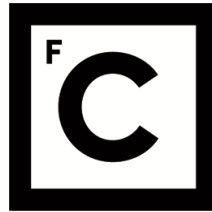


UNIVERSIDADE DE LISBOA
FACULDADE DE CIÊNCIAS



**Ciências
ULisboa**

**An ecosystem approach to pelagic fisheries management in
Portuguese continental waters**

“ Documento Definitivo ”

Doutoramento em Ciências do Mar

Dorota Szałaj

Tese orientada por:

Doutora Alexandra Silva

Professor Doutor Henrique N. Cabral

Professor Doutor Pedro Ré

Documento especialmente elaborado para a obtenção do grau de doutor

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According with the paragraph a) of the 2nd paragraph of the Article 26 of the Regulation of the Post-graduate Studies of the University of Lisbon (Diário da República N° 175 de 2020, 2^a série de 8 de setembro de 2020), this thesis includes papers published or submitted (Chapter 2 to 6) in collaboration with other co-authors.

The leading author of the papers of this thesis, was responsible for conceptualization, data acquisition and processing, methodology (model design, simulations), formal analysis (data and statistical analysis) and manuscript writing.

The candidate is the second author of the paper “First representation of the trophic structure and functioning of the Portuguese continental shelf ecosystem: insights into the role of sardine”, included in the Chapter 3, and was co-responsible for methodology, formal analysis, and manuscript writing.

In total, this thesis consists of five papers listed below, each one corresponding to a Chapter, from 2 to 6. Four papers corresponding to chapters 2 to 5 were published in international peer review journals while paper corresponding to chapter 6 has been submitted and is currently under review.

Chapter 2:

A GIS-based framework for addressing conflicting objectives in the context of an ecosystem approach to fisheries management—a case study of the Portuguese sardine fishery.

Szalaj, D., Wise, L., Rodríguez-Climent, S., Angélico, M.M., Marques, V., Chaves, C., Silva, A., Cabral, H. 2018.

Published in *ICES Journal of Marine Science* 75 (6), 2070–2087.

Chapter 3

First representation of the trophic structure and functioning of the Portuguese continental shelf ecosystem: insights into the role of sardine.

Veiga-Malta, T., **Szalaj, D.**, Angélico, M.M., Azevedo, M., Farias, I., Garrido, S., Lourenço, S., Marçalo, A., Marques, V., Moreno, A., Oliveira, P.B., Paiva, V.H., Prista, N., Silva, C., Sobrinho-Gonçalves, L., Vingada, J., Silva, A. 2019.

Published in *Marine Ecology Progress Series* 617-618. 323-340.

Chapter 4

Food-web dynamics in the Portuguese continental shelf ecosystem between 1986 and 2017: Unravelling drivers of sardine decline.

Szalaj, D., Torres, M.A., Veiga-Malta, T., Angélico, M.M., Sobrinho-Gonçalves, L., Chaves, C., B. Alcoforado, B., Garrido, S., Ré, P., Cabral, H., Silva, A. 2021

Published in *Estuarine, Coastal and Shelf Science* 251.

Chapter 5

Detecting Regime Shifts in the Portuguese Continental Shelf Ecosystem Within the Last Three Decades.

Szalaj, D., Silva, A., Ré, P., Cabral, H. 2021.

Published in *Frontiers in Marine Science*.

Chapter 6

Predictions of sardine and the Portuguese continental shelf ecosystem dynamics under future fishing, trophic and SST scenarios.

Szalaj, D., Silva, A., Ré, P., Cabral, H.

Under review in *Marine Pollution Bulletin*

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Abstract

The ecosystem approach to fisheries management (EAFM) is a new paradigm in fisheries management, that incorporates multi-species, habitat, environmental, and socio-economic elements. Within the scientific community and on the political agenda, EAFM has been recognised as a powerful approach to assist with the management of depleted stocks. However, a clear consensus on how this approach should be implemented in practice is still lacking.

The primary aim of this thesis was to apply an EAFM to pelagic fisheries in the Portuguese Continental shelf ecosystem (PCSE). Portuguese pelagic fisheries were chosen as a case study because its main resource sardine has considerably declined in the last two decades. To achieve this aim, a set of methodological approaches to EAFM were used in the context of this fishery. These methodological approaches included spatial analysis, ecosystem modelling (Ecopath with Ecosim) and statistical/indicators approach.

This research advances the application of the EAFM in the Portuguese pelagic fishery by, developing tools to support the management of the fishery and by deepening understanding of the PCSE and sardine dynamics. The key findings showed that trophic interactions followed by fishing were the main drivers of PCSE while a rise in sea surface temperature (SST) followed by fishing had the largest impact on sardine decline. This research highlighted that the management besides fishing restrictions should consider other factors that turn out to be important drivers of future sardine change. They are a rise in SST, trophic interactions, especially between sardine and predators of sardine eggs, and the possibility of regime shift occurrence. Moreover, results demonstrated that the pelagic fishery has conflicting objectives between conservation and fisheries and spatial analysis can support their addressing through the assessment of the trade-offs between them.

Briefly, this research can support strategic management advice for the pelagic fishery in the PCSE in the context of the EAFM.

Keywords: Ecosystem approach to fisheries management; Sardine; Portuguese continental shelf; Spatial analysis; Ecosystem modelling

Resumo alargado

Ao nível global, a pesca está em crise face a um grande número de unidades populacionais sobreexploradas, esgotadas e em colapso. A comunidade científica e as partes interessadas da pesca reconhecem esta situação e concordam que o sistema global de gestão das pescas, que se baseia em métodos de avaliação de unidades populacionais de uma única espécie, necessita de reforma. Existe um consenso global de que a gestão das pescas deve envolver um contexto mais amplo e holístico. Esta abordagem holística da gestão das pescas é frequentemente chamada a abordagem ecossistémica da gestão das pescas (EAFM, do inglês *Ecosystem Approach to Fisheries Management*) e descreve a gestão das pescas que engloba várias espécies, as suas interacções tróficas, a dimensão socio-económica e o impacto nos habitats e no ecossistema. A EAFM não é um conceito novo, e embora vários instrumentos internacionais, incluindo a Política Comum das Pescas (PCP) europeia, exijam a sua aplicação, a sua operacionalização é muito recente. Contudo, não é ainda muito claro como esta deverá ser implementada na prática. Neste sentido, o desenvolvimento de metodologias que possam apoiar a implementação desta abordagem (EAFM) é um passo essencial para apoiar a gestão de unidades populacionais de mananciais pesqueiros no futuro. Esta necessidade é particularmente crítica para unidades populacionais depauperadas, que requerem acções urgentes e eficazes para promover a sua recuperação. No ecossistema da plataforma continental portuguesa (PCSE, do inglês *Portuguese continental shelf ecosystem*), foi recentemente observado um declínio considerável na biomassa do manancial de sardinha (*Sardina pilchardus*), o qual teve implicações importantes no sector das pescas em Portugal.

A motivação principal para realizar a presente tese foi efectivamente a relevância e urgência da implementação da EAFM e, em particular, promover a sua aplicação ao caso da sardinha no PCSE. Os principais objectivos da tese foram: (1) Identificar as principais abordagens metodológicas propostas para a EAFM; (2) Aplicar as metodologias da EAFM ao PCSE; (3) Utilizar a pesca da sardinha como estudo de caso, devido à sua relevância para as pescas portuguesas e urgência da sua gestão sustentável; e (4) Explorar cenários futuros de mudanças globais, nomeadamente avaliando o impacto das alterações climáticas e cenários de pesca, no PCSE.

Esta tese é composta por sete capítulos, dos quais cinco correspondem a artigos científicos, publicados ou em revisão em revistas científicas internacionais. O primeiro capítulo introduz os principais conceitos relacionados com a pesca ao nível global e a sua gestão, centrando-se na pesca de recursos pelágicos no PCSE. Destaca-se a crise global da pesca e a necessidade de passar de métodos convencionais de avaliação uniespecíficos, para abordagens de gestão mais holísticas. Além disso, descreve-se a EAFM, os seus principais conceitos, os progressos na sua implementação e os principais desafios. Apresenta-se também neste capítulo a pescaria de cerco em Portugal, focando-se o caso da sardinha.

