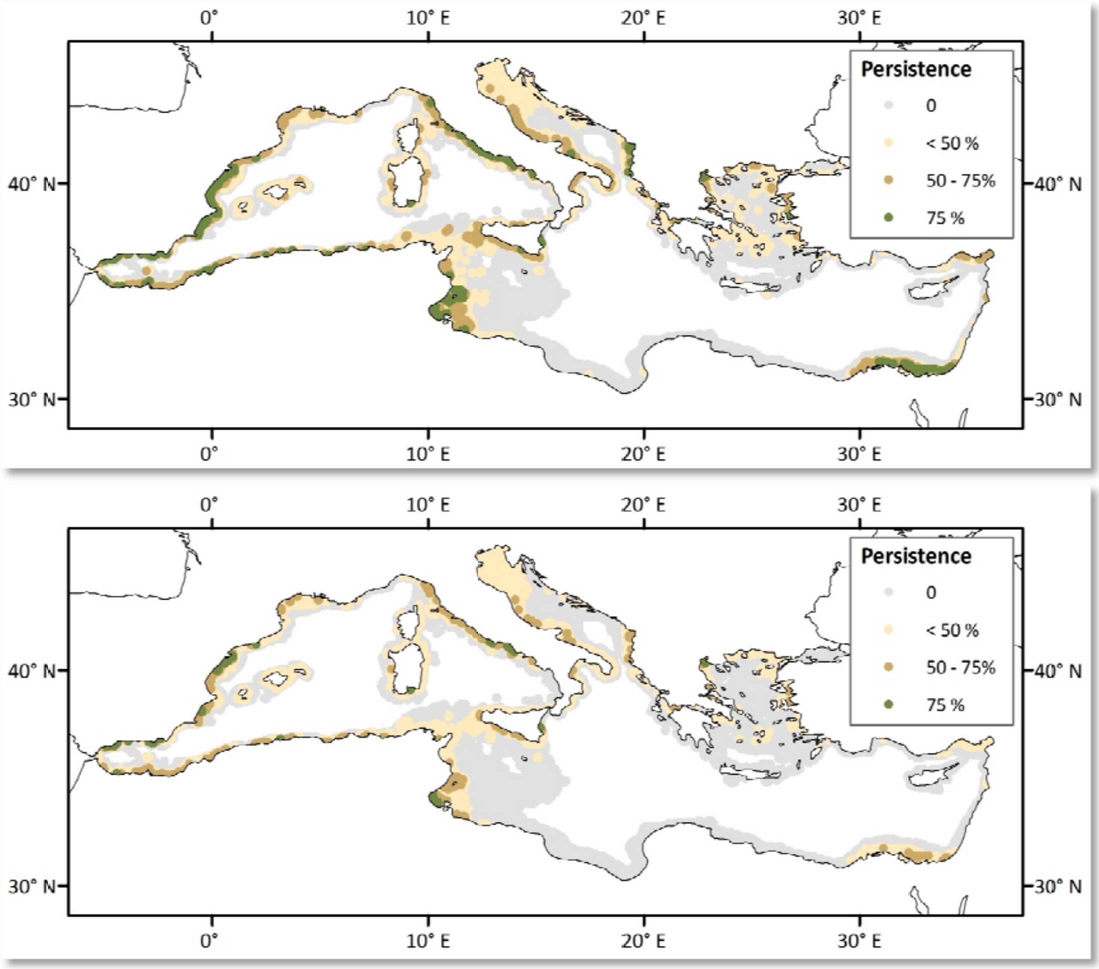


Figure 4.7. *S. pilchardus*. Overlapping areas between the potential spawning habitat (PSH) and the realised spawning habitat (RSH) in the Mediterranean Sea during late autumn. Maps show the persistence (% years) for which the probability of PSH and RSH are above a certain threshold, i.e. preferred habitat (probability>0.50) (above) and hotspot (probability >0.75) (bottom).

Sardine spawning habitat, fisheries landings and biological indicators

At the Mediterranean scale, no significant correlation was observed between landings of sardine and the PSH or RSH for the seven year time series (2003-2009). However, in the North Western Mediterranean Sea several relationships arose. Within the Spanish waters, sardine landings were positively correlated with the late autumn potential spawning habitat in GSA1 (cor=0.79, p-value=0.04) and GSA 6 (cor 0.84, p-value=0.02), as well as with the realised spawning habitat in GSA6 (cor=0.81, p-value=0.03). Furthermore, the potential spawning habitat in GSA 1 (cor=0.77, p=0.04) and in GSA 6 (cor=0.90, p=0.01), as well as the extension of the hotspot habitat in GSA 6 (cor=0.91, p-value=0.01) and the extension of the preferred habitat in the GSA 6 (cor=0.91, p-value<0.00) were correlated with sardine landings in the following year.

Within the Gulf of Lions (i.e. GSA7), the coefficient of condition (K_{rel}) of sardine during the summer was related with the potential spawing habitat of sardine (cor=0.75, p-value=0.05) and with the realised spawning habitat of sardine (cor=0.77, p-value=0.04) in that same area during late autumn, although correlations were not very high and significance, in both cases, were marginal.

When analysing the relationships between GSA6 and 7 it was found that, besides the relationships observed in the predictions of the late autumn PSH between GSA 6 and 7 in the previous section several relationships were observed. The condition factor of sardine in GSA7 during summer was related with the potential spawning habitat of sardine in GSA 6 in late autumn (cor=0.92, p-value<0.00), with the extension of the hotspot habitat (cor=0.91, p-value=0.01) and with the extension of the basin habitat (cor=0.91, p-value<0.00). Furthermore, landings of sardine from Spain were related with the late autumn realised spawning habitat in GSA 7 (cor=0.84, p-value=0.02) and with the summer condition factor in GSA 7 (cor=0.90, p-value=0.01). Landings of sardine from Spain in a following year was related to the late autumn potential spawning habitat of sardine en GSA7 (cor=0.82, p-value<0.00) and with the biomass in the summer of the previous year in GSA 7 (cor=0.77, p=0.02).

4.4 Discussion

The present work was aimed at modelling the habitat of sardine spawners (or PSH) and of sardine eggs (or RSH) during the species' spawning season through combining environmental data with the spatial distribution of the high quality acoustic data and egg data collected during regular small pelagic fish stock assessment surveys. The results will support the understanding of the potential distribution areas and ecology of sardine in the Mediterranean, far less studied than in large upwelling ecosystems (e.g. van der Lingen *et al.*, 2001; Bertrand *et al.*, 2008; McClatchie *et al.*, 2010; Barange *et al.*, 2009). One of the major goals and challenges of the current work was to select and implement a model based on data from an area of the Mediterranean Sea, which would identify similar suitable conditions for species occurrence in the entire Mediterranean basin. Notwithstanding, the present work constitutes the first attempt to model the realised spawning habitat of sardine in relation to environmental variables for the entire Spanish Mediterranean waters and to predict it for the whole Mediterranean Sea.

Potential spawning habitat (PSH)

At a regional scale (i.e. the Spanish waters), the variables that mainly defined sardine's PSH were, from highest to lowest contributors to explain variance, Depth, SST, SLA and CHLA. The depth range with higher probability of sardine PSH (up to 90 m) was similar to that observed in the Adriatic in autumn but deeper than summer sardine's distribution in Sicily and in the Aegean Sea (up to 65 m; Tugores *et al.*, 2011). The low summer productivity (Bricaud *et al.*, 2002; D'Ortenzio and Ribera d'Alcalà, 2009) would compel sardine to approach the coast in search of the most productive waters (Bosc *et al.*, 2004; D'Ortenzio and Ribera d'Alcalà, 2009). In autumn and winter, vertical mixing of the water column produces an increase of the productivity (Bosc *et al.*, 2004), allowing sardine to occupy a wider proportion of the continental shelf.

Further, higher probability of PSH was observed moderately negative values of SLA (-5 to 0 cm) combined with relatively low temperatures (14 to 17°C). Additionally, higher probability of PSH was seen in waters combining moderately positive SLA (1 - 5 cm) and warmer SST (16 to 18.5ºC). This is in the line with previous studies suggesting that maximum abundances of sardine spawners were observed at temperatures below 18ºC (Oliver, 1957; Olivar *et al.,* 2001). CHLA concentration had a positive effect on the presence of sardine spawners, but the positive effect starts reverting (becomes less positive) for the higher CHLA values. Sardine would avoid the most productive waters, similar to observations in large upwelling areas, suggesting wind-driven Ekman-type upwelling and a dome-shaped response to productivity (Roy *et al.,* 1989; Cury and Roy, 1989). The increased upwelling and transport occurring in the most productive areas will have negative impacts in sardine spawning success due to offshore transport (Roy *et al.,* 1989; Santos *et al.,* 2004). This uncoupling may not exist in areas where upwelling is not of the Ekman type (Cury and Roy, 1989).

Realised spawning habitat (RSH)

The main drivers shaping the RSH of sardine were SST and bottom depth which is in the line with previous observations in the Atlantic waters (Bernal *et al.,* 2007; Planque *et al.,* 2007). Further, depth up to which higher probability of finding sardine eggs were found (up to 110 m) were as well similar to previous works (70-100 m depth; Olivar *et al.,* 2001).

Higher probabilities of finding sardine eggs were observed in the colder range of the temperatures where the spawners were found (i.e. 14-17ºC), suggesting that sardine effectively spawned (or more efficiently spawned) in the colder waters. This is in line with previous studies in the Mediterranean, e.g. in the Western Mediterranean although sardine is known to spawn when temperature falls well below 20ºC, increased spawning activity is observed between 12 and 19 ºC and with preference for the lower temperatures, i.e. 12-14ºC (Olivar *et al.,* 2001, 2003; Palomera *et al.,* 2007). Overall SST preferences of sardine spawning are similar across the Northern Mediterranean basin (Regner *et al.,* 1987; Coombs *et al.,* 2006; Morello and Arneri, 2009 and references therein; Mandic *et al.,* 2013; Ganias *et al.,* 2007; Stratoudakis *et al.,* 2006) although local variations are observed.

In the Aegean and in the Gulf of Tunis, however, temperature choice seems not to be the lower temperatures. In December 2000 sardine spawned in temperatures between 17 and 19ºC in the Aegean Sea, although SST ranged from 15.4 to 19.8ºC (Somarakis *et al.,* 2006). The authors suggest that this could be related with the higher concentrations of meso-zooplankton found in these warmer waters and sardine choosing to feed on it rather than the colder less productive waters. Similarly, in the Gulf of Tunis the highest abundance of sardine eggs were found in winter where mean SST was 13.4ºC, but the higher concentrations were located in areas with relatively warmer (~14-14.4 ºC) waters but with high zooplankton concentration but low concentration of nitrates, chlorophyll-a and diatoms (Zarrad *et al.,* 2008).

Very low temperatures may have as well a negative impact on sardine spawning, i.e. <10ºC in the Adriatic (Po River influence) and <12 ºC in the Atlantic (Morello and Arneri, 2009 and references therein; Mandic *et al.,* 2013; Coombs *et al.,* 1996; Stratoudakis *et al.,* 2007). In our study such effect could not be evaluated due to the broader scale of our analysis in comparison to the very local effect of rivers in the Spanish Mediterranean waters. Similarly to sardine spawners, sardine eggs were absent in areas with the highest CHLA concentrations, suggesting again avoidance of the most productive waters (Roy *et al.,* 1989). Regarding SLA, low SLA values (-5 to 5 cm) had positive effects on RSH of sardine. The location of vortices, which are highly related to concentration/retention processes in the upper layers of the water column, have been detected by means of SLA across the Mediterranean (Isern-Fontanet *et al.*, 2006). Thus, SLA might indirectly indicate the effect of concentration/retention processes on the spatial distribution of sardine eggs. Similarly, in the Adriatic sardine spawning was found to be more intense at the frontal zones, i.e. areas where masses of different origins and properties meet (Regner *et al.*, 1988; 1987). Frontal zones originate water enrichment and vortices. Thus, the incorporation as possible explicative variables of the spatial distribution of fronts and/or vortices and/or spatial distribution of fronts should be explored in order to try to improve the performance of sardine eggs' model.

In the Western Mediterranean, SLA has a marked cyclic seasonal pattern being lower in winter and higher in summer and with intra-annual variations that can differ about 20 cm (Larnicol *et al.*, 1995). In winter, when the proportion of Atlantic water (AW) that concentrates in the W Mediterranean basin in relation to the denser Levantine Intermediate Waters (LIW) increases the SLA of the Western Mediterranean is lowered; the contrary happens in summer (Manzella and La Violette, 1990). Thus, any physical/climatological phenomenon that affects the timing or the quantity of AW that enter into the Mediterranean will have its impact on the SLA and in the marine ecosystems as well.

During the boreal winter months of 2009-2010, Mediterranean mean sea level rose 10 cm above the average monthly climatological values (Landerer and Volkov, 2013). Over the continental shelf of the Mediterranean basin, SLA in December 2009 ranged from 3.5 to 25.4 cm while in the period 2003-2008 it ranged between -12.1 to 18.6 cm. This huge increase in SLA could have produced the dramatically low prediction of sardine's RSH in 2009. The very low amount of stations with presence of sardine eggs in the samples in 2009 suggested that the model predicted pretty well the mean probability of finding sardine eggs even though their particular spatial location was not as good as desired as indicated by the poor model performance (i.e. very low AUC values). Additional "rare years" would be needed to allow achieving a good prediction in 2009. Further, the temporal variation of SLA was strongly anti-correlated with the North Atlantic Oscillation (NAO) index occasioning wind stress anomalies just west of the Strait of Gibraltar and standing into the strait itself (Landerer and Volkov, 2013). Excessive wind stress has shown to produce a negative impact on small pelagic fish early-life stages in areas where upwelling is related to Ekman-type upwelling (Cury and Roy, 1989; Ruíz *et al.*, 2013).

Sardine eggs were found up to somewhat deeper bottom depths than spawners, i.e. eggs up to 110 m and spawners up to 90 m depth. If data were synoptic, the realised habitat would be contained by the potential spawning habitat (Planque *et al.*, 2007). Passive offshore transport by currents can account for this deeper distribution of sardine eggs. As long as sardine eggs hatch 1.5-3.5 days after spawning (Riveiro *et al.*, 2004), differentiation between egg developmental stages should be performed in future surveys in order to incorporate only the eggs spawned synoptically with survey and thus define more precisely the realised spawning habitat.

Annual potential habitat and habitat suitability

The **potential spawning habitat (PSH)** of sardine, or potential distribution areas of spawners, coincide with the actual fish distribution as estimated by acoustic surveys in areas like the Gulf of Lion, the Ligurian Sea, the Aegean Sea and the Adriatic Sea (Guennegan *et al.*, 2000; Bigot 2007; Somarakis *et al.*, 2006;

Morello and Arnerni, 2009 and references therein; Romanelli and Giovanardi, 2000; Romanelli *et al.,* 2002). In the Spanish Mediterranean waters, the potential spawning habitat (PSH) of sardine, or potential distribution areas of spawners estimated in the present work are consistent with previous estimations in the same area but with fewer amounts of years (Bellido *et al.,* 2008). This suggests robustness of the model as additional years are incorporated in the modelling.