No capítulo 2 explorou-se a dimensão espacial que poderá apoiar a gestão da pesca de recursos pelágicos no contexto de uma abordagem ecossistémica. Foi utilizada uma combinação de sistemas de informação geográfica e um método de tomada de decisão multicritério para abordar múltiplos objectivos contraditórios entre conservação e a exploração por pesca. A análise destacou áreas espaciais importantes para implementar medidas de conservação para a sardinha. Além disso, indicou que algumas áreas são adequadas para conservação em vários cenários, tais como a área próxima de Aveiro e do estuário do Tejo. No entanto, as medidas de conservação implementadas na primeira destas áreas implicariam maiores contrapartidas económicas quando comparadas com as acções aplicadas na região próxima do estuário do Tejo. Os resultados deste capítulo demonstraram que a pesca que incide sobre recursos pelágicos em águas portuguesas tem objectivos contraditórios e a sua avaliação espacial é crucial para melhor compreender os custos e benefícios económicos e da conservação, e identificar medidas de gestão a implementar.

O capítulo 3 desenvolveu a componente Ecopath do modelo PCSE Ecopath com Ecosim (EwE). Os resultados apresentados neste capítulo evidenciaram que a biomassa no PCSE estava concentrada principalmente em níveis tróficos baixos e intermédios como se verifica noutras zonas de afloramento costeiro. Vários grupos de níveis tróficos baixos e médios foram identificados como grupos dominantes no ecossistema, incluindo a sardinha e a cavala (*Scomber colias*). Além disso, os grupos de baixo nível trófico foram responsáveis pelos principais fluxos de energia, e por um impacto global mais elevado no ecossistema, dando ênfase à importância do controlo ascendente na estrutura do ecossistema. Este trabalho deu origem ao desenvolvimento da componente Ecosim do modelo PCSE EwE (Capítulo 4), tendo-se utilizado a série temporal 1986-2017 para reflectir a dinâmica do PCSE e evidenciar os seus principais factores estruturantes. Os

resultados apresentados neste capítulo demonstraram que os principais factores que impulsionaram a dinâmica do ecossistema foram as interacções tróficas, a pesca e a temperatura da superfície do mar. Estes mesmos factores foram importantes para explicar o declínio da abundância da sardinha, sendo a temperatura da superfície do mar aquele que revelou uma maior influência na biomassa de indivíduos adultos de sardinha, seguida da pesca. Esta análise revelou ainda que as interacções tróficas responsáveis pela tendência da abundância da sardinha, entre 1986 e 2017, foram as relativas à predação de ovos de sardinha por parte da cavala, do carapau (*Trachurus trachurus*) e da boga (*Boops boops*).

O capítulo 5 fornece uma avaliação integrada do PCSE utilizando os resultados do modelo PCSE EwE como base para a análise. Foram utilizadas abordagens estatísticas combinadas com indicadores ecológicos para avaliar as mudanças nas principais tendências da biomassa, pesca e indicadores do ecossistema entre 1986 e 2017. Os resultados revelaram mudanças no PCSE e na abundância da sardinha nas últimas três décadas, as quais podem corresponder a uma mudança de regime (*regime shift*). Ao analisar as descontinuidades nas séries cronológicas, foram detectados três períodos distintos: "regime inicial", "regime de transição" e "regime tardio". As principais mudanças observadas no ecossistema foram a mudança do regime ("regime inicial") dominado pela sardinha e caracterizado por capturas elevadas, uma maior proporção de espécies demersais, e maior diversidade comparativamente ao "regime tardio" dominado por outros pequenos peixes pelágicos e durante o qual houve capturas mais baixas, um aumento do nível trófico e menor diversidade.

O capítulo 6 explora os cenários futuros dos principais factores de stress da sardinha e utiliza o modelo PCSE EwE para avaliar os impactos que estes podem ter sobre a sardinha e o ecossistema. Os resultados apresentados neste capítulo revelaram que o efeito da temperatura da superfície do mar na sardinha foi importante, e permitiram também estimar que o aumento desta poderia comprometer os esforços de gestão sustentável do manancial. Por outro lado, no cenário de simulação da pesca com rendimento máximo sustentável definido para os últimos anos, pelo Conselho Internacional para a Exploração do Mar, foi previsto um aumento da biomassa da sardinha e a recuperação do seu manancial para um nível equivalente ao período anterior ao declínio. Os resultados deste estudo mostraram que um aumento da cavala, dado constituir um predador de ovos de sardinha, poderá ter um impacto negativo no manancial de sardinha no futuro.

O aumento estimado para a cavala poderá implicar uma redução na estabilidade do ecossistema, o que é um indicador de stress, e que poderá sugerir a proliferação das outras espécies de pequenos peixes pelágicos e uma diminuição simultânea da sardinha. A pesca da sardinha a um nível de captura máxima sustentável poderá amortecer os efeitos negativos do aumento da cavala. Finalmente, o capítulo 7 apresenta as principais conclusões da tese e algumas perspectivas futuras para o desenvolvimento de investigação no contexto da abordagem do ecossistema e da gestão da pesca de recursos pelágicos em Portugal.

Os resultados obtidos nesta tese constituem um importante contributo para o desenvolvimento de uma abordagem ecossistémica da gestão da pesca de recursos pelágicos em Portugal, e permitiram aprofundar a compreensão do PCSE e da dinâmica da sardinha, fornecendo uma ferramenta (modelo EwE) capaz de apoiar o aconselhamento de gestão estratégica para a pesca.

Em conclusão, os resultados desta tese: (1) demonstram que a pesca de recursos pelágicos tem objectivos espaciais conflituosos e que a análise espacial pode apoiar a sua abordagem através de uma avaliação de custos e benefícios; (2) evidenciaram os principais factores responsáveis pelas mudanças no ecossistema ao longo das últimas três décadas; (3) melhoraram a compreensão dos factores responsáveis pelo declínio da sardinha; (4) indicaram que as mudanças que ocorreram no PCSE nas últimas décadas podem estar relacionadas com uma mudança de regime; e (5) permitiram salientar que, no contexto de uma abordagem ecossistémica, a gestão desta pescaria não deve limitar as suas acções às restrições de pesca, mas deve considerar adicionalmente um aumento das interacções tróficas, especialmente entre a sardinha, a cavala e a lula, bem como a possibilidade de ocorrência de mudanças de regime.

Palavras-chave: Abordagem ecossistémica da gestão das pescas; Sardinha; Plataforma continental portuguesa; Análise espacial; Modelagem de ecossistemas

List of symbols and abbreviations

A/C	Relative ascendancy
AC	Acoustic
AHP	Analytical hierarchy process
AIC	Akaike Information Criterion
AMI	Average mutual information
AMO	Atlantic multidecadal oscillation
AMOC	Atlantic Meridional Overturning Circulation
AR1	First order autoregressive model
B	Biomass
BA	Biomass accumulation
B _{lim}	Limit reference point for spawning stock biomass
B _{lim_low}	Limit reference point for spawning stock biomass at low stock productivity
BRPs	Biological reference points
B _{SRA}	Biomass trends estimated based on stock reduction analysis
BT	Bottom trawl
B _{trigger}	Value of spawning stock biomass that triggers a management action
CBD	Convention on Biological Diversity
CC	Chronological Clustering
CCUS	Canary Current Upwelling System
CFP	Common Fisheries Policy
Chla	Chlorophyll concentration
CPUE	Catch per unit of effort
CUFES	Continuous Underway Fish Egg Sampler
Dem C	Demersal catch
Dem/Pel B	Demersal per pelagic biomass
Dem/Pel C	Demersal per pelagic catch

DGRM	Directorate-General for Natural Resources, Safety and Maritime Services
DR	Daily ration for seabirds
EA	East Atlantic pattern
EA	Ecosystem approach
EAFM	Ecosystem approach to fisheries management
EBFM	Ecosystem based approach to fisheries management
EBM	Ecosystem based management
EE	Ecotrophic efficiency
EEZ	Exclusive Economic Zone
ENA	Ecological Network Analysis
ESDU	Elemental sampling distance unit
EU	European Union
EwE	Ecopath with Ecosim
$f(\text{Env}_{\text{function}}, t)$	Environmental response function
F	Fishing mortality
F	Mortality
F/Z	Exploitation rates
FAO	Food and Agriculture Organization
FCI	Finn's cycling index
$F_{\text{MSY}} / F_{\text{MSY}}$	Fishing mortality at maximum sustainable yield
$F_{\text{MSY\_low}}$	Fishing mortality consistent with achieving MSY at low stock productivity
F_{SRA}	Fishing mortality calculated based on biomass trends from stock reduction analysis
GE	Gross food conversion efficiency
GIS	Geographic Information Systems
GT	Gross <i>tonnage</i>
H	Entropy