In the Western Mediterranean, the mean probability of PSH was lower in the islands than in the mainland. These could be related with the generally lower productivity of the coastal waters of the islands in comparison to the mainland productivity in the Mediterranean Sea (Bosc *et al.,* 2004; D'Ortenzio and Ribera d'Alcalà, 2009). In the Spanish Mediterranean waters, this finding is supported by the fact that the purse-seine fisheries which is the main fisheries targeting on sardine and other small pelagic fishes, has had lower tradition in the mainland than in the Balearic Islands and as well as proportionally lower amount of censed purse-seiners, i.e. 239 in the mainland against 9 in the islands (BOE, 2013) despite the surface area where they can operate is of a similar size.

Regarding the **realised spawning habitat (RSH)**, although the information regarding sardine spawning grounds in the Mediterranean is limited, the predicted spatial location of the sardine RSH throughout the Mediterranean partially matches the known spawning grounds. Specifically, in the Spanish waters, the areas identified as suitable for sardine spawning were the surroundings of the Ebro River Delta and the North Alboran Sea, (Pérez de Rubín, 1996; Olivar *et al.,* 2001; Vargas-Yáñez and Sabatés, 2007). In the North Alborán Sea, the annual variation in the RSH is associated to the variability of the local upwelling and water circulation in the area (Pérez de Rubín, 1996).

In the Adriatic, the spawning area at the beginning of the spawning season is known to occur mainly along the Western coasts, although the main spawning area shift towards the open central and southern Adriatic when the river Po causes a drop of SST (<10ºC), finishing off closer to the eastern coast (Regner *et al.,* 1988). In Aegean and eastern Ionian Sea, RSH was more persistent inside the coastal waters and the gulfs of the western part, coinciding with the known spawning grounds of sardine in the early 00's (Somarakis *et al.,* 2006). It has to be taken into account, however, that the estimations of RSH in the northern of the Adriatic Sea in the years 2007 and 2008 were not available due to adverse environmental conditions (i.e. cloud cover).

Known distribution and/or fishing grounds of sardine exist along the Moroccan and Algerian coast (Djabali *et al.,* 1991; Ramzi *et al.,* 2006; Bedairia and Djebar, 2009), Tunisian and Libyan coastal waters as well as the Nile Delta region along the Egyptian coast (Farrag *et al.,* 2014) and south Lebanon (Carpentieri *et al.,* 2009). Further east, the information on the spatial distribution grounds of sardine in the Levantine basin is pretty scarce yet local landings denote sardine presence in the area (Bariche *et al.,* 2006, 2007). In Tunisian waters, and more specifically in the Gulf of Tunis, the predicted RSH either estimates high probability of finding sardine eggs throughout the gulf or, in years with more limited probability the areas of higher probabilities are estimated in the western part of the Gulf, coinciding with the spatial distribution of eggs in autumn (Zarrad *et al.,* 2008).

The comparison between PSH and RSH revealed that, the estimated spatial location of the RSH throughout the Mediterranean is similar to the estimated spatial location of the PSH, although in general less extended.

The high heterogeneity of the Mediterranean Sea suggests that the PSH and RSH would vary differently across different Mediterranean areas. However, the analysis of the synchrony among areas may reveal areas where environmental conditions vary simultaneously at a yearly scale, suggest potential connectivity among adjacent populations and/or similar exploitation patterns. Thus, areas showing synchronic temporal variation for a long enough time-series could be considered as management units. Sardine life span may reach up to 7 years. However, the bulk of sardine population live up to 3 years. Thus, the seven year time series used in the present study seem to suffice as it encompasses at least two cohorts.

In this sense, higher synchrony was observed among the annual variability in the PSH in the northern African and Eastern Mediterranean coasts, than in the Central and Western Mediterranean. In the Western Mediterranean, coastal areas from the mainland Spanish waters (GSA 6), France (GSA 7) and Northern Ligurian (GSA 9) revealed as well connected but at lower rates. The synchrony in the Spanish and French waters has been explained, at least partially, by the increased northerly winds and river runoff (due to increased rains over the Rhône basin and over the head of the Ebro River) that are observed in the NW Mediterranean when the anticyclone over the Azores encloses the SW Iberian Peninsula (Martín *et al.*, 2012). Nevertheless and although they have not been described (up to the authors knowledge), higher correlations in the northern African coasts and in the Eastern Mediterranean suggest that the environmental conditions favouring sardine habitat vary more synchronically than in the other areas and/or greater connectivity among sardine populations in these areas.

Regarding RSH, synchrony among adjacent areas was found in fewer cases. This, together with the fact that the mean RSH, as expected by the authors and by Planque *et al.*, (2007), show higher inter-annual variability than PSH, suggests that the habitat of RSH is more sensible to environmental changes than PSH. In the present study, synchrony was observed between the RSH in the Aegean (GSA 22) and the Ionian Sea (GSA 20) is in the line with previous observations that suggested that although Central Aegean (GSA 22) showed lower temperatures and a production of meso-zooplankton twice the concentration in the Ionian (GSA 20), both areas showed very similar sardine reproductive performance during the peak of the spawning period (Somarakis *et al.*, 2006).

Persistence of the habitat overlap among life-stages

The spatial overlap between the habitat of two different species will depend on the similarity of their biological requirements. In the case of two life stages of the same species and, in particular, in the case of sardine spawners and eggs, the spatial overlap of their habitat will be determined by the spawners' choice of the environmental conditions that are optimal for the spawners themselves and for the development of the eggs. The habitat of the spawners alone includes adults that effectively spawning but it includes as well adults that have not yet spawned or that have already spawned. On the other hand, the habitat of the eggs include eggs hatched in different days and yet not synoptic with the truly realised spawning. Thus, a mismatch between spawners and eggs may be originated by sea currents drifting eggs outside the spawning site or by the inactivity of a fraction of the population, whether it is for latitudinal variation in the onset of the spawning or due to a possible spatial differentiation of the age distribution. Younger individuals show a shorter spawning period which tends to start later in the year (Stratoudakis *et al.*, 2004).

The overlap among sardine spawners and eggs identifies the areas where the spawning is effectively being produced. So, the areas where the overlapping habitat is highly persistent are of outstanding importance for the subsistence of the species. It is important to mention that, data from different areas from the Mediterranean would be needed to have a true validation of the model at the Mediterranean basin. Additionally, in order to provide a picture of the temporal variability of the spawning and better define the most important areas to be protected, gathering information from several moments of the spawning season (or, if possible on a monthly basis) would be recommendable. Notwithstanding, the maps of the persistence of the habitat overlap presented here provide a starting point to construct an effective management tool to protect the effective spawning of sardine.

Sardine spawning habitat, fisheries landings and biological indicators

Within this work, the relationship between the potential spawning habitat (PSH) and realised spawning habitat (RSH) of sardine in late autumn were evaluated in relation to sardine landings for the seven year period 2003-2009. Up to a certain degree, landings can be representative of stock abundance, especially in a context of high exploitation rates or overexploitation as the current status of most sardine stocks in the Mediterranean denotes (Coll *et al.*, 2006; SGMED 2009, 2010).

At a Mediterranean scale, no positive significant correlation was observed although a previous study analysing a shorter time series had revealed a positive significant correlation between the PSH and landings (Tugores *et al.*, 2011). At a regional scale, i.e. in the Spanish Mediterranean waters, interesting relationships were found. Spanish landings were correlated with the yearly mean of potential spawning habitat in the Spanish Mediterranean continental shelf waters, i.e. Northern Mediterranean Spanish waters (GSA 6) and Northern Alboran Sea (GSA 1), being the correlation more intense and significant in the GSA6. This is not surprising as long as most of the Spanish sardine captures, with the highest captures in spring and autumn (Lloret *et al.*, 2004), are mainly landed in the ports of the Northern Spanish Mediterranean waters.

The existent relationships among sardine landings in one year and the habitat in late autumn of the same year suggest that higher landings in summer are in some way followed by a higher probability of good spawning grounds in late autumn of the same year. Together with the already mentioned high exploitation rates, sardine can increase the probabilities of larval survival in adverse conditions (e.g. low temperature) through increasing the fat content of spawned eggs (Riveiro *et al.*, 2004). As long as the production of eggs by sardine relies on visceral and muscular fat deposits accumulated during the summer season (Ganias *et al.*, 2007), it seems reasonable that certain relation exists between summer conditions and autumn/winter spawning.

Further evidence of this relationship between what it is observed in summer and the habitat in late autumn is provided by the relationship observed between sardine's coefficient of condition in the Gulf of Lions (GSA 7) during summer (Van Beveren *et al.*, 2014) and the potential and realised spawning habitat of sardine in late autumn. This suggests that good sardine condition during the feeding season (i.e. summer) would raise the probabilities of good sardine condition in the spawning season (e.g. late autumn) which will somehow be reflected in the potential and realized habitat. However, the fact that the summer condition and PSH and RSH were only moderately correlated (~0.70-0.80) and marginally significant suggest that, other factors will be interacting in the definition of the potential and realised habitat of sardine in late autumn, e.g. the size of the population, exploitation or predation rates or, for sure, environmental conditions in late autumn. For instance, the increase of upwelling events during the spawning season have been shown to have negative impacts on sardine recruitment due to increased larval mortality through offshore transport into unfavourable areas (Roy *et al.,* 1989; Santos *et al.,* 2004).

Additionally, the potential spawning habitat in the Spanish Mediterranean waters, as well as the extension of the preferred and hotspot habitat were positively and significantly correlated with Spanish landings in the following year. The correlations with the landings in the following year are generally more intense and more significant than the relationships with the landings of the same year. This highlights the possible use of the PSH of sardine in late autumn and its extension to predict the landings in the following year.

The relationships observed between biological conditions in GSA 7 and the PSH of sardine in GSA 6, or even with landings, most of them very highly correlated and highly significant, clearly points at the idea that environmental conditions that affect sardine habitat in both areas has similar temporal variability and that it may even extent to summer conditions.

Chapter 5. Identifying the potential habitat of European anchovy (*Engraulis encrasicolus*) recruitment in the Mediterranean Sea

Chapter 5. Identifying the potential habitat of European anchovy (*Engraulis encrasicolus*) recruitment in the Mediterranean Sea

5.1 Introduction

Small pelagic fish are known to play a key ecological role in coastal ecosystems, transferring energy from plankton to upper trophic levels (Cury *et al.*, 2000). Their populations are strongly dependent on the environment (Bakun, 1996) and have been found to be sentinels of ecosystem shifts (Alheit *et al.*, 2014). The effects of large-scale environmentally driven changes on the distribution and abundance of small pelagic fish populations have been a major concern for fisheries scientists and managers during the last decades. The frequent drastic reductions that their abundances suffer even in large productive upwelling areas worldwide have caused the collapse of the fisheries operating on small pelagic fish species (e.g. Santojanni *et al.*, 2003; Borja *et al.*, 2008; Takasuka *et al.*, 2008; Lindegren *et al.*, 2013).

In the Mediterranean, anchovy is mainly fished by purse seiners although mid-water pelagic trawls also operate in some areas (Tičina *et al.*, 1999; Lleonart and Maynou, 2003; Basilone *et al.*, 2006; Machias *et al.*, 2008), mostly landed in European countries (>90% in the period 2000-2012; FAO, 1990-2015). The operation and fishing practise of both gears are based on the spatial detection of major fish aggregations using echosounders. Anchovy stocks are highly variable in terms of their recruitment, abundance and distribution while Mediterranean anchovy fishery in many areas suffers from a high degree of exploitation with many stocks showing declining trends for the period 2000-2009 in terms of abundance (Study Group on Mediterranean Fisheries, SGMED 2009, 2010). This makes the examination of the relationship between species spatial distribution and environmental conditions vital.

The increasing interest concerning the climate change effect on fisheries has given the ignition for a number of studies on habitat suitability modelling (e.g. Guisan and Zimmermann, 2000; Francis *et al.*, 2005; Weber and McClatchie, 2010). This approach links species location information to environmental data, determining the combination of these environmental conditions that are suitable for the survival of the species (Guisan and Zimmermann, 2000; Planque *et al.*, 2007; Zwolinski *et al.*, 2011), however in the absence of biotic interactions (like competition or predation). Quantifying the distribution of a species on environmental gradients can provide fish habitat maps that present geographic areas within which the range of environmental factors can determine the presence of a particular species.

The current work takes advantage of acoustic surveys that were routinely applied in the Spanish Mediterranean waters in late autumn for stock assessment purposes. European anchovy spawns in the Mediterranean from spring to autumn (Palomera *et al.*, 1992; Somarakis *et al.*, 2006) largely depending on temperature and presenting a maximum during June and July. Therefore, in late autumn and winter a large proportion of anchovy population consists of recruits (Abad *et al.*, 1998a). Satellite environmental data and bottom depth data, as proxies or surrogates to causal factors, were used to model the factors that are suitable for anchovy presence, inferring spatial variations due to environmental factors and assessing possible ecological relationships.

The potential habitat of anchovy for the entire Mediterranean basin was recreated for each year in order to evaluate persistent areas presenting high probability of anchovy presence as well as its inter-annual variability. Results were evaluated in the framework of existing information from surveys and landings, as well as the hydrographic and productivity patterns that occur in the study area.

The main goals of the present work were, (i) describe the environmental conditions that favour the presence of anchovy recruits in the Spanish Mediterranean waters in mid November-mid December (late autumn), (ii) identify the areas with favourable environmental conditions for anchovy recruits throughout the Mediterranean, (iii) describe the temporal variability of the suitable habitat in different areas of the Mediterranean, (iv) analyse habitat suitability in terms of high probability and temporal persistence in the time series and (v) investigate the degree of spatial overlap between the potential habitat of anchovy recruits and sardine spawners in this period. Finally, we analysed possible relationships between the potential habitat of anchovy recruits and anchovy landings in the Spanish waters and in the Mediterranean.

5.2 Materials and methods

Study area and data collection

The study area comprises the continental shelf of the Mediterranean Spanish Mediterranean waters, between the Strait of Gibraltar and the Spanish-French border (see Figure 1.1, section 1.2). Anchovy presence/absence data (2003-2009) from regular monitoring surveys were used to model and validate the potential recruitment habitat (PRH) of anchovy in late autumn (i.e. mid November-mid December) in the Spanish Mediterranean waters (Western Mediterranean), during the species recruitment season. Details regarding the acoustic sampling and the sampling design are found in the General Introduction (Chapter 1, section 1.4).

Satellite environmental data and bottom depth data were used as explanatory variables to model the habitat of anchovy in the Spanish Mediterranean waters and predict its occurrence throughout the Mediterranean basin, similar to the modelling used in the previous chapter for sardine (Chapter 4, section 4.2).

Data analysis

Model estimation

Generalized Additive Models (GAMs) were applied to define the set of the environmental factors that describe anchovy recruits' distribution in the Spanish Mediterranean waters. Model construction and selection were thoroughly explained in section 4.2. Anchovy recruits' model was constructed using pooled data from the Spanish Mediterranean acoustic surveys from late autumn (mid November-mid December 2004 to 2008). Data from the different years were collated in order to grasp the temporal variability in anchovy distribution area, obtain more possible observed conditions and ensure potentiality (ICES 2005; Planque *et al.*, 2007; Giannoulaki *et al.*, 2008).

Model validation

In a subsequent step, the final selected model was tested and evaluated for its predictive performance for periods not included in model selection. For this purpose, we estimated the Receiver Operating Characteristic curve (ROC) (Hanley and McNeil, 1982; Guisan and Zimmermann, 2000) and the AUC metric, the area under the ROC. The model was validated with data from years not included in model construction, i.e. data from Spanish waters from the years 2003 and 2009. See more details regarding model validation in section 4.2.

Annual potential habitat and habitat suitability

Selected models were used to predict the probability of encountering anchovy for each year over a 4 km cells grid covering the entire Mediterranean basin. Thus, annual maps of potential habitat of anchovy recruitment in late autumn were produced for the entire Mediterranean for a seven-year period (2003-2009).

Habitat suitability was defined according to level of probability and the stability of a particular grid cell over the period 2003-2009. The mean and the coefficient of variation (cv) of anchovy recruitment habitat over the time series were estimated at each grid cell. Habitat suitability maps were constructed, following the description in section 4.2, as follows:

a) **Persistent hotspot**: high average probability (> 0.75) and low temporal variation (cv<0.50)
b) **Persistent preferred habitat**: intermediate average probability (>0.50 and <0.75) and low temporal variation (cv<0.50)
c) **Occasionally preferred habitat**: intermediate average probability (>0.50 and <0.75) and high temporal variability (cv>0.50) and
d) **Unfavourable habitat**: low average probability (<0.50).

Temporal synchrony among adjacent areas

The yearly predictions of potential habitat were averaged on an annual basis over the Mediterranean Geographical Subareas (GSAs) established by GFCM (GFCM, 2009; see section 4.2; Figure 4.2). A yearly-time series consisting of the mean probability of finding adequate habitat of anchovy recruits were constructed for each GSA. Further, the existence of synchrony between the time series of adjacent GSAs was explored by means of Pearson correlation coefficient and tested for its significance. Temporal synchrony among adjacent areas would imply that the mean habitat prediction in two contiguous GSAs increase and decrease concurrently in the yearly time series.

Persistence of habitat overlap among anchovy and sardine

The **persistence of the habitat overlap** among the PRH of anchovy and the PSH of sardine was analysed in order to identify key areas for management purposes. The overlapping habitat was analysed for the hotspot habitat and preferred habitat, following the definition used when analysing habitat suitability. Thus, two levels of probability of concurrently finding suitable conditions for anchovy recruits and sardine spawners were considered: overlapping hotspot habitat (probability of anchovy recruits and sardine spawners >0.75) and overlapping preferred habitat (probability of anchovy recruits and sardine spawners >0.50). For each probability level, every grid cell was classified as 1, if the probability of finding adequate habitat was above the specific level both for anchovy recruits and sardine spawners, and 0 otherwise. The persistence of the overlapping habitat was estimated as the proportion of years for which a particular grid cell was classified as overlapping area in the time series.

Temporal synchrony among anchovy and sardine

The temporal synchrony among anchovy recruits and sardine spawners was analysed at GSA level, in order to determine whether can potentially be considered as a management unit. It was also analysed in adjacent GSAs. For this, the Pearson's correlation coefficient and its significance test at each GSA were calculated for the time series of the yearly average of the PRH of anchovy and of the PSH of sardine at each GSA.

Anchovy recruitment habitat and fisheries landings

The potential habitat of anchovy was analysed at the Mediterranean basin level and in the Spanish waters in relation to sardine fisheries catch data, obtained from the Food and Agriculture Organisation (FAO, 1990-2015), for the period 2003-2009. The analysis was performed by means of R software (R Core Development Team, 2009).

5.3. Results

Data description

The amount of acoustic samples varied between 681 and 1290, owing to the fact that in some years adverse environmental conditions prevented to cover the whole study area (Table 5.1). The amount of nautical miles with presence of anchovy varied from 23.1% to 63.6% (Table 5.1). Regarding the satellite environmental data (Table 5.1), the lowest SLA value was observed in 2008 and the highest in 2004. Regarding temperature, the maximum in the year 2006 was about 2°C hotter than the maximum of the other years (Table 5.1). CHLA values showed the highest minimum value in 2006 while the highest maximum values were observed in 2009 (Table 5.1).

Table 5.1. Description of anchovy presence in the surveys: total amount of acoustically prospected nautical miles (N) and number of positive nautical miles for anchovy (N+).

	Anchovy		SLANOV (cm)		SSTNOV (°C)		CHLANOV (mg m^{-3})	
Year	N	N+ (%)	min	max	min	max	min	max
2003	1290	410 (31.8%)	4.6	14.4	15.13	19.01	0.216	2.501
2004	1130	522 (46.2%)	1.4	19.0	15.63	20.13	0.174	1.966
2005	1126	716 (63.6%)	0.1	5.6	15.75	19.88	0.180	3.719
2006	980	428 (43.7%)	7.6	13.7	15.50	22.38	0.253	1.745
2007	681	174 (25.6%)	4.8	9.7	15.50	19.25	0.202	0.827
2008	1084	250 (23.1%)	-8.6	17.2	15.63	19.25	0.152	2.235
2009	1005	376 (37.4%)	1.2	8.2	15.37	20.38	0.151	11.890
2003-2009	7296	2876 (39.4%)	-8.6	19.0	15.13	22.38	0.151	11.890

Model estimation

Model results are presented in Table 5.2 and the effect of the environmental parameters on anchovy presence is shown as plots of the best-fitting smooths, with 95% confidence intervals (Figure 5.1). Interaction effects are shown as a perspective plot without error bounds. The y-axis reflects the relative importance of each parameter of the model and for the interaction effects this is presented on the z-axis. It should be noted that the effect of each variable is the conditional effect, i.e. the effect of this variable, given that the other variables are included in the model. The percentage of the total deviance explained by the final model was 28.1% (Table 5.2).

The selected GAM included as main effects: the interactive effects of Depth (cubic root transformed) and SLA and the interactive effect of SST and CHLA (log transformed). Depth was the variable that initially entered the model explaining most of the total variation (Table 5.2). Model results indicated higher probability of finding anchovy recruits at two different combinations of SLA and Depth: i) for SLA between -5 and 5 cm anchovy recruits occupy the entire continental platform up to 200 m and ii) SLA between 5 and 10 cm but less deeper waters, i.e. up to about 90 m depth. High probability was also predicted at SST values between 17 to 19 ºC when co-existing with CHLA values of 0.36 to 2 mg m^{-3}. For temperatures above 19ºC and low CHLA values (0.22 – 0.81 mg m^{-3}) a positive relationship could exist but confidence interval do not seem to fully support it (Figure 5.1).

Table 5.2. GAM model selection for anchovy recruits: analysis of deviance for GAM covariates and their interactions of the final models fitted. Res. Df.: residual degrees of freedom; Res. Dev.: residual deviance; Dev. Expl. %: deviance explained %; AIC: Aikaike Information Criteria; p-value: probability that the effects of a variable are not significant (<<0.000: p-value of all variables in the model is <<0.000).

Model	Res. Df	Res. Dev.	Dev. Expl. %	AIC	p-value
Null model	4997.00	6792.89		6794.89	
s(Depth)	4988.59	6047.44	11.0	6066.25	<<0.000
s(Depth)+s(CHLA)	4953.25	5769.90	14.6	5805.41	<<0.000
s(Depth)+s(CHLA)+s(SLA)	4877.19	5183.99	22.3	5265.62	<<0.000
s(Depth)+s(CHLA)+s(SLA)+s(SST)	4782.65	4939.21	24.5	5007.91	<<0.000
s(Depth, SLA)+s(CHLA,SST)	4761.56	4705.82	28.1	4816.70	<<0.000
Total variation explained (%)			28.1		

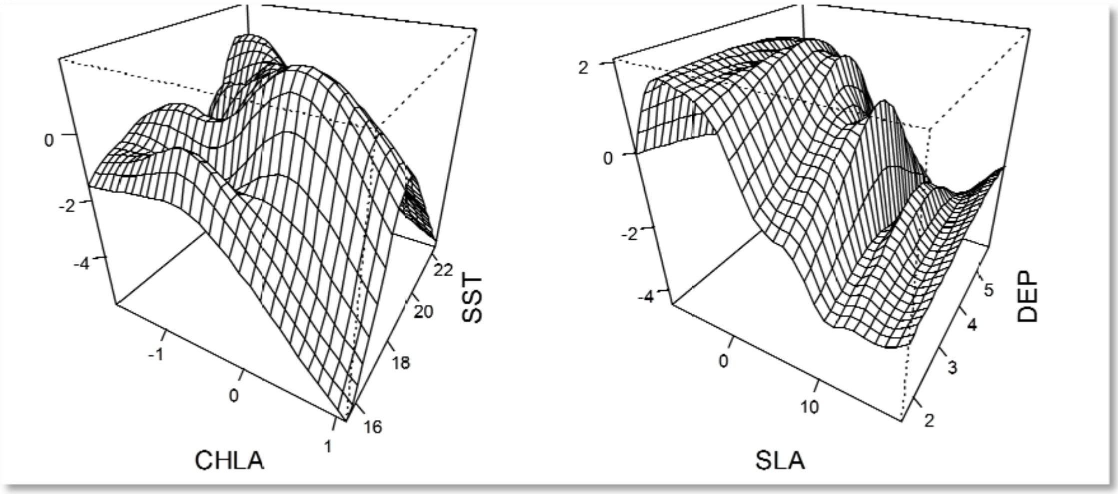


Figure 5.1 Interaction plots of the Generalized Additive Models (GAMs) concerning anchovy recruits in late autumn model.

Model validation

Based on the AUC estimates, validation results indicated from moderate to high model performance, excepting the year 2003 (Table 5.3). The poor performance indicates low reliability of model estimates for that year, being the model more able to predict absences rather than true presence as seen in the specificity parameter being higher than the specificity parameters (Table 5.3). Nevertheless, the overall performance of the model was moderate (AUC 0.78), suggesting the overall estimation of the habitat is pretty good. The ideal case would be that the model showed a good performance both for sensitivity and specificity, so the accuracy measures would show high and similar values for the two measures, which is the case of the year 2007 (Table 5.3).

Table 5.3. *Engraulis encrasicolus* recruits' model evaluation: number of records (N); estimated area under the Receiver Operating Curve (AUC); se: standard error; mean values of sensitivity (s) and specificity (sp) accuracy measures for two threshold criteria: MDT (maximize the specificity-sensitivity sum) and prevalence (PRV) values.

Year	N	AUC (±se)	MDTs	MDTsp	PRVs	PRVsp
2003	1264	0.65±0.02	0.52	0.72	0.21	0.88
2004	1093	0.78±0.01	0.81	0.62	0.72	0.68
2005	1086	0.86±0.01	0.86	0.70	0.73	0.80
2006	954	0.81±0.01	0.75	0.76	0.62	0.84
2007	672	0.88±0.01	0.81	0.80	0.86	0.70
2008	1012	0.80±0.02	0.79	0.69	0.90	0.56
2009	993	0.73±0.02	0.68	0.69	0.35	0.85
2003-2009	7074	0.78±0.01	0.67	0.76	0.65	0.78

Annual potential habitat and habitat suitability

The mean probability of finding adequate habitat for anchovy recruits throughout the Mediterranean varied between 0.09 to 0.33, with highest probability found in 2005 (Table 5.4) while the variability of potential habitat across the Mediterranean varied from 0.50 to 0.90, the lowest variability observed in 2005 as well (Table 5.4). Annual maps of potential recruitment habitat of anchovy showed that most of the Mediterranean areas follow this general pattern of increase from 2003 to 2005 and further decrease 2005 to 2009 although some particular areas like the Balearic Islands (GSA 5) do not follow this general pattern. In the Balearic Islands (GSA 5), the highest predictions are observed in 2003, 2005 and 2008 (Figure 5.2).

Table 5.4. Average potential recruitment habitat of anchovy estimated over the entire Mediterranean basin. N: number of cells in the prediction grid; in brackets: relative standard error (%).

Year	N	PRH
2003	42094	0.09 (0.86)
2004	42021	0.17 (0.70)
2005	42043	0.33 (0.50)
2006	42262	0.20 (0.63)
2007	41942	0.20 (0.65)
2008	41517	0.14 (0.77)
2009	37433	0.09 (0.90)

Habitat suitability maps showed that the persistent hotspot habitat (very high mean, low cv) for anchovy recruitment in late autumn is mainly found in the Western Mediterranean and, specifically in the Spanish coast, mainly in association with the outflow of the Ebro River and in Western Italian coasts (Ligurian) (Figure 5.3). Spots of persistent hotspot habitat were observed in the South Adriatic, Western Ionian, Aegean Sea and in the Moroccan waters (Figure 5.3). Persistent preferred habitat (high mean, low cv) was observed throughout the Mediterranean Sea excepting the Gulf of Gabes, Levantine waters and the Cretan shelf (Figure 5.3). In the Western and Central Mediterranean, persistent preferred habitat appear closely associated to the biggest Mediterranean rivers, i.e. the Rhône and the Po outflow areas respectively. No persistent hotspot or preferred habitat was observed in relation to the Nile River and in the Levantine coasts (Figure 5.3). Occasionally preferred habitat was observed in the Gulf of Lions, in the Tunisian and Libyan coasts, in the Adriatic and Aegean Sea (Figure 5.4).

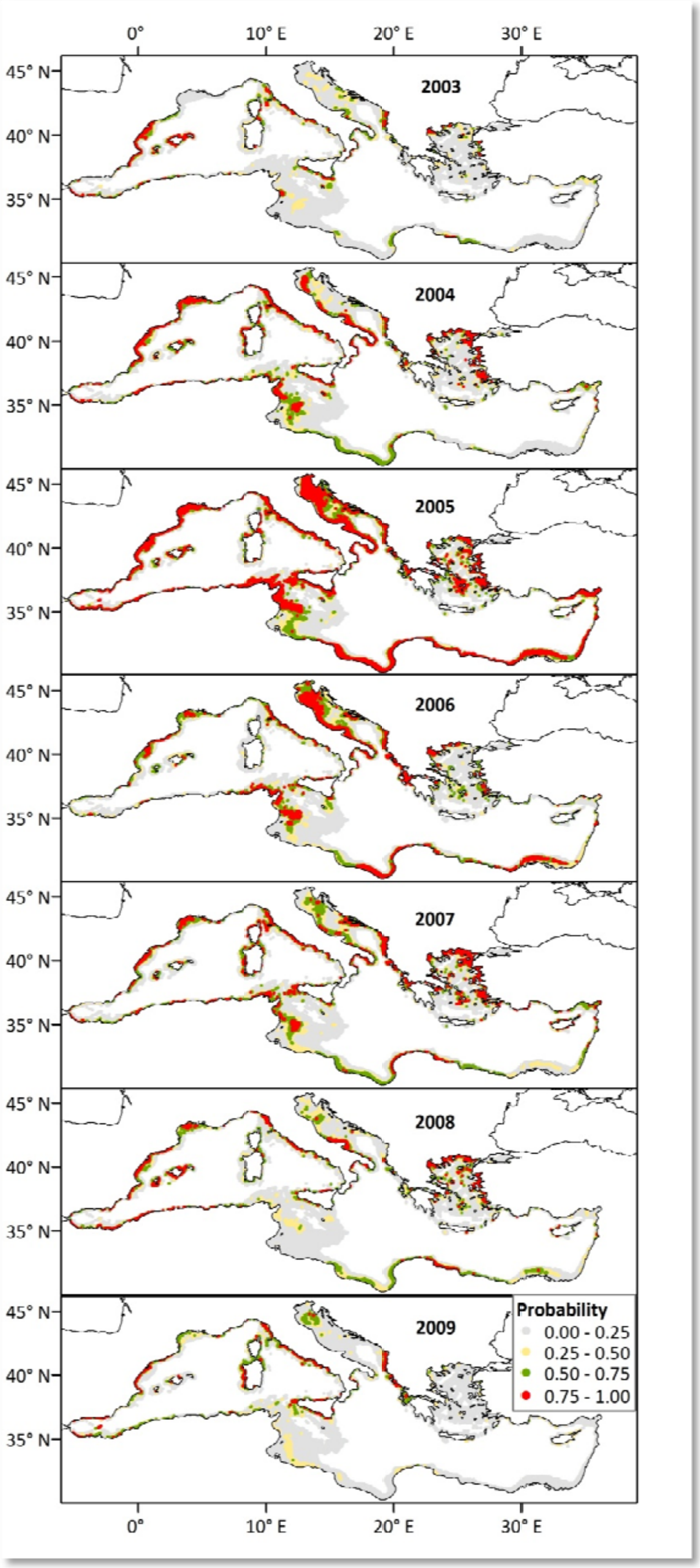


Figure 5.2. *Engraulis encrasicolus*. Potential annual habitat maps indicating the probability of anchovy recruits' presence in the Mediterranean Sea in late autumn (2003-2009) estimated by the GAM model.