HCR	Harvest Control Rule
IBTS	International bottom trawl surveys
ICES	International Council for the Exploration of the Sea
Invertebrates B	Invertebrate biomass
IPC	Increment of percent range
IPCC	Intergovernmental Panel on Climate Change
IPMA	Portuguese Institute of Sea and Atmosphere
ITA	Integrated Trend Analysis
Kempton Q	Kempton's index
LOA	Length overall
LPUE	Landings per unit effort
M	Natural mortality
MCDM	Multi-criteria decision making
MPA	Marine protected areas
MSFD	Marine Strategy Framework Directive
MSY	Maximum sustainable yield
MTI	Mixed trophic impact
mTLc	Mean trophic level of the catch
mTLco	Mean trophic level of the community
NAO	North Atlantic Oscillation
NGOs	Non-governmental organizations
OAT	One-at-a-time method
OLS	Ordinary least squares
P/B	Production/biomass ratio
PC	Principal components
PCA	Principal Components Analysis
PCSE	Portuguese continental shelf ecosystem
PCSE	Portuguese continental shelf ecosystem
Pel C	Pelagic catch

PP anomaly	Primary production anomaly
PPR	Primary production required to sustain the fishery
PREBAL	Pre-balance diagnostic
Pred B	Predatory biomass
Pred C	Predatory catch
Q/B	Consumption per unit of biomass
R	Redundancy
SA	Sensitivity analysis
Shannon	Shannon diversity index
SPF	Small pelagic fish
SPG	Subpolar gyre
S-R	Stock-Recruitment
SRA	Stock Reduction Analysis
SS	Weighted sum of squared deviations
SST	Sea surface temperature
STARS	Sequential t-test Analysis of Regime Shifts
STECF	Scientific Technical and Economic Committee for Fisheries
TE	Transfer efficiency
TL	Total length
TL	Trophic level
Tot C	Total catch
Total B	Total biomass
TotP/TotB	Turnover rate
TST	Total system throughout
UI	Upwelling Index
UN	United Nations
VBA	Visual Basic for Application
VGPM	Vertically generalized production model
VMS	Vessel Monitoring System

WGSAM	Working Group on Multispecies Assessment Methods
WLC	Weighted linear combination
Z	Total mortality

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Chapter 1

General introduction

Chapter 1 – General introduction

1.1. World fisheries in crisis

Fish constitute an important share of the global population's consumption of animal protein and according to the latest Food and Agriculture Organization (FAO) report on *The state of the world fisheries and aquaculture* (FAO 2020), fish accounts for about 17% of total consumption, while in developing islands and coastal areas, it may reach 50% or more. Moreover, a large proportion of the world's population relies on fishing for their livelihood, and according to the same FAO (2020) report, capture fisheries create around 39 million job posts, of which 12% are occupied by women. Furthermore, while the world population is growing and is expected to reach between 9.6 and 12.2 billion in 2100 (Gerland et al. 2014), simultaneously the global demand for seafood worldwide is projected to grow (AES 2013).

Fishing is a historical trade and localised negative impacts on fish stocks and ecosystems have been registered throughout history (Ludwig et al. 1993). However, the noteworthy impact on ocean fish resources and associated ecosystems only began in the early 1890s with the introduction of English steam trawlers, followed by power winches and diesel engines after World War I (Jackson et al. 2001). Fishing industrialisation continued and after World War II it included the introduction of fishing freezer trawlers, radar, acoustic fish finders and GPS that made fishing much faster and cheaper (Pauly 2006). This massive increase of global fishing effort led to a substantial increase in fish catches, which masked local stock collapses and created a misleading impression that the ocean can provide unlimited/endless living resources (Pauly 2006). This caused the overexploitation, depletion, and collapses of fisheries (Froese et al. 2012). The Peruvian anchovy collapse in 1972 was the first fishery collapse documented that had large scale economic repercussions (Muck 1989), followed by a decline in total catches from the North Atlantic in the late 1980s (Pauly and Maclean 2003) and the collapse of most of the cod stocks off New England and Eastern Canada in the early 1990s (Walters and Maguire 1996).

Industrialised fisheries seemed to not be concerned about the observed depletion and collapses, and in order to maintain an economic profit, once a stock was over-fished, they gradually moved their fishing efforts to deeper waters (Morato et al. 2006; Swartz et al. 2010), other

unexploited low latitude and southern hemisphere regions (Pauly et al. 2005) and finally, when they removed the larger, fast-growing individuals, they started to withdraw lower trophic level, previously unexploited fish, a phenomena called fishing down the food web (Pauly et al. 1998). It was only in the mid-90s when the global fisheries crisis started to be recognised as a serious issue (Garcia and Newton 1997; Sissenwine and Rosenberg 1995; Pauly et al. 1998; Safina 1995). Also, it was about this time, when it has been recognised that global fishery management system that is based on conventional stock assessment models focusing on single species fish populations and Maximum Sustainable Yield (MSY) needed a reform (e.g., Walters and Maguire 1996). The foundation of these models is still very much in use today (though in strongly modified forms) however, there is a widely recognised and growing consensus that the management of fisheries should encompass a much larger, holistic context (Garcia et al. 2003; Piktich et al. 2004, Hall and Mainprize 2004; Link 2002). This holistic approach to fisheries management is called the “ecosystem approach to fisheries management” (EAFM) (Garcia et al. 2003) or the “ecosystem-based approach to fisheries management” (EBFM) (Piktich et al. 2004). At some point there was a differentiation between EAFM and EBFM (Dolan et al. 2016), however currently, in European Policy and among the scientific community these terms have been generalised (e.g., Fanning et al. 2011; Link and Browman 2017). In this thesis, the term “Ecosystem Approach to Fisheries Management” (EAFM) (Garcia et al. 2003) will be used and treated as a synonym for EBFM.

1.2. Placing fisheries in the ecosystem context

1.2.1. Definition and key concepts of the Ecosystem Approach to Fisheries Management (EAFM)

The ecosystem approach to fisheries management (EAFM) is not a novel concept and its underlying principles and conceptual objectives evolved over a long time. Since 1980, the institutional foundations of EAFM are mentioned in numerous instruments and events that reflected a growing societal concern for the environment and urgency for the sustainable use of resources (Garcia et al. 2003). The term ecosystem approach (EA) was adopted for the first time in the 1992 United Nations (UN) Convention on Biological Diversity (CBD) and was defined as

“a strategy for the integrated management of land, water and living resources that promotes conservation and sustainable use in an equitable way” (CBD 2000). In the context of fisheries management, the 1995 FAO Code of Conduct for Responsible Fisheries, which is a reference framework for sustainable fisheries, addresses practically all the ecosystem considerations, principles, and conceptual goals that EAFM describes (Garcia et al. 2003). According to FAO (Garcia et al. 2003), EAFM is a more comprehensive approach to the implementation of the Code in all its aspects, including assessment, management, capture, processing, and trade.

EAFM in the definition provided by US National Research Council, (1998) and then adopted by FAO (Garcia et al. 2003, Garcia and Cochrane 2005) is described as ‘*an approach that takes major ecosystem components and services – both structural and functional – into account in managing fisheries. It values habitat, embraces a multispecies perspective, and is committed to understanding ecosystem processes. Its goal is to rebuild and sustain populations, species, biological communities and marine ecosystems at high levels of productivity and biological diversity so as not to jeopardize a wide range of goods and services from marine ecosystems while providing food, revenues and recreation for humans.*’ (US National Research Council 1998). The recently reformed European Union (EU) Common Fisheries Policy (CFP) (Regulation (EU) No. 1380/2013) defines EAFM as. “*an integrated approach to managing fisheries within ecologically meaningful boundaries which seeks to manage the use of natural resources, taking account of fishing and other human activities, while preserving both the biological wealth and the biological processes necessary to safeguard the composition, structure and functioning of the habitats of the ecosystem affected, by taking into account the knowledge and uncertainties regarding biotic, abiotic and human components of ecosystems*”. [2, art. 4 par 9]. In short, key characteristics of EAFM include multispecies consideration, trophic interactions, socio-economic dimension and impact on habitat and ecosystem (Garcia et al. 2003).

1.2.2. Methodological approaches used to advance EAFM

EAFM received a lot of attention in the two decades and publications that reviewed the EAFM concept (e.g., Garcia et al. 2003; Garcia and Cochrane 2005; Morishita 2008; Rice 2011), challenges for implementation (e.g., Kempf 2010; Cowan et al. 2012; Ramirez-Monsalve et al. 2016a), progress in operationalisations and future recommendations (e.g., Jennings and Rice 2011;

Koen-Alonso et al. 2019; Stefansson et al. 2019) are abundant. However, the review of scientific methods that can be used as a science base in EAFM has received relatively little attention (Smith et al. 2007) reflecting a need to review the methodological approaches that can facilitate EAFM operationalization. In order to fill this gap, in this PhD thesis, a review of EAFM methods that are published in peer review literature has been performed. A systematic clearly defined search method, using the *Google Scholar* and *Science direct* databases, was performed. As a criterion for the search were keywords *Ecosystem fishery management* and *Ecosystem fisheries management* that appeared in the title and additionally in the abstract and keywords when the search was done using the *Science direct* database. The search was performed between November 2016 and January 2017. The results in *Google Scholar* and *Science direct* provide 1092 and 1137 records respectively (575 from science direct analysed). After scanning the abstract for relevance and exclusion of non-relevant, non-peer review articles, working reports and thesis manuscripts, a total of 201 articles, were selected for further analysis. We found 16 methodological approaches that were proposed more than once in published peer review literature as a tool for an Ecosystem approach to fisheries management (Figure 1, Table A1.1 in annex 1). The methods were divided into 7 groups that represent different types of approaches that can assist the implementation of EAFM (Table A1.1 in annex 1). The most popular and frequently studied were modelling approaches, with 118 records in searched databases, followed by spatial methods with 24 records, indicators with 23 records and socio-ecological frameworks with 19 records (Figure 1). The methods that have 15 and fewer records in search databases were bioeconomic (15), risk assessment (11), and network analysis methods (3). The methods that appeared only once in the literature were not (included in) considered for further analysis.



Figure 1.1 Word cloud (<https://www.wordclouds.com>) of main methodological approaches to EAFM that were published in peer review literature based on the systematic search in Google scholar and Science direct databases using as keywords: *Ecosystem fishery management* and *Ecosystem fisheries management* in the title (Google scholar) and in the title, abstract and keyword (Science direct). The search was performed between November 2016 and January 2017. Description of the methodological approaches, explanation of their abbreviations and the context of their application to EAFM are provided in annex 1, Table A1.

1.2.3. The rationale behind a selection of EAFM methodological approaches applied in this thesis

Results of the literature review presented above constituted the foundation based on which the methodological approaches that were applied in this thesis, were selected. The choice of methods was based on both, the popularity (largest number of records) and relevance to the pelagic component of the ecosystem. Selected methods belong to methodological groups representing ecosystem models, specifically the Ecopath with Ecosim (EwE) methodological approach

(Christensen and Walters 2004), spatial analysis and indicators. These methodological approaches had the highest number of records in searched databases. This indicated that they were frequently used by the scientific community to address ecosystem issues in the context of EAFM. Moreover, the choice was based on their relevance to the pelagic component of the ecosystem to assure that they would be adequate to represent the issues that are important for this part of the ecosystem. Even though EAFM is a holistic concept that by definition should incorporate broad ecosystem aspects, its application should be refined based on the specific issues and research questions. For example, as different concerns are pertinent to demersal and pelagic ecosystems, the methods that would be the most appropriate to represent these systems would differ. For example, the ecosystem approach to the management of demersal fisheries should consider aspects related to seabed habitats that are documented not only to be highly affected by these fisheries (Eigaard et al. 2017) but also are recognised to be crucial for vital life-history functions of demersal stocks (Caddy 2014). On the other hand, management of the pelagic fisheries should be designed in a way to incorporate the aspects related to environmental variability since this aspect has been well documented to influence the productivity of pelagic stocks (e.g., Fréon et al. 2005; Keyl and Wolff 2008). Nevertheless, there are some universal components of EAFM such as species interactions that should be considered regardless of the ecosystem component. Therefore, while selecting the methodological approaches to be used in this research, the specific aspects/characteristics of the pelagic community and its recent issues on the Portuguese continental shelf were considered.

1.2.4. Challenges and progress in implementation of EAFM in EU

Currently, the ecosystem approach to fisheries management is a widely accepted concept and various international instruments such as EU CFP require its application. In the latest CFP reform (Regulation (EU) No. 1380/2013) significant progress has been made towards a better operationalization of an EAFM and now the approach can be considered embedded/formalised in the policy framework (Ramirez-Monsalve et al. 2021). Simultaneously, a large set of guidelines and frameworks designed to facilitate EAFM operationalization have been proposed and published (e.g Garcia and Cochrane 2005; Stephenson et al. 2019). However, there is still a lack of clarity on how this approach should be implemented in practice (Cowan et al. 2012; Ruckelhaus et al. 2008). Lack of: (1) capacity among stakeholders in terms of financial availability and self-related

resources; (2) specific management goals; (3) transparent and legitimate framework to address and balance conflicting objectives and trade-offs and (4) political will to support EAFM, are reported as the main obstacles for the effective implementation of EAFM (Ramírez-Monsalve et al., 2016ab; Link et al. 2019). Furthermore, even though policy framework such as CFP and Marine Strategy Framework Directive (MSFD) provided the legal setting for EAFM advice, a formalised process to integrate EAFM advice into EU fisheries policy is lacking and the capacity of the advisory bodies to inform actual policy decisions is still limited (Ramirez-Monsalve et al. 2021). Even though scientific advisory bodies, such as the International Council for the Exploration of the Sea (ICES), deliver advice on a range of elements with EAFM relevance, recipients do not have a clear path on how to use it. Moreover, policy-makers are reluctant to receiving advice that cannot link directly to their current list of tactical and strategical management decisions. Even considering these challenges, significant progress has been made towards a better operationalization of an EAFM in a recent CFP reform. The ICES is actively moving to deliver ecosystem-based advice (Lassen et al. 2014; Ballesteros et al. 2018). Recently, Ballestseros et al. (2018), and Ramirez-Monsalve et al (2021) building on the findings of a large research project MareFrame, (Co-creating Ecosystem-based Fisheries Management Solutions), provided a detailed analysis on how to improve Ecosystem Approach Fisheries Management advice within the European Union's Common Fisheries Policy and how ICES can improve the delivery of fishery advice that includes ecosystem considerations. They discussed: (1) what kind of scientific advice ICES is currently delivering; (2) what are the shortcomings that ICES can address and remedied and (3) what are the shortcomings that are beyond the scope of ICES control. Moreover, as an output of this project, a set of concrete actions have been suggested/proposed for stakeholders, scientific advisory bodies and decision-makers to foster the transition towards an EAFM in the EU. For examples, stakeholder advisory bodies should assure that investments and initiatives are designed taking into account the specificities of the socio-ecological context (Rudd et al. 2018). On the other hand, scientific advisory bodies should assure stakeholder engagement in the advisory process to ensure that outputs are relevant to societal needs (Dickey-Collas and Ballesteros 2019). Furthermore, an increased effort should be placed on the improvement of the social and economic dimension in the ecosystem advice as they are the weakest aspects of the advisory process (Ramirez-Monsalve et al. 2021). Finally, decision-makers need to be open and responsive to continued adjustments in the light of new knowledge (Langlet and Rayfuse 2019). Also, further

development in how the advice is requested, and an enhancement of EAFM implementation on the political agenda, are necessary (Ramirez-Monsalve et al. 2021).