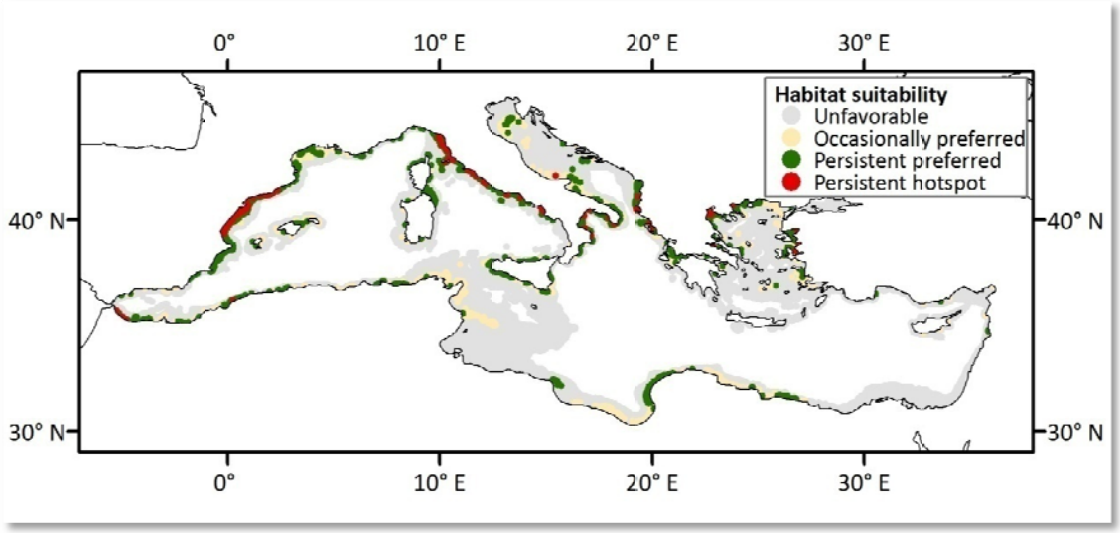


Figure 5.3. *E. encrasicolus*. Habitat suitability map of potential anchovy habitat (2003-2009) in the Mediterranean Sea in late autumn.

Temporal synchrony among adjacent areas

In the Western Mediterranean, positive-significant correlation between anchovy PRH in adjacent GSA areas existed mainly in the most eastern part, i.e. between Ligurian Sea, Tyrrhenian Sea and Southern Sicily, i.e. GSAs 9,10 and 16 respectively, and between the Northern Tunisia, the Gulf of Hammamet and Southern Sicily, i.e. GSAs 12, 13 and 16 (Table 5.5; Figure 5.4). In the Central Mediterranean positive significant correlation of the PRH of anchovy was observed between the Northern and the Southern Adriatic (GSAs 17 and 18). Some less significant correlation was observed in the Northern African coasts, from Morocco (GSA3) to Lebanon and Syria (GSA 27) and between some of the Northern basin GSAs, as the Gulf of Lions (GSA 7) and the Ligurian Sea (GSA9), between Southern Tyrrhenian and Western Ionian and between Western Ionian and Southern Adriatic (GSAs 10, 19 and 18 respectively). Significant correlation exists as well between the Northern Tunisia and Southern Sicily (GSAs 12 and 16; Figure 5.4).

Table 5.5. Synchronies of the PRH of anchovy time series in adjacent areas. cor: Pearson's correlation coefficient; p-value between brackets; W: Western Mediterranean basin; C: Central Mediterranean basin; E: Eastern Mediterranean basin.

	GSAs	Cor		GSAs	Cor
W	1-4	0.78 (0.04)	W-C	10-16	0.93 (<0.00)
	3-4	0.88 (0.01)		12-13	0.93 (<0.00)
	7-9	0.81 (0.03)		12-16	0.86 (0.01)
	9-10	0.95 (<0.00)		10-19	0.85 (0.02)
	8-11.2	0.84 (0.02)			
	10-12	0.87 (0.01)			
C	13-14	0.89 (0.01)	C-E	21-26	0.86 (0.01)
	17-18	0.91 (<0.00)			
	18-19	0.86 (0.01)			
	19-21	0.84 (0.02)			
	16-19	0.79 (0.03)			
E	26-27	0.90 (0.01)			

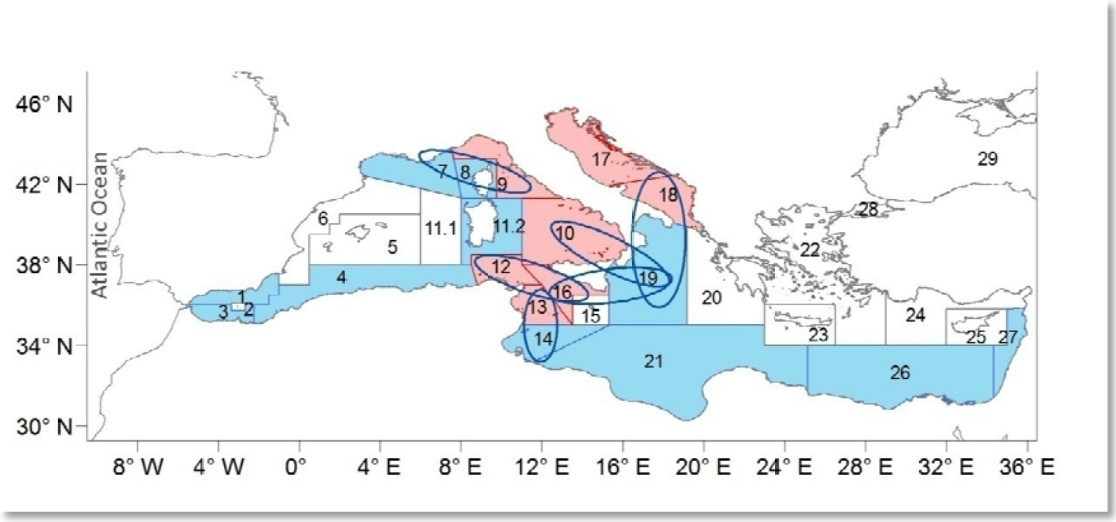


Figure 5.4. *E. encrasicolus*. Temporal synchrony of the time series PRH of anchovy among adjacent GSAs. Red: GSAs with high correlation coefficient (>0.90) and high significant (p-value<0.001); blue: middle correlation coefficient (>0.80 and < 0.90) and low significance (p-value<0.05). Blue ovals indicate intermediate correlation as well.

Persistence of the habitat overlap among anchovy and sardine

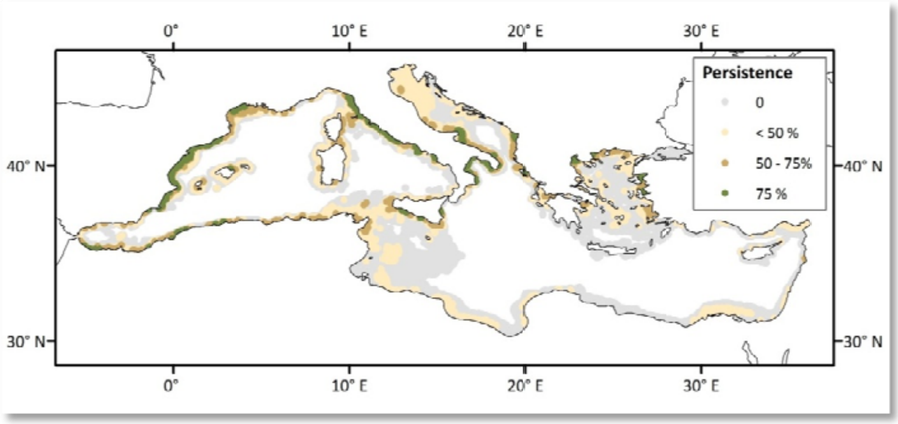
The persistent overlapping habitat among anchovy and sardine, or habitat occupied concurrently by anchovy recruits and sardine spawners, was analysed at two probability levels, i.e. overlapping hotspot habitat (p>0.75) and overlapping preferred habitat (p>0.50). The areas were overlapping preferred habitat showed a high persistence (> 75% of the years) were mainly located in the Western Mediterranean, in the South-West Adriatic, Western Ionian, South and East Sicily and in the Aegean inside the gulfs (Figure 5.5). The overlapping preferred habitat showed a persistence of 50-75% of the years in most of the Western Mediterranean and Sicilian waters but remained absent in the Central and Eastern North-African coasts, where persistence of the overlapping preferred habitat was only observed for less than a half of the analysed years (Figure 5.5). Regarding the overlapping hotspot habitat was scarce throughout the Mediterranean both for the high persistent (> 75% of the years) and for the persistent (50-75%) habitat (Figure 5.5).

Synchrony among adjacent areas between PRH of anchovy and PSH of sardine was pretty scarce and limited to the Western Mediterranean basin (Table 5.6; Figure 5.6). Specifically, positive significant correlation existed between the Alboran Island and the Algerian coast, i.e. GSA 2 and 4 respectively, and between the Gulf of Lions and the Ligurian Sea, i.e GSA 7 and 9 respectively (Table 5.6; Figure 5.6). Positive although less significant correlation existed between the Ligurian and the Southern Tyrrhenian Sea, i.e. GSA 9 and 10 (Table 5.6; Figure 5.6).

Anchovy recruitment habitat and fisheries landings

No significant correlation was observed between landings of anchovy and the PRH for the seven year time series (2003-2009), neither at the Mediterranean scale nor at the Spanish scale. Although not statistically significant, in the Spanish waters the correlation was positive if 2009 was not included.

a)



b)

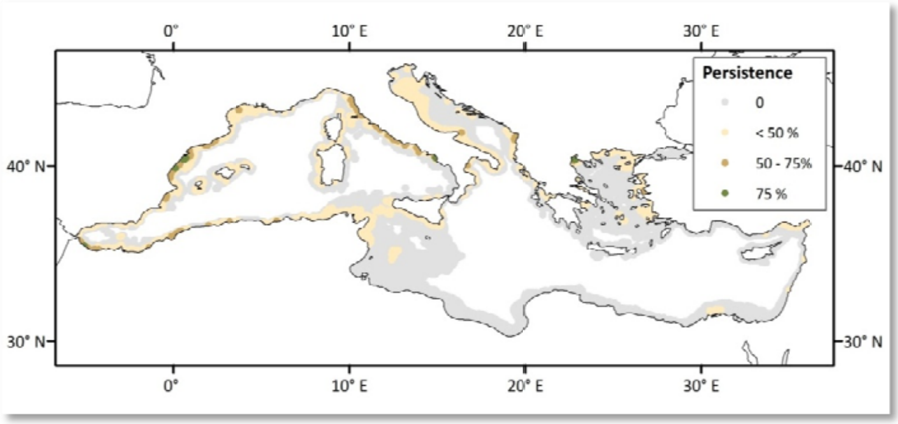


Figure 5.5. *E. encrasicolus* and *S. pilchardus*. Persistence of the overlapping habitat between the PRH of anchovy and the PSH of sardine during late autumn in the Mediterranean Sea. Maps show the persistence for: a) the overlapping preferred habitat ($p>0.50$) and b) the overlapping hotspot habitat ($p>0.75$).

Table 5.6. Synchronies between the time series of anchovy PRH and sardine PSH in adjacent areas. cor: Pearson's correlation coefficient; p-values between brackets; W: Western Mediterranean basin.

	GSAs	cor
W	2-2	0.82 (0.03)
	2-4	0.93 (<0.00)
	7-7	0.79 (0.04)
	9-7	0.92 (<0.00)
	9-9	0.88 (0.01)
	10-9	0.77 (0.04)

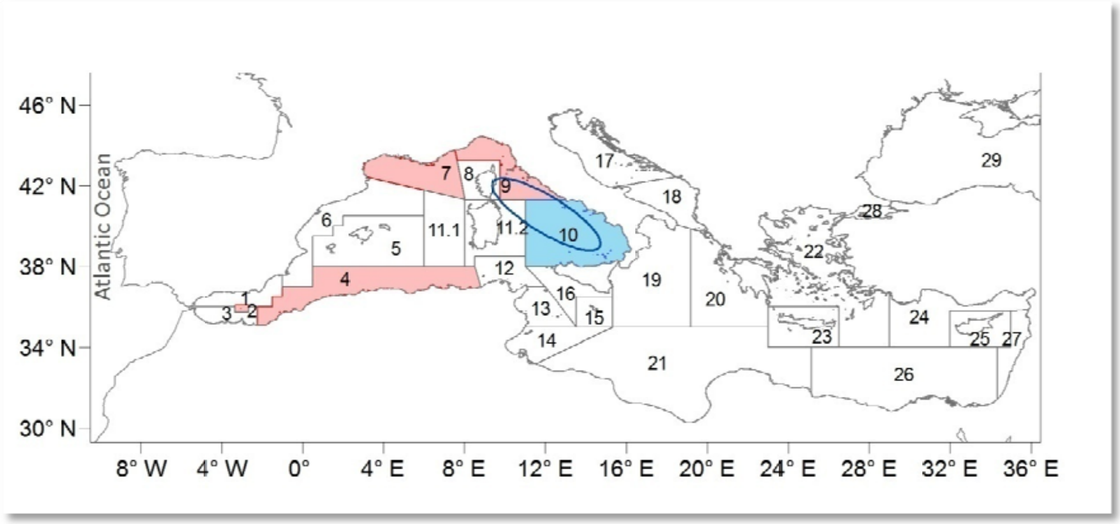


Figure 5.6. *E. encrasicolus* and *S. pilchardus*. Temporal synchrony between the PRH of anchovy and the PSH of sardine among adjacent GSAs. Red: GSAs with high correlation coefficient (>0.90) and high significant (p-value<0.001); blue: middle correlation coefficient (>0.80 and < 0.90) and low significance (p-value<0.05). Blue ovals indicate intermediate correlation as well.

5.4 Discussion

The present work was aimed at obtaining a comprehensive picture of the potential recruitment habitat (PRH) of European anchovy in the Mediterranean Sea in late autumn in relation to environmental conditions. Our initiative was to take advantage of acoustic surveys to increase our knowledge on the spatial distribution of anchovy resources in the Mediterranean and provide a significant tool for the management of anchovy stocks. Gaining knowledge regarding anchovy population during the recruitment season is of due importance, as long as these fraction of the population is highly exploited in the following fishing season (Pertierra and Lleonart, 1996). However, within the Mediterranean Sea little information is available regarding anchovy recruitment (Abad *et al.,* 1998; Santojanni *et al.,* 2001), although other periods of the life cycle like spawning have been more thoroughly documented (Palomera *et al.,* 2007; Morello and Arneri, 2009). Maps indicating habitat suitability for anchovy recruitment were produced for the first time throughout the Mediterranean basin.