Moreover, the need to produce ecosystem information (based on the ecosystem models), that can be directly used to inform stock assessment methods that are in use today, has been highlighted as an important step forward to progress implementation of EAFM (Howell et al. 2021). An example of how this could be done in practice has recently been presented by two independent case studies: (1) Atlantic menhaden in the United states (Chagaris et al. 2020) and (2) the multi-species fisheries of the Irish Sea in the Celtic Sea ecoregion (Bentley et al. 2021). These examples, although performed independently on two distinctive coasts separated by the Atlantic Ocean and designed to fit different international management frameworks, adopted a similar approach. They both, combined strategic advice from ecosystem modelling with the tactical advice of single-species assessment models to provide practical management advice in the context of the ecosystem approach. Specifically, in both cases, the ecosystem information provided by the EwE model, in the form of ecosystem indicators, was used to rescale the target fishing mortality (F) computed from a single species model, within the range of precautionary fishing mortality at maximum sustainable yield (F_{MSY}) recommended by current stock assessment methods. Even though this approach has some limitations and the use of ecosystem information to feed management advice is quite limited it has the potential to address several ecosystem objectives effectively and efficiently in the fisheries management context (Howell et al. 2021). Moreover, this approach is flexible and can be used much more extensively. Importantly, it complements the existing management framework and does not require instant and extensive reform of the current management system that can be easier to accept by management and fisheries stakeholders.

1.3. Case study – Pelagic fisheries in the Portuguese Continental shelf

1.3.1. Study area – Portuguese Continental Shelf

The Portuguese continental shelf ecosystem is located in the northeast Atlantic between 36.5° and 42° N and between 10.5° and 7.5° W. It covers an area of around 25,000 km² between the 30 and 200 m isobaths. The continental shelf width varies along the coast, ranging from

approximately 5 to 70 km, being wider on the northwest coast (Figure 2), and having an average width of 45 km. Mean sea surface temperature in the studied area ranges from 13°C and 17°C in the north and 15°C and 21°C in the south in the winter and summer, respectively. The western Portuguese coast is located alongside the northernmost part of the Canary Current Upwelling System (CCUS), one of the four major eastern boundary upwelling systems of the World Ocean classified as a Class I highly productive ecosystem ($>300 \text{ g cm}^{-2} \text{ year}^{-1}$) (Carr 2001). Consequently, it is affected by seasonal upwelling that occurs during spring and summer due to steady northerly winds (Wooster et al. 1976; Fiúza et al. 1982). Moreover, Also, the Iberian Peninsula is influenced by mid-term atmospheric phenomena such as Atlantic multidecadal oscillation (AMO) and North Atlantic Oscillation (NAO) (Trigo et al. 2004; Santos et al. 2011).

The Portuguese continental shelf ecosystem is situated in a biogeographic transition zone, between temperate and subtropical waters. Consequently, it is abundant in both temperate and subtropical fish species that have their southern or northern distribution limits along the coast (Briggs 1974). It is particularly abundant in small and medium pelagic species such as sardine (*Sardina pilchardus*), chub mackerel (*Scomber colias*) and horse mackerel (*Trachurus trachurus*) (Arístegui et al. 2009; García-Seoane et al. 2019). Among other abundant species that are ecologically and commercially important are hake (*Merluccius merluccius*), blue whiting (*Micromesistius poutassou*) (Silva et al. 1997; Sousa et al. 2005) and cephalopods *Loligo* spp and *Octopus* spp. (Moreno et al. 2009).

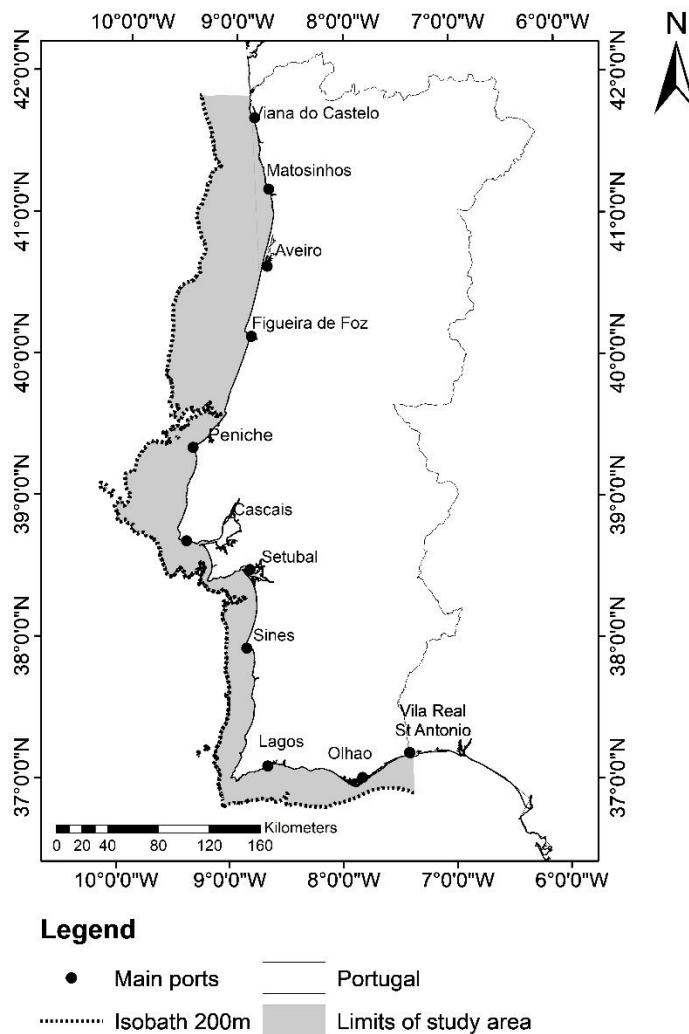


Figure 1.2 Map showing study area (limits of the Portuguese continental shelf ecosystem).

1.3.2. Portuguese pelagic fisheries

In 2019 the fishing fleet of Portuguese purse seiners that target pelagic fish, consists of 176 with a mean vessel tonnage of 69.9 GT and engine power category of 359 kW (ICES 2020a). Purse seine vessels employ 1,951 fishers (INE 2020). Those vessels usually perform daily trips, close to the port of origin where the net is set once or twice, usually around dawn (Stratoudakis and Marçalo 2002; Feijó 2013). In 2018 they operated for 11,569 days (Caseiro-Dias 2020). Although historically this fishery mainly targeted sardine, it is not a single species fishery and the importance of other species is growing due to the recent decline of sardine. Until 2011 sardine was the most

important species not only for the purse seine fleet but for the whole Portuguese fleet (INE 2012). However, between 2011 and 2014 a decline of the stock and catch regulations caused a 70% decrease in sardine landings (55,179 tonnes to 15,808 tonnes). Then, since 2012, sardine importance gradually diminished and other small pelagic species such as chub mackerel, horse mackerel and anchovy (*Engraulis encrasicolus*) become more important in terms of landings weight and value (INE 2013–2020). Consequently, since 2013 chub mackerel became the most landed species in purse seine fishery (except for the year 2017 when reported sardine catch was a bit higher 13,756 vs 14,169). In 2019 its landings were approximately four times higher than landings of sardine.

1.3.3. Focus species of the study - Sardine

1.3.3.1. Distribution

European sardine (*Sardina pilchardus*, Walbaum, 1792) is a pelagic and migratory fish species that belong to the *Clupeidae* family (e.g., sardines, sprat and herring). It has a wide distribution in the Northeast Atlantic and the Mediterranean Sea. In the Atlantic, sardine extends along the continental shelf from the Celtic Sea and the North Sea to Senegal, with residual populations off the Azores, Madeira, and the Canary Islands (Parrish et al. 1989). Based on integrated genetic and phenotypic data five biological populations of sardine are distinguished: (1) an African population (south of 30°N); (2) a Northeast Atlantic population (north of 30°N to the North Sea and the Alboran Sea); (3) a Mediterranean population (east of the Almeria-Oran front); (4) one in the Azores and (5) one in Madeira (Kasapidis et al. 2012; Shaw et al. 2012).

1.3.3.2. Biology and ecology

Sardine is a fast-growing (~23 cm in 4–5 years) and medium longevity (up to 14 years, in Atlantic less than 10 years) species. It reaches maturity early, between the first and second year and is characterised by high fecundity, releasing about 400,000 eggs per year per female (Nunes et al. 2011) in batches over a few months (Zwolinski et al. 2001). Sardine spawns throughout most of the continental shelf when the temperature is between 12°C and 18°C (Ettahiri et al. 2003;

Coombs et al. 2006; Bernal et al. 2007). In Portugal, the main sardine spawning grounds are localised in the north of the country (Bernal et al. 2007; Rodríguez-Climent et al. 2017) and the optimal spawning temperature is about 14–16°C (Coombs et al. 2006). The duration of the spawning season depends on the geographic region and in the north-eastern Atlantic, it generally increases from north (1–2 months) to south (6 months). In the north, the peak of spawning activity occurs in late spring while in the south it happened in winter (Ettahiri et al. 2003; Coombs et al. 2006; Stratoudakis et al. 2007). Besides temperature, the other factors that affect sardine reproductions are food availability, body size and energy reserves of spawning females (Zwolinski et al., 2001; Riveiro et al. 2004; Ganas et al. 2007; Garrido et al. 2017).

Sardine feeds on zooplankton, mainly copepods (Bode et al. 2004; Costalago et al. 2012; Garrido et al. 2008, 2015), but also have alternative preys such as phytoplankton and fish eggs (Garrido et al. 2008, 2015). In the Portuguese continental shelf, sardine prey mainly on crustacean eggs, copepods, decapods, cirripedes and fish eggs (Garrido et al. 2008, 2015). Sardines is considered a “forage fish” because they can be classified as generally abundant, lower trophic level organisms that serve as important prey for higher trophic level marine predators, including mammals (Thompson et al. 1996; Silva 1999; Santos et al. 2014; Marçalo et al. 2018), seabirds (Jahncke et al. 2004; Paiva et al. 2010; Käkälä et al. 2010) and larger fish species (Cabral and Murta 2002; Campo et al. 2006; Spitz et al. 2013). In Portugal, the main predators of juvenile and adult sardine are cephalopods, hake (Cabral and Murta 2002) and the common dolphin (*Delphinus delphis*) (Silva 1999; Marçalo et al. 2018) but also other small pelagic species such as juvenile chub mackerel, and bogue (*Boops boops*) that prey on sardine eggs (Garrido et al. 2008, 2015). Moreover, the study by Garrido et al. (2015) highlighted the importance of cannibalism in the predation of sardine eggs.

Sardine abundance, biomass and distribution display a considerable variation in response to environmental variability and climate change (Alheit et al. 2014; Peck et al. 2020). Clupeoid fishes, like sardine, usually show high variability in the recruitment process related to environmental conditions such as temperature and productivity (Guisande et al. 2001; Santos et al. 2012). In Portuguese continental waters, sardine recruitment has been associated with sea surface temperature (SST), chlorophyll concentration (Chla) (Garrido et al. 2017), North Atlantic

Oscillation (NAO), Atlantic multidecadal oscillation (AMO) and coastal upwelling (Malta et al. 2016).

1.3.3.3. Sardine fishery in the Portuguese continental shelf

For fisheries management purposes, 13 stocks of European sardine are considered, two stock units in EU Atlantic waters, three off northwest Africa and eight in the Mediterranean Sea (Silva et al. 2015). Sardine stocks in EU Atlantic waters consist of the Northern stock that is distributed between the Celtic Sea English Channel and the French-Spanish border in the Bay of Biscay, as well as the Southern stock that is distributed from the French-Spanish border in the Bay of Biscay to Gibraltar Strait (ICES Sub-areas 8c and Division 9a). Division 9a expands from Galicia (Cape Finisterre), through the Portuguese continental shelf to the Strait of Gibraltar (Figure 3) and is characterised by most of the sardine Southern Stock population in numbers (mean=91%) (ICES 2020b). This area is jointly managed between Spain and Portugal and around 80% of sardine is caught by the Portuguese fleet (ICES 2020a). In this thesis, the term west Iberian stock will be used when referring to Division 9a of the sardine Southern Stock.

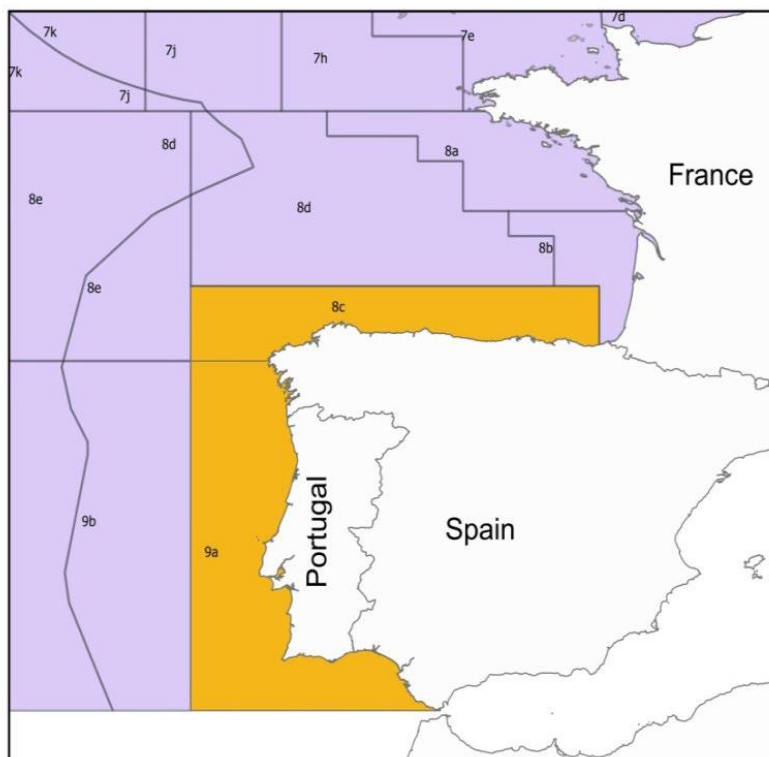


Figure 1.3 Delimitation of the Southern sardine (*Sardina pilchardus*) stocks in divisions 8c and 9a (Cantabrian Sea and Atlantic Iberian waters). Source: adapted from sardine stock divisions 8c and 9a ICES stock annex available at: https://www.ices.dk/sites/pub/Publication%20Reports/Stock%20Annexes/2019/pil.27.8c9a_SA.pdf.

In Portugal, sardine is captured mainly by the purse seine fishery with a small proportion taken as by-catch in the bottom trawl fishery and local small-scale fisheries. Moreover, sardine is caught by the small-scale fisheries fleets that are negligible in terms of landings weight and value but are important in social and cultural terms (Silva et al. 2015). Until 2011, sardine was the most important species not only for the purse seine fleet but also for the whole Portuguese fleet with around 35% in terms of volume of total landings and 18% in value (INE 2012). However, since 2012, due to the considerable decline in sardine stock and catch regulations, sardine landings decreased by ~70% (INE 2012–2019). In 2019, 9,796 tonnes of sardine were landed by the Portuguese fleet corresponding to 19 million euros in first sale value (INE 2020).

Sardine is almost totally used for human consumption and a high proportion (around 45%) of the landings supply the processing industry, that produces canned products (Silva et al. 2015). Currently, 20 canneries are transforming mainly sardine, tuna, and chub mackerel. For some factories, sardine accounts for over 50% of production. In 2018, 8,713 tonnes of canned sardine

products were produced from which 95% (8,318 tonnes) was sold for a total value of 45 million euros, mainly for the foreign market (INE 2020). The canning industry employs around 3,500 people of which about 85% are women (Silva et al. 2015).

1.4. Steps toward an ecosystem approach to pelagic fisheries management in Portugal (with the focus on sardine)

1.4.1. Historical development and status of the sardine stock off the Iberian coast

Changes in sardine biomass are closely linked to the timing and magnitude of recruitment: periods of high and low biomass occur shortly after one or two years of strong and weak recruitment, respectively. Recruitment of the Iberian sardine stock is showing a downward trend with a lower magnitude of both low and high recruitments and wider separation between strong recruitments (Silva et al. 2015). Sardine biomass started to decrease considerably between 2006 and 2009 and in 2010, its biomass was 60% lower when compared to the year 2006 (Figure 4). Moreover from 2010 the biomass of fish aged one and more (biomass 1+ or B1+) was below the MSY $B_{trigger}$ (value of spawning stock biomass that triggers a specific management action) reference point recently updated by ICES and defined to be 252,523 tonnes (2019a). Furthermore, in 2016 sardine recruitment reached a critical level, the lowest in 40 years (ICES 2017).