The environmental variables explaining higher proportion of deviance of the PRH model were bottom depth and CHLA. However, the finally selected model included the interaction between bottom depth and SLA and the interaction between CHLA and SST. The PRH of anchovy was spread over all the continental platform (up to 200 m depth) when SLA was moderate (between -5 and 5 cm) while for high SLA values (5 to 10 cm) it showed a more coastal distribution (up to 90 m depth). On the other hand, highest probability of PRH of anchovy was found in intermediate productivity waters, identified by intermediate CHLA and SST values between the available ones (i.e. CHLA: 0.36 - 2 mg m^{-3}; SST: 17-19ºC).

The interaction between bottom depth and SLA, may be surrogates of mesoscale circulation, which is related to water enrichment and retention/concentration processes and are known to have significant influence on small pelagic fishes. Sea floor morphology and coastline (and hence bottom depth) introduce changes in water circulation, such as in mesoscale eddies (Kamykowsky, 2014; Arnau *et al.,* 2004) while SLA is being used to identify such eddies (Isern-Fontanet *et al.,* 2003; 2006). Eddies and fronts are responsible of a significant fraction of water enrichment at a mesoscale level, especially in poor waters like the Mediterranean, while in winter vertical mixing is responsible for larger scale enrichment.

Higher CHLA concentrations are located close to upwelling areas although generally not in the area of highest upwelling intensity as long as recently upwelled waters, although being nutrient rich, may have not been enough time in contact to light to let CHLA increase (Bakun, 2006; Mahadevan *et al.,* 2008).Thus, CHLA preferences of anchovy could be related to areas close to upwelling areas. The intermediate CHLA concentrations preferred by anchovy recruits may be related to the choice of areas close to upwelling regions and to the anchovy feeding preferences. As long as anchovy is a zooplanktivorous fish (Tudela and Palomera, 1997) anchovy would be preferentially found in areas with relatively high zooplankton concentration and where CHLA concentration is low possibly explained by a to top-down control of zooplankton on phytoplankton concentration (and hence on CHLA).

In the late autumn Spanish Mediterranean continental shelf waters, lower SST waters are found in the Alboran Sea, related to the gyres originated by Atlantic water entrance, and in the Northernmost waters of the Spanish Mediterranean shelf, more related to the winter vertical mixing of the water column (Figure 5.7). In areas like South Africa or the Alboran Sea, strong upwelling has negative impacts on anchovy as it would lead anchovy early-life stages to open-sea less productive waters, reducing their chances of survival (Ruíz *et al.,* 2013; Boyd *et al.,* 1998; Hutchings *et al.,* 1998).

The suitable recruitment grounds observed in the present study are well known anchovy spawning habitats (Palomera, 1989; García and Palomera, 1996) for anchovy and coincide with the spatial distribution of anchovy larvae from previous studies in the area (Palomera, 1992; Olivar *et al.,* 2001). These highlight the importance of these areas for the subsistence of the anchovy population as long as provide habitat for both larval and recruits.

Our results show that suitable recruitment grounds are found over the continental shelf, close to locations presenting enrichment processes like upwelling areas or the vicinity of river mouths. In the Gulf of Gabes recruitment grounds were indicated for some years in open water, but still over the continental shelf. Anchovy spawning grounds in some areas like North Western Pacific (Oozeki *et al.,* 2007) and distribution of anchovy juveniles, i.e. age-0 individuals not having been recruited to the adult grounds, in the Bay of Biscay (Petitgas *et al.,* 2004; Irigoien *et al.,* 2008) show extended offshore grounds , yet the survival of juvenile anchovy in these offshore grounds and their net contribution to the whole population is not clear (Petitgas *et al.,* 2004). In the Mediterranean Sea, offshore advection of early-life stages could be restricted in space and intensity (e.g. Somarakis and Nikolioudakis, 2007), in comparison with large upwelling areas. Besides the indirect negative effect of intense upwelling on recruits through decreased survival chances for early life stages, a possible direct negative effect of intense upwelling on anchovy recruits would imply that fish would actively avoid offshore waters, recognized as being notably oligotrophic (Bosc *et al.,* 2004, D'Ortenzio and Ribera d'Alcalà, 2009).

All in all, the most plausible explanation is that, at least in the Mediterranean, the spawning areas represent highly suitable areas where anchovy would remain or survive in higher proportions until recruitment in late autumn, in response or as a result of concentration/retention processes. Even if intense upwelling did not have a direct negative impact on anchovy recruits it could be indicating areas where concentration/retention has occurred from summer, when eggs are spawned, till late autumn when recruits are found. Environmental conditions affecting the survival of anchovy from spawning till recruitment should be inspected (Komatsu *et al.,* 2002).

Annual maps of the PRH of anchovy show great **variability in the year-to-year** extension of the habitat and, consequently, habitat suitability maps show high probability and stability in very restricted areas. Although these are general traits throughout the Mediterranean, they seem especially remarkable in the Adriatic Sea (GSA 17 & 18) or the Gulf of Lions (GSA 7). Both the Adriatic Sea and the Gulf of Lions, are known important anchovy spawning sites (Palomera, 1989; Palomera, 1992; Morello and Arnieri, 2009) and they encompass the environmental conditions favourable for a successful anchovy recruitment (Agostini and Bakun, 2002; Nicolle *et al.,* 2009). The two regions have been traditionally important Mediterranean anchovy fisheries. While the Adriatic Sea accounted for about 40-50% of the annual anchovy landings in the whole Mediterranean in the last three decades (1990-2013; FAO, 2009), the fishery in the Gulf of Lions is less important but survey based estimations of anchovy biomass are usually one order of magnitude higher than in the Northern Spanish Mediterranean waters (Palomera *et al.,* 2007). Consequently, either in the Adriatic or in the Gulf of Lions one would expect higher suitability of PRH than it is actually predicted. This can be related to variations in the oceanographic factors that combine to produce an optimal environmental window (Cury and Roy, 1989; Guisande *et al.,* 2004; Fréon *et al.,* 2005). Nevertheless, despite a possible understatement of the PRH of anchovy in these areas (specially in some years), in the Gulf of Lions locations identified with a higher persistence of PRH of anchovy spatially coincide with the areas with higher probability of individual late larval recruitment success from a recent study (Ospina-Álvarez *et al.,* 2015).

The analysis of **the synchronies among adjacent areas** revealed that there is higher synchrony between the GSA areas bounding between the Western and Central Mediterranean as well as between Central Mediterranean GSAs. Areas showing synchronic temporal variation should be taken into consideration as management units as long as the PRH of anchovy show the same temporal trend. Although there are some evidences of connectivity between early life stages of anchovy between the Northern Spanish waters (GSA 6) and the Gulf of Lions (GSA 7) (Sabatés *et al.,* 2001; Ospina-Álvarez *et al.,* 2015), and although river discharges from the Rhône river and the Ebro river are as well related (Lloret *et al.,* 2001; Martín *et al.,* 2012), no positive significant correlation was observed between these two areas. Thus, for what refers to recruitment habitat, there no seem to be evidences for a joint management of Gulf of Lions (GSA 7) and Northern Spanish Mediterranean waters (GSA 6).

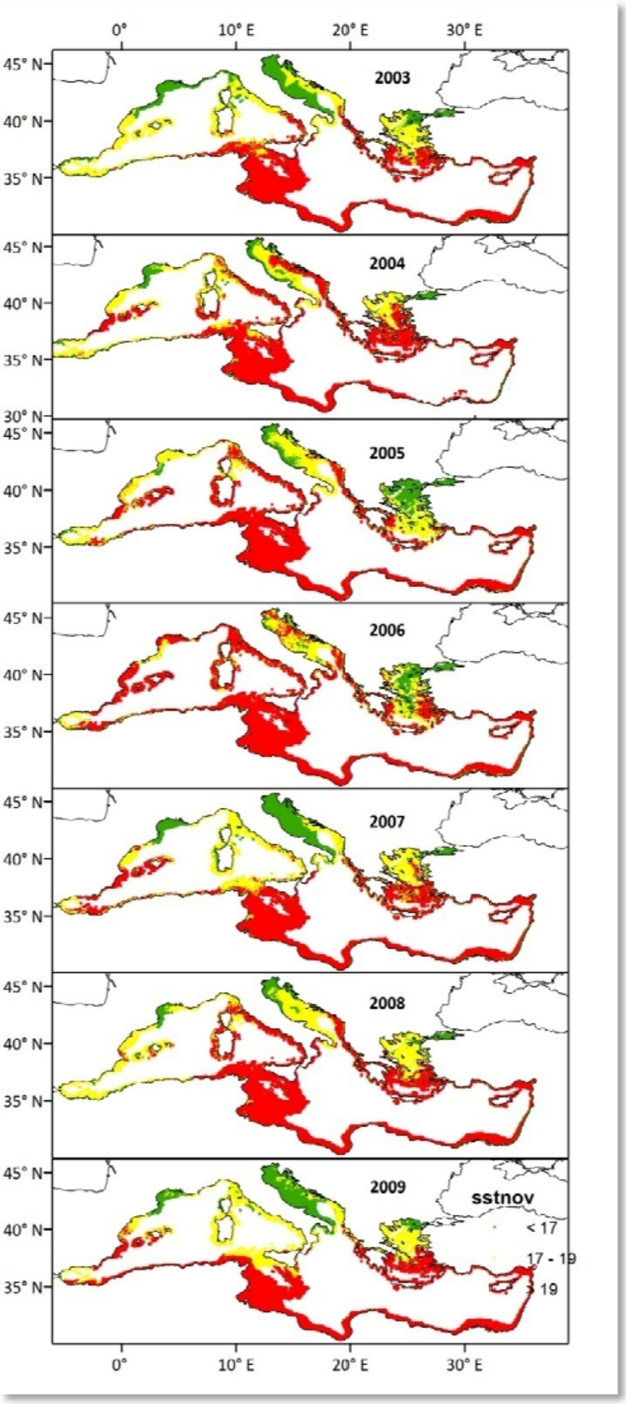


Figure 5.7. Spatial distribution of monthly average of sea surface temperature (SST) in November from satellite data.

The comparison of the **PRH of anchovy and the potential spawning habitat (PSH) of sardine** in late autumn (presented in Chapter 4), reveal that the PRH of anchovy show higher inter-annual variability than the PSH of sardine (see “Results” in Chapter 4, section 4.3). This could be related to different sensitivity to (or dependence on) environmental conditions of anchovy rather than sardine (Ruíz *et al.*, 2013) or to different sensitivity of different life-stages. Furthermore, sensitivity to environmental conditions could be as well indirectly related to abundance of the population (Brander, 2005; Cahuin *et al.*, 2013).

The overlapping habitat between **anchovy recruits and sardine spawners** in this period was rather limited and mainly restricted to the Spanish Mediterranean waters, the Gulf of Lions, Ligurian, South Adriatic and Western Ionian and some small Gulfs in the Aegean Sea. The protection of the overlapping habitat would imply protecting two important Mediterranean species at the same time. Nevertheless, the reduced overlapping persistent area suggest low probability of inter-specific competition between anchovy recruits and sardine spawners and further low probability that anchovy would feed on sardine eggs. This is in the line with previous studies indicating very low or null egg content in anchovy's stomachs (Costalago *et al.*, 2014; Borme *et al.*, 2009).

No significant linear relationship was found between **the PRH of anchovy and landings** in the Mediterranean basin or in the Spanish waters. However, relationships could arise in other Mediterranean regions as in the Adriatic, where annual maps of anchovy PRH show a decrease in the predictions from 2005 till 2009 while anchovy landings suffered a huge decrease one year latter (Figure 5.8). Thus, it would require further investigation.

Our results show that although both species inhabit the continental shelf, anchovy recruits seem to occupy a wider range of bottom depth than sardine and inhabit a wider area than sardine spawners. This is in the line with previous studies suggesting that both species, although pretty similar, do not occupy exactly the same ecological niche (Gutiérrez *et al.*, 2007).

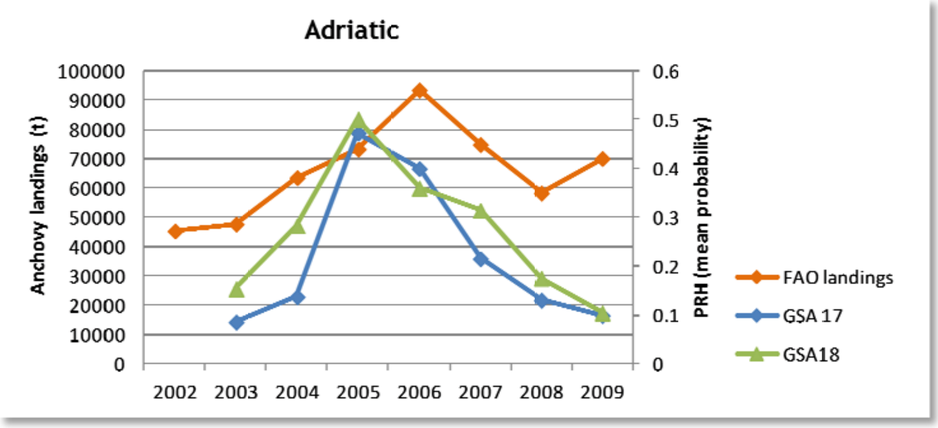


Figure 5.8. Anchovy landings from the Adriatic (FAO, 2009) and time series of the potential recruitment habitat of anchovy (PRH) in the Adriatic (GSA 17 and 18).

Besides environmental and hydrographic features that define potential habitat, realized habitat further depends on factors such as the population abundance or predators' abundance (Planque *et al.*, 2007). However, potential habitat is still of interest from an ecological aspect as long as the models can be conditioned in order to predict potential changes in the habitat according to different climate scenarios. Habitat suitability maps (as well as annual PRH maps) are a simple way to visualize possible regime shifts, reflected in the shrinkage and expansion of suitable habitat, which are known to occur between small pelagic fish (Cury and Shannon, 2004). Moreover, spatially explicit information is considered essential in operational systems for ecological-based planning and management (Cardinale *et al.*, 2011). Large-scale conservation planning requires the identification of sensitive or priority areas in which species have a high likelihood of long-term persistence, areas of particular importance for the maintenance of the stock.

Future work should include the definition of indexes more effectively describing the spatial variability of the water masses and that could explain better the spatial location of the habitat of anchovy. More useful indicators than the bare satellite data could be include upwelling indexes, concentration/retention indexes or variables describing the location of fronts and eddies. The effects of environmental variables and/or derived indices of summer (or during the previous 3-6 months) on the PRH in late autumn should as well be explored.

Chapter 6. General Discussion

Chapter 6. General discussion

Marine living resources have constituted important sources of food and economic resources worldwide since ancient times. From the World fisheries captures, pelagic fish represent a significant share, i.e. 35-40%. Besides their economic importance, small pelagic fish are essential components of the ecosystem by transferring energy from lower to upper levels of the trophic chains (Cury *et al.,* 2000). Their populations are highly sensitive to environmental variability and changes (Cole and McGlade, 1998; Lloret *et al.,* 2004) and have been identified as sentinels of climate shifts (Alheit *et al.,* 2014).The decline and collapse, even temporary, of their populations can have dramatic impacts on the ecosystem by reducing food supply to species in higher trophic levels (Pinsky *et al.,* 2011).