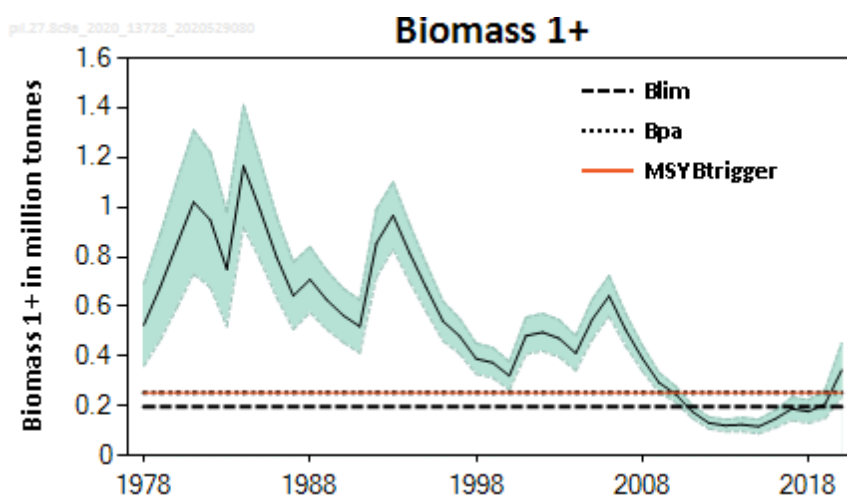


Figure 4. Biomass of sardine stock based on ICES 2019 stock assessment (ICES 2020b).

From 2017, an increase in biomass (and recruitment) was observed and in 2020 the biomass of age one and older fish (biomass 1+ or B_{1+}) is above $MSY B_{trigger}$ for the first time since 2009 and recruitment in 2019 is the highest since 2004 and above the long-term geometric mean (ICES 2020b). Even considering the observed improvement of recruitment and increase in biomass, the Iberian sardine stock is still in a fragile state, and according to biological reference points for sardine exploration recently updated by ICES (ICES 2019a), fishing mortality (even though it is the lowest in the time-series since 1978), is still above F_{MSY} (ICES 2020a).

1.4.2. Management of sardine fisheries

As a response to a pronounced decline in sardine biomass and recruitment, a first sardine Fishery Management Plan (2012–2015) was implemented (DGRM 2012). This plan established a set of actions that had a goal to promote recovery and prevent the further decline of the Iberian sardine stock. The main measures that were regulated included: (1) adoption of harvest control rule (HCR) that was designed to allow for stock recovery above $B_{trigger}$ by 2015; at that time $B_{trigger}$ was established for 368,000 tonnes; (2) a compulsory fishing ban that totalled 45 days imposed in the period between 1st January and 31st April; in practice, three 15 days bans in three different periods for each production region (North, Centre and South) were defined; (3) a limit of 9,000 tons for total landings was imposed for the period between 1st January and 31st April; (4) the 48 h fishing ban on weekends was maintained.

However, these measures turned out to be insufficient and sardine continued to decline well below the $B_{trigger}$ that was in operation at that time. Therefore, in 2018 the second multiannual management plan for the recovery of sardine stock was implemented (DGRM 2018). This plan was applied by both Portuguese and Spanish governments and included much more restrictive harvest rules and fishing measures to address an ongoing decline of sardine stock. The plan adopted a set of specific measures that were adopted by both Portugal and Spain. The main measures specified in the new plan included: (1) a progressive recovery of sardine to at least 80% of B_{lim} (limit reference point for spawning stock biomass) before the end of 2023; (2) employment of harvest control rule defined by ICES and evaluated as precautionary (ICES 2019b) to manage sardine fishery that states: fishing mortality (F) will be set every year “at” or “below” F_{MSY} 0.12.

If the biomass is below 80% of B_{lim} , F will be set at 0.1 and if the biomass is over 80% of B_{lim} , F will be set at F_{MSY} 0.12. Moreover, mortality will be modulated to produce at least a 10% of biomass increase in the following year and never less than 5%. In 2019, considering the recent low stock productivity (corresponding to the period 2006–2017) ICES updated biological reference points (BRPs) (ICES 2019c) on which the advice is currently based (ICES 2020b). According to updated BRPs, B_{lim_low} (limit reference point for spawning stock biomass corresponding to low stock productivity) was estimated to be 196,300 tonnes and F_{MSY_low} (Fishing mortality consistent with achieving MSY at low stock productivity) was estimated to be 0.032 year⁻¹ (ICES 2019c); (3) agreement to a reference indicative ratio of catches of 2/3 (66.5%) and 1/3 (33.5%) for Portugal and Spain respectively; (4) closure of the fishery for sardine from 1st November until 30th of April to protect the stock during the reproduction period. Moreover, both countries: implemented real-time closures of areas to protect juveniles; limited the fleet that can participate in the sardine fishery and reduced the quantities allowed to be landed per day, trip, and vessel. Additionally, Spain, allowed bycatch of sardine to be landed in anchovy and horse mackerel fishery (to avoid discards of sardine caught as by-catch) and change the quota division system to include individual and transferable quota and by this means to reduce the effort and improve the selectivity and the use of the quota. On the other hand, Portugal limited the area where purse-seine fishing operated to avoid catches of juvenile fish and committed to improve the monitoring of the fishing activity by the VMS and other systems.

1.4.3. Research in the context of the EAFM

Sardine decline raised the interest of the scientific community and the urgency of in-depth research on sardine became apparent. Consequently, during the last decade, a large number of studies aiming to improve the understanding of sardine decline and improvement of its management were performed. For example, Malta et al. (2016) explored the relationship between sardine recruitment and environmental conditions, Garrido et al (2017) studied the effect of food availability on sardine recruitment and Wise et al. (2019) assessed potential competition between the fishery and sardine top predators. Also, some authors linked the decline of sardine with pressure from top predators (Marçalo et al. 2018) and intraguild predation (Garrido et al. 2015)

Moreover, research focusing on juvenile sardine habitat protections was undertaken (Rodriguez-Climent et al. 2017) and the development of a bio-economic model for sardine management was started (Rosa et al. 2018). In addition, a multidisciplinary project, led by IPMA with the collaboration of several universities and aiming at improving the understanding of sardine decline and its management “*SARDINIA2020: ecosystem approach to fisheries management of the sardine*”, was launched in 2017. The goal of this project is “*the development of a Management Plan for the purse-seine fishery, aligned with the Common Fisheries Policy and Marine Strategy Framework Directive, based on the principles of sustainability of fisheries resources, recovery of the pelagic habitat biodiversity and the fisheries industry profitability*” (Nunes et al. 2019). Some outcomes of this project were already published in peer review journals exploring the degree of connectivity between southern and northern sardine stock (Silva et al. 2019) and investigating the spatial and temporal variation of the pelagic community composition in the Atlantic Iberian waters (García-Seoane et al. 2019).

This research showed that Portugal is proactive and on track to find the answers and solutions for sardine management in the context of EAFM. However, even considering these efforts and considerable advancement and improvement of knowledge, the attempts to develop ecosystem models capable to assess the impact of inter-specific trophic interaction, fisheries and environment on sardine stock and pelagic community is limited.

Thesis motivation and objectives

The scientific community and fisheries stakeholders agree that fisheries should be managed considering a larger and holistic, ecosystem approach. Various international instruments including the European Common Fisheries Policy (CFP) call for its application in practice. Therefore, the development of methodologies that can support the implementation of this approach (EAFM) is an essential step to assist the management of future stocks. This is especially relevant in the context of the stocks that are depleted and require urgent and effective action to support their recovery. In the Portuguese continental shelf ecosystem (PCSE), a considerable decline in the biomass of sardine has been observed between 2006 and 2009 that had an important implication to the Portuguese pelagic fishery.