Fisheries management has traditionally been based on single-stock assessment and aimed at avoiding overexploitation (Bosford *et al.,* 1997; Pauly *et al.,* 1998). The focus was at determining the maximum sustainable yield that will allow a sustainable exploitation of the resource so that the level of fishing in the present would not compromise the future profit. In the last decades, growing attention has been given to the application of an ecosystem approach to fisheries management (Pikitch *et al.,* 2004). This implies the practical recognition of the living organisms as important elements within the ecosystem (Tansley, 1935) rather than isolated items. Thus, a part from the living organisms and the physical (or habitat) factors and the complex interplay of relationships among them will need to be considered. However, **the ecosystem based approach to fisheries management (EBFM) aims at maintaining ecosystem quality and sustaining the diverse benefits expected from marine ecosystems** (Brodziak and Link, 2002).

The European Union legislation incorporates this ecosystem based approach to fisheries management within the Marine Strategy Framework Directive (MSFD, DIRECTIVE 2008/56/EC), which is aimed at achieving a good environmental status (GES) by 2020. The MSFD incorporates eleven qualitative descriptors for determining GES that range from marine litter to biological diversity or hydrological conditions. However, single species stock assessment remains crucial as long as the third of the MSFD descriptors stands "*Populations of all commercially exploited fish and shellfish are within safe biological limits, exhibiting a population age and size distribution that is indicative of a healthy stock*" and it is still of interest in the research community (Worm *et al.,* 2009; Mora *et al.,* 2009; Petitgas *et al.,* 2010).

This thesis is both an attempt to increase the knowledge regarding small pelagic fish within the Mediterranean while providing useful information for fisheries management purposes. Thus, it starts with a conventional stock assessment point of view, taking sardine and anchovy as case studies, and then evolves to a broader approach by identifying the environmental factors that shape the habitat of these two species in late autumn (mid November-mid December). For these purposes, data from ECOMED acoustic surveys, which were conducted annually in late autumn over the Spanish Mediterranean continental shelf by Instituto Español de Oceanografía (IEO) were used.

6.1 Stock assessment, spatial distribution and fisheries management

In order to know if *a population is within safe biological limits* and be able to manage fish stocks, the first and most basic question is how much resource is available or, in the present case, "*How many fishes are there in the sea*"? Sardine and anchovy abundance estimates derived from the ECOMED acoustic surveys were annually reported by IEO to General Fisheries Commission for the Mediterranean Sea (GFCM) stock assessment groups. In a second instance, the manager would like to know whether those abundance estimates have a small associated error or not, or "*How trustful are the abundance estimates?*" This question was not routinely estimated and was the first objective to be achieved in this thesis.

A revision and qualitative estimation of the many sources of error associated to acoustic surveys was performed and included in the present work as an Annex (Annex 1), for the Spanish late autumn acoustic surveys. We then focused in the estimation of one of the errors that are thought to be one of the main contributors to random error, i.e. **the error associated to the sampling scheme**. Data used for this comprised a four year time series (2003-2006) of the ECOMED surveys and the study area was restricted to the Northern Spanish Mediterranean waters, where the higher amount of abundance and landings of both species are generally observed (IEO unpublished data; CGPM, 2005).

The estimation of the error associated to sampling scheme is statistically complex due to the type of sampling (systematic) and due to non-normal and spatially autocorrelated data. We used geostatistics, a methodology that estimates sampling variance taking into account the autocorrelation observed in the data (Matheron, 1965; Petitgas, 1993). However, the huge non-normality of acoustic derived data (and of many natural resources) made us wonder about the reliability of the uncertainty estimates obtained by means of geostatistics (Carr *et al.,* 1985; Guiblin *et al.,* 1995; Rufino *et al.,* 2006a; Webster and Oliver, 2007; Kerry and Oliver, 2007a,b). Hence, our approach applied two geostatistical methods and different methodological options within the geostatistical analysis in order to have an idea of the robustness of the methods applied. Because, **where is the point in estimating uncertain estimates of uncertainty?**

In the present work, estimates of the uncertainty in abundance estimates of sardine and anchovy were derived for the first time in the Northern Spanish Mediterranean shelf, analysed the spatial structure of their distributions, derived from late autumn Spanish acoustic surveys. This exercise served as well to increase the knowledge regarding these two species. This was performed by means of transitive geostatistics in 1D (see Chapter 2), which reduces the 2D information to 1D by summing up the abundances in each transect. This simpler method requires few statistical assumptions than other more elaborated 2D methods. The precision of abundance estimates in the whole study area estimated by transitive geostatistics in 1D were among acceptable ranges (10-18%) for the two analysed species. Similar studies analysing the precision of other pelagic species in Norway or Senegal yielded results varying between 4 and 15% (Petitgas, 1993; Samb and Petitgas, 1997).

A two dimensional estimation of the precision of global abundance estimates was explored in a following chapter (Chapter 3) for anchovy, as long as its probability distribution function in the area is more skewed than that of sardine and thus, it is more likely to show problems. We focused in a smaller area, the surroundings of the Ebro river. For anchovy, precision estimates were consistent with those obtained with the more complex intrinsic geostatistical method in 2D, supporting the idea that the simpler T1D method would suffice for acoustic surveys or for other surveys applying similar sampling designs (e.g. CUFES). For sardine, it was revealed that in a declining stock context, the temporal evolution of precision should be assessed to ensure it continues to being within an acceptable range as long as a negative relationship between abundance and precision was observed.

The simplified 1D data revealed varied degree of overlap between sardine and anchovy but with segregation in the highest abundances. It further revealed that, while the abundance of sardine varied synchronically in the entire study area the variation of anchovy diverged between the most northern and narrow continental shelf area (with some relation to the Gulf of Lions) and the southernmost and wider continental shelf area (under the direct influence of the Ebro river). However, the analysis of the 2D structure provide additional information for survey design and maps of the spatial distribution of anchovy in the shelf surrounding the Ebro river were produced revealing a patchy distribution of anchovy.

The origin of low precision in the abundance estimates of anchovy in one year (i.e. 2006) and of the high skewness of the probability distribution function of anchovy was related with a few amount of samples that represented very high abundance and yet not outliers but significant fraction of the population. These high values were producing poor precision estimates in a particular year. So, the spatial location of the high abundance values of anchovy (or of any species if such phenomenon is observed) should be routinely identified and their location followed across time in order to increase sampling intensity where these high values occur and try to increase the precision of the estimates.

As expected, abundance estimates were robust to all tested methodological options while the 2D spatial analysis and the global precision were not robust to data transformation, but it was generally needed to retrieve the spatial autocorrelation structure due to the huge skewness (skewness >7) of the probability distribution functions. In similar occasions (data with similar pdf), the logarithmic transformation should be used in order to apply a conservative approach. Although retrieving the spatial structure with a transformed dataset, the interpolation should be performed on the original data to obtain closer mean abundance estimates to that observed in the samples. Furthermore, in the variogram construction, care should be taken in the family of model to be applied (to accommodate as much as possible to the variogram), using least squared fitting methods and lag width between the EDSU and the inter-transect distance to avoid non-sensical results.

Automatic tools for spatial analysis and interpolation through kriging have been designed (Hiemstra *et al.*, 2008), which are highly useful for normally distributed data. This would ensure 100% objectivity and reproducibility of the analysis. Although we tried as much as possible to make the analysis reproducible and objective, our experience showed that geostatistical analysis for highly correlated and skewed data requires expert judgement if non-sensical results are to be avoided. While the intrinsic 2D methods are implemented within RGeoS library, within an open access environment like the R software, the simpler but effective transitive 1D geostatistics is not. The implementation of the 1D approach within the R software would be of interest.

6.2 Habitat identification, suitability and overlap

The natural environment shapes the habitat of every single species on Earth and determines where a species can potentially be found (*potential habitat*). However, the particular locations where a species is actually found (*realised habitat*) also depends on a complex net of inter-relationships among the different species and between the every species and the environment, further delineating the ecosystem. Thus, increasing the knowledge about the habitat of a species contributes to the ecosystem based approach to fisheries management as it helps delineating the areas that are critical to species for vital population processes.

For pelagic species, inhabiting the water column, the processes that are thought to be of major significance in the description of their habitat are those related with water circulation, water enrichment and concentration and retention processes (Bakun, 1996). In the semi enclosed and oligotrophic Mediterranean Sea, the most important enrichment mechanisms are related with land runoff from rivers, mesoscale oceanographic features such as gyres, eddies and fronts, coastal upwelling and winter water mixing due to the cooling of surface waters (Estrada and Vaqué, 2013). As an example, shelf-slope fronts and outflows of major rivers were related to anchovy spawning (Palomera, 1992) while mesoscale eddies were found to shape the spatial distribution of anchovy larvae (Sabatés *et al.*, 2014).

Thus, in the second section of the thesis (Chapters 4 and 5), we identified the environmental factors that shape the habitat of sardine and anchovy in late autumn, through relating the data from ECOMED acoustic surveys with satellite and bathymetric information. A nine-year time series was made available (2003-2009) in this occasion and the study area was widened to encompass the whole Spanish Mediterranean continental shelf, so that a wider combination of environmental scenarios were analysed. Late autumn corresponds to sardine spawning season and to anchovy recruitment season, so the analysed habitats correspond to sardine spawning habitat and anchovy recruitment habitat. Further, sardine egg data was retrieved from 2006 to 2009 and estimates of the realised habitat of sardine produced for the entire Mediterranean basin.

As environmental variables we used satellite and bathymetric data which do not allow a fine spatial resolution but allow making inferences and predict the habitat of the species throughout the Mediterranean basin. Bottom depth, sea surface temperature, chlorophyll-a concentration and sea level anomaly were the environmental variables defining the habitat of both sardine and anchovy although the percentage of variance explained by each variable differed for sardine, sardine eggs or anchovy recruits and the final models included different interactions among the variables. Thus, the similar albeit not identical habitat together with the spatial segregation of the highest abundances (observed in the 1D geostatistical analysis), give forward evidences to the idea that sardine and anchovy, although similar, do not occupy exactly the same ecological niche (Gutiérrez *et al.*, 2007).

Maps of annual predictions of habitat were produced for the entire Mediterranean basin that allows the inspection of spatio-temporal variability of the habitat of these species. Additionally, habitat suitability maps allowed the identification of areas where the habitat is highly probable and persistently in time (if they exist), constitute interesting areas for protection purposes as they more likely contribute to the species subsistence/persistence (or whatever) over time. Furthermore, maps showing the areas where the habitat of sardine and anchovy overlap were produced.

Areas with higher probability and stability, as well as areas with overlapping habitat for two (or more species) would deserve additional efforts in order to be protected rather than areas that vary more greatly in time or show lower average probabilities. Thus, the spatial component of the habitat and spatial distribution of a species, a bunch of two species, community or ecosystem is essential for management purposes if one objective is to try to avoid interferences between different human activities making use of similar or of the same space, the spatial location of important areas to be protected is crucial, as it has been recognised within the EBFM (Pikitch *et al.,* 2004).

However, the temporal scale should not be forgotten. Similar to an approach taken within the STOCKMED project (Fiorentino *et al.,* 2014), an analysis of the temporal correlation among the mean annual habitat prediction at each GSA area was performed, so that positive and significant correlations would indicate areas that may potentially be managed as one unit. Between the Gulf of Lions (GSA 7) and the Northern Spanish Mediterranean waters (GSA6), no correlation was observed for anchovy but positive significant correlation was observed for sardine. Anchovy larval advection from the Gulf of Lions (GSA7) to the Northern Spanish Mediterranean waters (GSA6) has been described (Sabatés *et al.,* 2004; Ospina-Álvarez *et al.,* 2015). However, anchovy in the years 2003-2006 showed picks of abundance in the most northern area of the Northern Spanish Mediterranean waters that were not observed in the southern area (the area of wide continental shelf surrounding the Ebro river) and the recruitment habitat was not correlated among GSA7 and GSA6. Our results, thus, suggest that the relationship observed in the larval stage only has significant effects on the local anchovy population in some years and/or at a local scale.

For sardine, conversely, relationships among the temporal time series of PSH, landings and summer condition factor from GSA7 derived from a recent work (van Beveren *et al.,* 2014) suggest that GSA7 and GSA6 might constitute a management unit for this species.

Future prospects

The acoustic surveys conducted by IEO are not stand alone surveys but they are standardised and coordinated with the international community in an effort to make stock assessment throughout Europe comparable. So, in the year 2009 the ECOMED acoustic surveys were replaced by MEDIAS acoustic surveys, conducted in summer and EU financed. Acoustic surveys conducted now in spring-summer cover the entire Iberian Spanish continental shelf for stock assessment purposes and are coordinated by ICES in the Atlantic waters and by GFCM in the Mediterranean.

Additionally, the RV Cornide de Saavedra has been replaced by the newer RV Miquel Oliver. So, to start with, a quantitative estimation of the main sources of errors associated to the RV Miquel Oliver and an effort to mitigate the most significant errors as much as possible would be needed. Some sources of error need further research, as species allocation and the target strength.

Acoustic surveys are significant platforms for collecting information from a wide range of aspects, from the biology of the species of interest (e.g. condition factor, etc) to ecological interaction with other fish (e.g. stomach contents analysis) or for the observation of top predators like marine mammals or marine birds (e.g. space overlap). They can be used as well to provide information about lower trophic levels such as plankton (Pinot and Jansá, 2001), environmental data regarding water quality, nutrient contents, pollutants, hydrodynamics or information regarding detection and distribution regarding jellyfish (Peña *et al.,* 2014), of due interest for recreational activities. This holistic approach is being applied in the new surveys but some could be retrieved from re-examining and re-processing of the ECOMED acoustic surveys, if not regarding the biology and interaction of the species, at least regarding their spatial co-occurrence as a proxy of probability of interaction.

The estimation of the precision of abundance estimates should accompany the routine estimates of abundance of assessed species. The amount of assessed species should be increased to all the encountered species however having in mind that the errors associated with the estimates of each species may differ.

The mapping of the spatial distribution and of the habitat of the species should be extended to the whole pelagic community. The exploration of different spatial scales, from local, regional and up to the Mediterranean scale, provides complementing information that would increase the knowledge of the functioning of the species and of the ecosystems.

Further investigation on the relationships among landings, abundances and the habitat of the species of interest would be another remarkable field in an attempt to predict landings in future years. This would allow the adoption of a dynamic management, which will vary annually according to expected catches and population metrics, such as the one implemented in the Bay of Biscay.

Habitat models could be used to provide estimates under different climate scenarios. However, additional years and seasons of the year would be needed in order to have a picture of the within year variability and evolution of the habitat, trying to evaluate the periods and life-stages more sensible to environmental variability and to other factors. Generation of derived oceanographic variables that could better identify productivity and retention/concentration processes would be of interest in order to try to improve the habitat identification.

Finally, the economical and social aspects of the fisheries deserve attention as long as the possible interactions with other human activities in order to provide sound management advice within the ecosystem based approach to fisheries management. Even the rise of meat price could have impacts on fishing pressure and fish abundance.

Chapter 7. General conclussions

Chapter 7. General Conclusions

7.1 Stock assessment, precision and spatial distribution of sardine and anchovy in the Northern Spanish Mediterranean continental shelf waters

1. European sardine and anchovy stocks showed declining trends between 2003 and 2006. The highest abundances of these species were located near the Ebro River Delta, spatially segregated and anchovy being closer to the river mouth. Maps of anchovy distribution were produced for the first time in the study area and showed a patchy spatial distribution.
2. The precision of the global abundance derived from sampling design was in general good (10%-18%) for the two species and the results were consistent among the two geostatistical methods applied, i.e. transitive in 1D and intrinsic in 2D.
3. The poor precision of anchovy abundance in 2006 was improved after removing a few amount of very high values located in shallow waters (up to 100 m) near the Ebro River mouth. These high values were not outliers but a significant fraction of the population. So, an increase of the sampling intensity in this area would be recommendable to avoid low precision in similar situations.
4. For sardine, the inverse relationship between abundance and precision bringing to light that attention should be paid to avoid low precision, in the stock context.
5. The 2D spatial modelling required the *a priori* adoption of several methodological options to avoid nonsensical results. Data transformation, use of spherical or exponential models, the application of least squares methods and a lag width between the minimum and maximum distance among samples were required.
6. Data transformation should be avoided as far as possible. However, for hugely skewed data (skewness>7) it is unavoidable to use a data transformation to be able to retrieve the spatial structure. In that case, log-transformation provides the lower probabilities of overestimating the precision.
7. The spatial structure and the global precision were not robust to data transformation while abundance was robust to all methodological options and, showed a small negative bias, in relation to sample estimates, provided that the interpolation was performed on the untransformed data.
8. The information retrieved from the 1D and 2D approaches is complementary. The 1D approach is sufficient to estimate the precision of global abundance and provide valuable information in a proxy of a latitudinal direction and regarding inter-annual variation. The 2D method allow providing distribution maps which are of due interest for management and planning.
9. The analysis of the precision of global abundance contributes to improve the accuracy of the estimations that were annually presented in stock assessment groups and/or to increase knowledge regarding the species ecology and spatial distribution.

7.2 Habitat identification of sardine and anchovy in late autumn

10. Suitable sardine spawning and anchovy recruitment grounds in late autumn are found over the continental shelf, occupying a similar habitat but not identical, giving further support to the idea that both species do not occupy exactly the same ecological niche. The habitat of both species was positively influenced by intermediate sea surface temperature and chlorophyll-a, suggesting a location close to water enrichment and retention/concentration processes (e.g. river discharges and upwelling areas) known to influence small pelagic fish. However, anchovy can be found up to deeper depths, depending on SLA values.
11. Sardine eggs drift was evidenced by the fact that eggs were encountered in the colder temperatures of those preferred by spawners and up to deeper bottom depths.
12. Habitat suitability maps showed that sardine eggs occupied similar locations than sardine sapwners throughout the Mediterranean although less extended. The estimated spawning grounds of sardine match with fish distribution estimated by acoustic surveys and known spawning grounds.
13. Suitable recruitment grounds of anchovy identified in the present study are well known spawning habitats for anchovy and coincide with the spatial distribution of anchovy larvae from previous studies in the Spanish Mediterranean waters, highlighting the importance of these areas for the subsistence of the anchovy population as long as provide habitat for both larval and recruits.
14. The habitat estimated for sardine eggs and for anchovy recruits showed higher year-to-year variability than the habitat of sardine spawners, suggesting higher sensitivity of the early life stages to environmental variability.
15. Temporal synchronies among adjacent areas throughout the Mediterranean showed, for sardine spawners and eggs, higher synchrony in the northern African and eastern Mediterranean coasts. For anchovy recruitment, the higher synchronies were observed in the GSA areas bounding the Western and the Central Mediterranean Sea as well as within the Central Mediterranean areas. The areas showing temporal synchrony should be considered as possible management units.
16. Habitat suitability maps are useful tools to identify areas with high likelihood and long-term persistence of a species or life-stage habitat, being areas of critical importance for the maintenance of the species stock and should be considered for management purposes like temporal closures or marine protected areas. Additionally, the habitat overlap maps represent a useful tool in order to establish protected areas in overlapping areas that are highly persistent encompassing the protection of two species or two life-stages.

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ANNEX. Main erros associated to abundance estimates of pleagic fish stocks the case of late autumn Spanish Mediterranean acoustic surveys (2003-2006)

ANNEX. Main errors associated to abundance estimations of pelagic fish stocks: the case of late-autumn Spanish Mediterranean acoustic surveys (2003-2006)

Errors associated to the estimations of any variable can be classified, depending on how they affect the observation, in a) systematic errors, when they affect all the observations in the same way and with the same intensity, reducing the accuracy of the estimates and introducing a bias or b) random error, if they can have variable effects on the estimations, sometimes increasing and sometimes decreasing the estimate, without any defined pattern, reducing the precision of the estimates. Thus, accuracy is similarity between the estimated value and the real value of the studied phenomena (e.g. fish density) and is inversely related to bias, while precision is the similarity between successive samples of the same phenomena and is affected by random errors.

The origin of the errors might be diverse, e.g the sampling instruments, the person in charge of the sampling (sampler), the nature of the analysed variable or the environment in which it is found. The main errors usually encountered in acoustic surveys and their expected relative importance were compiled by Simmonds and MacLennan (2005) (Table A1.1).

Table A1.1. Expected percent error for the most common sources of error found in abundance estimates derived from acoustic surveys (adapted from: Simmonds and MacLennan, 2005).

Source of error	Systematic (Bias)	Random (Accuracy)
Calibration	± 3 a 10	± 2 a 5
Transducer motion	0 a -25	
Bubble attenuation	0 a -90*	
Hydrographical conditions	± 2 a 25	± 2 a 5
Target strength (TS)	0 a 50	± 5 a 25
Species identification		0 a 50
Random sampling		5 a 20
Migration	0 a 30	
Daily behaviour		0 a 50
Avoidance	0 a 50	

*for hull-mounted transducers

However, when acoustic surveys are used to obtain estimates of abundance over an area, the precision of these estimates will depend as well upon the sampling design, the spatial distribution of the species, the echogram partitioning to obtain the proportion of fish species by means of pelagic fish trawls or abrupt changes in fish distribution due to stormy events. Of these, the random error which is considered to be the most important in acoustic abundance estimates is the sampling design (ICES, 1998). Although the application of a random sampling design would simplify the estimation of the precision, it has been considered counterproductive to the abundance estimates and to its accuracy (Simmonds and Fryer, 1996).

This Annex revises the most common sources of systematic error that are commonly found in the acoustic surveys directed to stock estimation, making a quantitative analysis of their importance in the Spanish Mediterranean late autumn acoustic surveys (ECOMED) for the period 2003-2006.

Accuracy in abundance estimations: sources of systematic error

1. Calibration and sensitivity of the instruments

In late autumn Spanish Mediterranean acoustic surveys the calibration of the 38 kHz transducer, the one used for abundance estimation, is performed prior to each survey with a 60 mm diameter copper sphere and following the standard method (Foote *et al.,* 1987). The method consists in locating a standard target of known reflective properties below the transducer, usually a copper or tungsten-carbide sphere, with the aid of three winches (Figure A1.1). The calibration is accepted if the root mean square (RMS) between the echo received from the standard target and the theoretical model is equal or less than ± 0.1 dB. This corresponds to a 0.3% of the expected echo of the 60 mm copper sphere at a sound velocity in sea water of 1500 m s^{-1}, which is -33.6 dB. Thus, systematic error due to acoustic instruments is negligible. The sound speed in sea water used until 2005 was the standard 1500 m s^{-1}. In the year 2006, however, with the incorporation of the new echosounder EK-60, the sound speed used is 1 510.7 m s^{-1}, which is the sound speed at 100 m for sea water at 15 ºC and 37 ppm (Mackenzie, 1981).

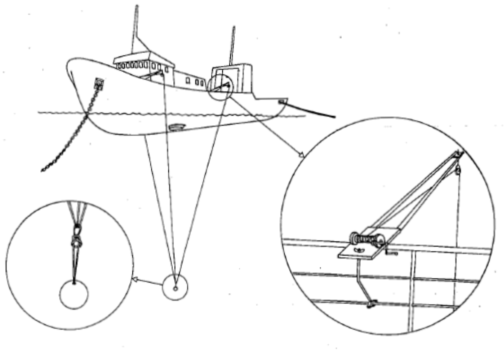

Figure A1.1. Disposition of the winches used to allocate the calibration sphere below the transducer (Source: Foote *et al.,* 1987).

2. Transducer motion

Acoustic surveys aimed at pelagic fish stock assessment generally use a hull-mounted transducer and, thus, measurements will be affected by the vessel movement: pitch, roll and forward vessel movement. The misalignment between the emission and the reception reduces the mean amplitude of the received signal and introduces bias in the estimates. This bias is more intense for narrow beam-angle transducers, which are generally used in scientific echosounders, and increases in bad weather conditions due to the increase of pith and roll (Simmonds and MacLennan, 2005).

The bias introduced by the forward vessel movement depends on the sound speed and on the vessel speed and can be easily quantified. Given a constant speed of 10 knots (5.14 m s^{-1}) and a sound velocity of 1,500 m s^{-1} the deviation between the emission and the reception angles is thought to be of about 0.4º (Simmonds and MacLennan, 2005). The bias introduced in abundance estimates due to cruise progression is <1.4% (Stanton, 1982) and thus, it is not critical when compared to the effects that pitch and roll might have on the estimates. On the other hand, pitch and roll cause a misalignment directly related to the rotation of the transducer (Figure A1.2) and to the depth where the insonified target is encountered and inversely related to the transducer beam-angle (Stanton, 1982).

In order to minimise this error, compensation of the vessel movement should be sought by means of mounting the transducers on a protruding keel at the vessel hull (Ona and Traynor, 1990) or the vessel itself could be equipped with active stabilisation systems. Both measures, however, are costly to implement and were not installed in the research vessel used in late autumn Spanish Mediterranean acoustic surveys, i.e. R/V Cornide de Saavedra.

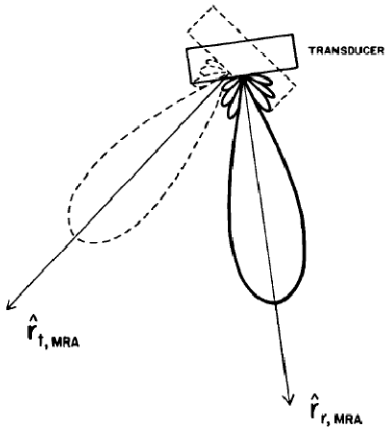

Figure A1.2. Transducer movement generating a misalignment between emission (solid line) and reception (dashed line) of sound (Source: Stanton, 1982).

For narrow transducers, like the 38 kHz hull-mounted on the R/V Cornide de Saavedra (7x7°), deviations of only 5-6 degrees (or higher) between emission and reception angles are critical, >50% bias (Stanton, 1982). Thus, the vessel pitch and roll should be measured by means of a tilt sensor and its effects on the transducer directivity should be estimated and incorporated as a correcting factor on the estimates (Stanton, 1982).

3. Surface bubble layer

Air bubbles located below the transducer can cause extra attenuation to the emitted and received sound, causing measurement bias. Especially wind, but also vessel movement, can generate a layer of air bubbles, with higher vertical extension in bad weather conditions. Theoretical and semi-empirical works (Novarini and Bruno, 1982; Feullidade, 1996; Ye, 1997) predict the extra attenuation caused by bubble layers. These models do not take into consideration the vertical displacement of water caused by the vessel during the surveys and, thus, underestimate the extra attenuation that occurs in acoustic surveys (Weston, 1989). Nevertheless, extra attenuation can be measured by analysing the resonance of the bubble layer or differences in bottom integration observed at the echogram (Dalen and Lovik, 1981).

The installation of a protruding keel can efficiently reduce the effects of the bubble layer for wind speeds up to 19 m s^{-1} (Ona and Traynor, 1990). In 2006 the transducers in the R/V Cornide de Saavedra were installed in a protruding keel of 1 m width, attached to the vessel hull. This may reduce the bias caused by the surface bubble layer but, as the transducers are located at 6-7 m from the sea surface (considering hull+keel) and the bubble layer may reach 20 m deep in bad weather conditions, the effect is not removed. Prior to 2006 hull-mounted transducers were used and thus, estimates obtained prior to 2006 may suffer higher extra attenuation. Moreover, as long as in the late autumn Spanish Mediterranean acoustic surveys the transects are located in more or less the same geographical position since 2003, an attempt could be made to compare the integration of the bottom to quantify the possible existence of extra attenuation.

1. *Hydrographical conditions*

Sound intensity diminishes while travelling through water. This reduction is mostly caused by the geometric dispersion and the absorption. Geometric dispersion is caused by the fact that the further the sound goes from the transducer, the bigger is the area in which the sound is distributed. It only depends on the distance from the transducer. The absorption of the sound waves by the water is inversely related to wavelength and also depends on hidrographical conditions, such as water temperature, salinity and pressure (depth) (Mackenzie, 1981; François and Garrison, 1982).

Given temperature and salinity, at a 38 kHz working frequency and a maximum depth of 200 m, the error due to hydrographical conditions is < 3% (MacLennan, 1990). However, hydrography may vary in different areas and times of the year and thus the error can be bigger. The presence of a thermocline, and the depth at which it is found, is particularly important because sound velocity changes.

In the Mediterranean Sea, stratified waters are observed in summer, with thermocline at 5-30 m depth with high temperatures at the surface and lower temperatures (~ 13-13.5ºC) below 60 m. In winter, the whole water column homogenises reaching low temperatures (~13.1-13.4ºC, Olivar *et al.,* 2001). In autumn and spring, an intermediate situation is observed with surface temperatures of 18-20ºC and homogeneous cold waters (~13ºC) below 100 m (Segura, 2007).

In the Spanish Mediterranean waters, acoustic surveys were annually performed between the end of November and mid-December (i.e. late autumn/early winter) when an intermediate situation exists, as a transition between summer stratification and winter homogeneity. For this reason, the presence of a thermocline is not considered an important source of bias by the time of the year the surveys are performed. Nevertheless, the bias could be quantified and corrected on the basis of CTD stations performed throughout the study area.

In the Spanish Mediterranean continental shelf, the hydrography is complex and could introduce variability in the sound velocity and absorption. For instance, in the Strait of Gibraltar, colder and less saline Atlantic waters enter the Mediterranean Sea; in the Gulf of Rosas colder water from the Gulf of Lions may reach the area, or in the vicinity of the Ebro delta, fresh water river inputs . Moreover, periods of intense winds, typical of the time of the year the surveys are carried out, enhance vertical mixing of the water column and should be taken into consideration.

4. Fish target strength

The target strength (TS) is a logarithmic measure of the proportion of sound intensity that reaches a target (I_i) and is backscattered by the target at a 1 m distance (I_r), of the form:

$TS= 10 \log (I_r/I_i)$ (i.e. Burczynski, 1979) (Eq. A1.1)

The swimbladder, an organ generally air-filled but sometimes fat-filled, takes part in fish buoyancy and hearing. At 38 kHz, which is the frequency commonly used to estimate the abundance of pelagic fish stocks, 90-95 % of the eco backscattered by a fish comes from the swimbladder (Foote, 1987). For fishes without swimbladder, their echo at 38 kHz is weak, making their identification and abundance estimation more difficult at this frequency (McClatchie and Coombs, 2005). Nevertheless, for fishes without swimbladder (i.e. Atlantic mackerel, *Scomber scombrus*) and opposedly to swimbladdered fish, the relative response at 200 kHz is higher than at 38 kHz (Nesse *et al.,* 2009), allowing the identification of the species.

TS depends on the species, the existence of a swimbladder and its type (open or closed) (MacLennan, 1990), fish length, the depth at which the target is located or even physiological factors like fat content or maturity (Ona, 1990; Machias and Tsimenides, 1995; Jorgensen, 2003; Zhao, 2008). Although an expanded target strength relationship for herring was developed (Ona, 2003), for stock assessment of anchovy and sardine the simple model relating the TS with the fish length (see Eq. A1.1) is of common use.

The estimation of fish TS can be performed by means of laboratory experiments with immobile fish (Foote and Nakken, 1978; Kinacigol and Sawada, 2001), life fish in cages (Lillo *et al.,* 1996; Gauthier and Rose, 2001) or with in-situ measurements of fish at sea (Degnbol *et al.,* 1985; Foote *et al.,* 1986), which are usually assumed to be more representative of schooling fish observed during surveys. However, in-situ measurements require i) the presence of one dominant species in the trawls or two species but with very different size ranges (Foote *et al.,* 1986) and ii) dispersed fish (or dispersed enough) to allow single-fish detection which is usually observed during the night. Nevertheless, it has to be assumed that target strength from dispersed fish is representative of target strength in fish schools may need a correction for tilt angle distribution (Kloser *et al.,* 2013). Multi-specificity of the Spanish Mediterranean waters makes this situation hardly found. In fact, in the years 2003-2006 the amount of fish trawls that accomplish these pre-requisites are not enough.

Given the lack of in-situ data bibliographical values of b_{20} values are used and, in many occasions, adapted from other species (see Chapter 1, section 1.4 on “Data processing”). Thus, this source of error is supposed to be important in abundance estimation of pelagic fish stocks. Nevertheless, the importance of TS is lower if the aim is obtaining abundance indices rather than absolute values, which will be comparable between years. Due to the multi-specificity of the Spanish Mediterranean waters, the method used for splitting the s_A between species (see Chapter 1, section 1.4 on “Data processing”) takes into account the proportion of each species and its TS thus, an error in one species’ TS propagates to the other species’ abundance estimations.

5. Species migration

For any survey aimed at estimating the population of a certain species it is important that the sampled area covers the entire habitat occupied by the population. Many fish species make annual migrations for reproduction, feeding or wintering purposes. If the population is migrating while the sampling takes place, abundance estimations can suffer from bias even if the entire habitat is sampled. Acoustic surveys for pelagic fish stock assessment are usually conducted in the same period of the year to avoid different annual biases due to migration. The intensity of this bias will vary depending on the relative direction and relative speed between the fish migration and the progression of the survey.

Given the direction and velocity of the migration and of the vessel progression the bias in abundance estimation (E_Q) is computed as follows:

$$E_Q = Q\,(1 + v_f/v_s) \qquad \text{(Eq. A1.2)}$$

where Q is the abundance estimation, v_f is the velocity of the migration and v_s the velocity of the survey in relation to the migragion; v_s is positive when both fish and survey progress in the same direction. If the transects are long and perpendicular to the migration, v_s is much smaller than v_f, i.e. if vessel speed is 5 m s^{-1} and transect length is 10 times the inter-transect distance, then the survey progress at v_s=0.5 m s^{-1}, a value that could be comparable to fish speed (Simmonds and MacLennan, 2005).

Nevertheless, no migration patterns have been described in the Western Mediterranean neither for sardine nor anchovy and thus, the bias from this source is expected to be negliglible or nule.

6. Daily behaviour

Pelagic fish generally perform aggregation-dispersion behaviours on a daily basis, forming schools close to the bottom or at mid-water during the day and ascending and getting dispersed by dusk (Blaxter and Holliday, 1969; Muiño *et al.,* 2003; Milne *et al.,* 2005). In some cases the dispersion is not linked to ascension to the water surface (Bertrand *et al.,* 2004; Zwolinski *et al.,* 2007) and in coastal waters the ascension and dispersion is linked to an horizontal migration towards the coast, moving offshore during the day (Fréon *et al.,* 1993a and references therein). In clupeoid fishes, daily migrations are thought to be triggered by light intensity (Blaxter and Hunter, 1982).

The aggregation-dispersion behaviour can bias the estimations mainly because of three reasons. First, the criteria for reading the echograms may vary between day and night. Second, because a varying proportion of the stock may ascend to the sub-surface blind zone (upper than the transducer) or descend to the bottom blind zone. Third, during ascension-descent, fish TS may change because of the angle formed between the fishes and the transducer (e.g. Foote and Nakken, 1978; Huse and Ona, 1996) and/or due to variations in the swimbladder volume, especially in physostome fishes, i.e. open swimbladder (Simmonds and MacLennan, 2005). If the acoustic sampling is carried out during the day and during the night further bias may exist if some demersal species behave as pelagic during night (Fréon *et al.,* 1993b).

In late autumn Spanish Mediterranean acoustic surveys, acoustic sampling was only performed between dawn and dusk, thus reducing the bias caused by the fraction of stock located in the blind zones and eliminating the bias caused by echogram reading. Nevertheless, the bias caused by the ascension-descent of the fishes has not been described or quantified in our area. In the surroundings of the Ebro delta, anchovy and sardine schools aggregate at dawn more rapidly than they disperse at dusk, i.e. lasting 1 hour the aggregation and 2 hours the dispersion (Fréon *et al.,* 1996). Taking this into consideration, if we take for instance the survey in 2005, a gross estimation rises that up to 13% of the acoustic sampling (that comprised in the 1+2 hour of ascencion/descent) could underestimate abundance of small pelagic fish stocks.

On the other hand, during the late autumn Spanish Mediterranean acoustic surveys fishing trawls are performed during night. The possible bias of demersal fishes entering into the catch is avoided by taking into account only pelagic species for estimating species proportions. Moreover, demersal fishes are not considered in the partition of the echo received as they do not form schools and echointegration is performed only for schools observed during the day.

7. Vessel avoidance

Some pelagic fish species when surpassed by a vessel may develop avoiding reactions (e.g. Gerlotto and Fréon, 1992; Mitson, 1995; Gerlotto *et al.,* 2004) or may not (Skaret *et al.,* 2005; Handegard and Tjostheim, 2005). Avoiding reactions can include vertical descents and horizontal movements. Vertical descents have been studied with echosounders and are observable some minutes prior and after the vessel surpass (Vabo *et al.*, 2002; Mitson and Knudsen, 2003; Ona *et al.*, 2007) while horizontal movements have been studied with sonars (Aglen, 1994 and references there in).

Avoidance reactions have been generally considered to be related to hearing (e.g. Olsen *et al.*, 1983b; Engas *et al.*, 1995; Mitson, 1995) and influenced by the directivity of the noise generated by the vessel (e.g. Misund and Aglen, 1992). In the 1990s and 2000s, efforts were made to construct vessels under ICES noise reduction specifications (Mitson, 1995) but studies conducted with this type of vessels have not demonstrated a reduction of fish avoidance (Ona *et al.*, 2007; De Robertis *et al.*, 2008). Other sources of fish avoidance could be the infrasound noise, as fish are particularly sensitive to sound between 20 and 0.001 Hz (Chapman and Sand, 1974; Sand and Karlsen, 2000; Wahlberg and Westerberg, 2005) or particle acceleration produced by the vessel movement or by sound emission. The volume of water displaced (Sand *et al.*, 2008), the visual stimulus of the vessel shadow (Aglen, 1994) or lights during night observations (Ona and Toresen, 1988; Lévénez *et al.*, 1990) can have an influence in avoidance reactions. Furthermore, motionless vessels can cause attraction to fishes even with the engines on (Rostad *et al.*, 2006).

Factors affecting the existence and intensity of avoidance reactions are many, e.g. the depth where the fishes are found (Gerlotto and Freón, 1992; Vabo *et al.*, 2002; Mitson and Knudsen, 2003; Ona *et al.*, 2007; De Robertis *et al.*, 2008), hydrographical conditions affecting sound propagation (Misund and Aglen, 1992), ambient noise that could mask vessel noise (Ona *et al.*, 2007), the vessel speed, the season, the time of the day (Vabo *et al.*, 2002; Jorgensen *et al.*, 2004), learning processes related to the level of explotation of the stock (Marler and Terrace, 1984 in Gerlotto and Fréon, 1992) or the use of new vessels of unknown noise patterns for fish (Ona *et al.*, 2007). The species hearing and/or visual capabilities play also a determinant role. The same species can show avoidance reaction or not depending on the life cycle or the time of the year (Jorgensen *et al.*, 2004; Skaret *et al.*, 2005).

Underestimation of abundance due to avoidance reactions can occur if fishes move outside the vessel track or, if the movement is downwards to deeper waters, due to swimbladder compression or due to changes in tilt angle that can affect fish TS (Simmonds and MacLennan, 2005). Vertical avoidance can produce the compression of the fish school which do not necessarily imply a variation in the mean density in the area (Gerlotto and Fréon, 1992; Fréon *et al.*, 1992). Nevertheless, avoidance reactions can reduce reflected energy and, thus, underestimate the abundance (Olsen *et al.*, 1983a; Olsen *et al.*, 1983b). Sometimes the bias may be limited to night observations (Vabo *et al.*, 2002; Jorgensen *et al.*, 2004) or, even if avoidance reactions exist, the effect on abundance estimations may be negligible or absent (Gerlotto and Fréon, 1992; Lévénez *et al.*, 1990; Fernandes *et al.*, 2000) or the effect may be observed just after the vessel of echosounder surpass, and thus will have no practical effects on abundance estimations (Ona *et al.*, 2007).

Avoidance reactions can be structured in two phases. In the first phase, at long distance, a number of schools would be trapped at the vessel track due to the hull acoustic shadow, while another group of schools would escape laterally. In the second phase, at short distance, the schools initially trapped in the vessel track would escape laterally and vertically and a second group of schools would only move vertically (Soria *et al.*, 1996). Methods applied so far to correct avoidance reaction effects on abundance estimates have only corrected for the second phase reactions (Vabo *et al.*, 2002; Hjellvik *et al.*, 2008) and the combined effect of the long and short distances avoidance has not been properly studied yet (Aglen, 1994).

In the surroundings of the Ebro River mouth, where sardine and anchovy dominate the pelagic fishing trawls, it was observed that the density of schools was higher at a certain distance from the vessel and a 50% reduction of school density was described in the vessel trajectory (Soria *et al.,* 1996). Due to the variable nature of avoidance reactions it is necessary to analyse the avoidance reactions of the species under study, during the time of the year the survey is conducted, with the same vessel and, if possible, with the same weather and environmental conditions in which the survey was conducted.

8. Precision of species proportion estimation: Net avoidance

One commonly accepted assumption in pelagic fish estimations is that the samples obtained in pelagic fishing trawls are representative of the analysed populations. This is a simplification of the reality, because studies have described avoidance reactions during fishing operations depending on the species and age (Fréon *et al.,* 1993a) that could be even more intense than the reactions observed during acoustic sampling (Ona and Godo 1990; Handegard and Tjostheim, 2005). Fish escape from the net by immediate visual contact and its intensity diminishes during the night (Glass and Wardle, 1989). However, endogenous rythms may also have an impact as it has been observed sudden increments in the capturability just before dawn, without an increment of the light intensity (Baudin-Laurencin, 1967). Moreover, fish have learning abilities that may increment avoidance in front of a fishing gear (e.g. Soria *et al.,* 1993).

With the aim of having a qualitative approach, the size ranges of the fishes caught during the echosurveys were compared to the size ranges of the fishes caught by the purse seine fisheries in the area under study (between Albufera de Valencia and the Spanish-French border) between November and December of the years under study (unpublished data, IEO). The size ranges were similar both for sardine and anchovy (Table A1.2) and thus, no major bias is expected in the estimated size ranges.

Table A1.2. Size ranges (cm) in late autumn Spanish Mediterranean acoustic surveys and in sampling obtained from the landings of purse seine fisheries during November-December.

	Sardine		Anchovy	
Year	Echosurveys	Fisheries	Echosurveys	Fisheries
2003	8.0 – 25.5	9.0 – 22.0	5.5 – 16.0	6.5 – 17.0
2004	7.5 – 22.5	10.0 -23.0	4.0 – 16.5	9.5 – 16.0
2005	8.0 – 22.5	11.0 – 22.5	6.0 – 17.0	7.5 – 17.5
2006	8.0 – 23.0	9.0 – 22.5	7.0 – 18.0	10.0 -16.0

9. Non linearity

One of the main echointegration assumptions is linear relationship between the energy received at the transducer and the amount of fishes (Simmonds and MacLennan, 2005). This linearity principle may not hold in high density schools, slowing down the increase of energy with the increase of the number of fishes (Rottingen, 1976).

This effect may be caused by shadowing or multiple scattering. The shadowing effect is produced by the absorption of a fraction of the emitted acoustic energy by the fishes that are in the upper side of the school. Thus, fishes below receive lower sound intensity and their backscattered echo is lower than the expected in the linearity case. Multiple scattering occurs when the sound received by a target does not come only from the transducer but also from the surrounding fishes. If the sound coming from the surrounding fishes is more intense than the sound coming directly from the transducer, the sound escapes out of the school more slowly than in linear case and the school rings like a bell (Figure A1.3).

In such case the effect may introduce a significant bias and thus it should be quantified by some of the available methodologies by in situ measuring the intensity variation along the school (Toresen, 1991; Foote *et al.*, 1992; Foote, 1999; Zhao and Ona, 2003) or by means of hydrophons (Furusawa *et al.*,1992). In Moroccan coasts correction factors of between 1.03 and 1.36 where estimated for some sardine schools (Uumati, 2004).

In late autumn Spanish Mediterranean acoustic surveys this effect is not likely to be a major concern as generally schools' densities are not too high. In the Spanish Mediterranean acoustic surveys recorded maximum s_A values of about 48,000 m^2 mn^{-2}, 21,000 m^2 mn^{-2}, 24,000 m^2 mn^{-2} and 12,00 m^2 mn^{-2} in the surveys of 2003 to 2006, respectively, and generally in the Alboran Sea. Thus, echograms should be checked for the possible existence of such error and, if occurred, it should be corrected, especially in the areas where high density values are registered.

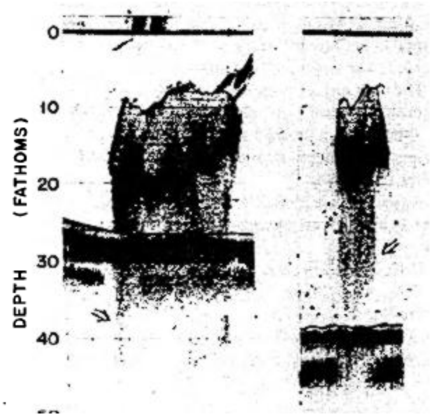

Figure A1.3. Multiple scattering observed in two herring schools: indicated by the "tails" of echo are seen just below the school (Source: Stanton, 1984).

10. Non-accessibility: blind zones and unsampled areas

Blind zones, or portions of the water column not accessible to the echosounder, are due to their proximity to the sea bottom or because they are located between the sea surface and the depth where the transducer is located (Simmonds and McLennan, 2005). In the R/V "Cornide de Saavedra" transducers are located at about 6-7 m depth. In the late autumn Spanish Mediterranean acoustic surveys blind zones are not thought of as an important source of error as long as the acoustic sampling is performed during the day, when fish schools are located at mid water (Fréon *et al.*, 1996).

Unsampled areas are locations or regions not covered by the acoustic sampling but where a part of the population is found (Simmonds and McLennan, 2005). Although for a given survey the unsampled area may remain constant from year to year, the fraction of unsampled population is likely to vary (Brehmer *et al.*, 2006). In the late autumn Spanish Mediterranean acoustic surveys, the volume of water comprised between the shoreline and 30 m depth (an area of ~1,591 nm^2 and ~19% of the continental shelf) is not sampled due to constraints in navigation and in pelagic trawl operations. Quantifying this type of error requires the use of complementary platforms sampling the shallower waters at the same time than the acoustic survey is performed.

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