An attempt to address the global call to implement EAFM and support the management of the sardine stock in the PCSE was the motivation for this thesis whose general objective was to advance an application of the ecosystem approach to pelagic fisheries management in Portuguese continental waters. To achieve this general objective, this thesis aims to: (1) identify the main methodological approaches that have been proposed for EAFM; (2) apply EAFM methodologies to the PCSE; (3) use the sardine fishery as a case study, due to its relevance in terms of its importance for Portuguese fisheries, as well as the urgency needed to remedy the current situation; (4) explore future scenarios of global changes, particularly evaluating the impact of climate change and fisheries scenarios, in the PCSE.

Thesis outline

This thesis consists of seven chapters.

In *chapter 1*, the main themes related to an Ecosystem approach to fisheries management and pelagic fisheries in Portuguese continental waters are described. Also, in this chapter, the results of a systematic literature review on EAFM methods are presented.

A general, spatial framework supporting an ecosystem approach to European sardine management is provided in *chapter 2*. This approach allowed for the synthesis of information about the sardine fishery system in the spatial context. Moreover, it addressed conflicting objectives by identifying the areas that have the highest importance for conservation and pelagic fisheries and assessing the trade-offs between conservation and fisheries objectives.

In *chapter 3*, the output of the collaboration in the development of the static, Ecopath component of the Portuguese continental shelf EwE model has been presented. This model represents the trophic structure and functioning of the Portuguese continental shelf ecosystem and as a result, improves the understanding of the Portuguese continental shelf ecosystem dynamics. Moreover, it creates a foundation for further work presented in the following chapters.

A dynamic ecosystem model of PCSE has been developed and the drivers of ecosystem dynamics and causes of sardine decline have been investigated in *chapter 4*. This research deepened the understanding of the drivers underpinning sardine stock dynamics. Moreover, the development of the dynamic ecosystem model in this chapter was the first step to provide a tool ready to run simulations of different ecological and management scenarios in *chapter 6*.

In *chapter 5*, an integrated assessment of the PCSE has been performed and the impact of drivers identified in *chapter 4* on the ecosystem through the last decades has been investigated. Specifically, by using statistical methods, the changes observed in the fishery system, in biomasses of functional groups and in indicators (that describe the structure and function of the ecosystem), have been reported. Furthermore, potential regime shifts in the ecosystem have been identified.

The impact of different fishing, trophic and SST scenarios on future ecosystem dynamics and sardine stock have been explored in *chapter 6*. Moreover, the impacts of combined multiple stressors on sardine and the ecosystem have been assessed.

In the final chapter (*chapter 7*) an overall summary and general discussion of the work presented in this thesis has been provided. Specifically, the use of applied methodological approaches (Spatial analysis, Ecosystem modelling (EwE) and statistical methods with indicators) to advance EAFM in Portuguese continental waters, has been discussed.

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Chapter 2

A GIS-based framework for addressing conflicting objectives in the context of an ecosystem approach to fisheries management – a case study of the Portuguese sardine fishery

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Chapter 2 – A GIS-based framework for addressing conflicting objectives in the context of an ecosystem approach to fisheries management – a case study of the Portuguese sardine fishery

Abstract

An ecosystem approach to fisheries management (EAFM) is a new paradigm in fisheries management. In this study, a combination of geographic information systems (GIS) and multi-criteria decision-making method (MCDM) is proposed as a framework supporting an ecosystem approach to European sardine (*Sardina pilchardus*, Clupeidae) fishery management in Portugal. This case study was chosen due to the recent severe decline shown by the species. To develop an EAFM for the sardine fishery, a set of criteria were defined based on literature review and expert knowledge. To address multiple conflicting objectives, namely conservation and fisheries, five scenarios were considered: (1) *baseline*; (2) *nurseries protection*; (3) *spawning areas protection*; (4) *fishery profit driven* and (5) *safeguarding dependent fishing communities*. Combination of GIS and MCDM methods highlighted important areas to implement spatial conservation measures for sardine. The analyses indicate that some areas are suitable for conservation in several scenarios, such as the area near Aveiro and the area near the Tejo estuary. However, conservation measures implemented in the area near Aveiro would imply higher economic trade-offs when compared to the actions applied in the region near the Tejo estuary. Results also suggested some of the conservation objectives, such as the protection of sardine eggs and juveniles, to not be compatible. The proposed framework is an important tool supporting EAFM by addressing conflicting objectives, trade-offs and identifying areas that could be considered as potential fishery closure sites or subjected to further analyses.

Keywords: Marine Protected Areas (MPA), Ecosystem approach to fisheries management (EAFM), Marine spatial planning, Multi-criteria decision making (MCDM), Sardine, Spatial analysis

2.1. Introduction

Depletion of fish stocks worldwide (Fletcher and Bianchi 2014) signals a failure of conventional fisheries management practices and ineffective governance (Ruckelshaus et al., 2008). Common Fisheries Policy (CFP) was settled with the aim to integrate environmental concerns and move towards a more holistic ecosystem approach to fisheries management (EAFM) (Ramírez-Monsalve et al. 2016). Key characteristics of this approach include multispecies consideration, trophic interactions, socio-economic dimension and impact on habitat and ecosystem (Garcia et al. 2003).

There is a large body of literature presenting guidelines and frameworks aiming to facilitate EAFM operationalization (Fletcher 2008; Link 2010; Staples et al. 2014) and several methods have been explored. The most popular and frequently studied have been: (1) modelling approaches e.g. Ecosystem models (Polovina 1984; Christensen and Pauly 1992; Walters et al. 1997, 1999, Fulton et al. 2004a, 2004b); (2) statistical methods that support Integrated Ecosystem Assessment (Link et al. 2002); (3) spatial methods, such as the use of Geographic Information Systems (GIS) (Olson 2011); (4) application of indicators (Link 2005; Yeon et al. 2011) and finally (5) the use of socio-ecological frameworks (Leite and Gasalla 2013). Even though, significant progress has been made towards a better operationalisation of an EAFM in a recent CFP reform (regulation (EU) No. 1380/2013), several challenges, such as lack of transparent and legitimate framework to address and balance conflicting objectives and trade-offs, impede the implementation of an EAFM in EU fisheries (Ramírez-Monsalve et al. 2016).

The use of GIS, a versatile tool that can be applied at different stages of the fisheries management process, has been recommended by the Food and Agriculture Organisation (FAO) as a tool for an EAFM (Carocci et al. 2009). GIS application in fisheries management has been already implemented in coastal regions around the world (Aswani and Lauer 2006; Hall and Close 2007; De Freitas and Tagliani 2009). Despite its potential, the use of GIS in EAFM is still limited (Carocci et al. 2009; Meaden et al. 2013).

Multi-criteria decision making (MCDM) methods have the ability to assist in the management of renewable resources by taking into account conflicting objectives, therefore attaining interests within a wide range of management fields (Romero and Rehman 1987). They

have also been frequently applied to fisheries (Mardle and Pascoe 1999; Chiou et al. 2005; Kjærsgaard 2007; Innes and Pascoe 2010). Nevertheless, spatial MCDM methods, that allow for the evaluation of multiple conflicting criteria to solve complex spatial problems (Malczewski 2006), have had limited use in fisheries and coastal management studies (Hossain and Das 2010; Daputo et al. 2015; Villa et al. 2002; Portman 2007). In the EAFM context, this approach can be used to indicate suitable areas for biodiversity conservation, while minimising the negative effect on fisheries.

European sardine (*Sardina pilchardus*, Walbaum, 1792) represents an economically and socially significant fishery resource in Portugal and Spain (Silva et al. 2015). Sardine in the Iberian Peninsula Atlantic waters (ICES Divisions 8.c and 9.a) is considered stock for management purposes (ICES 2017a). In the last decade, its severe decline in the Iberian waters has been observed: biomass decreased around 80% and recruitment reached the lowest historical level in 40 years (ICES 2017a). The majority of the Iberian sardine stock is distributed in Portuguese waters and its main recruitment and spawning areas are northern Portugal and south of Spain (Gulf of Cadiz); (Bernal et al. 2007; Rodríguez-Climent et al. 2017). Clupeoid fishes, like sardine, are usually short-lived and the success of their recruitment is crucial to further increase the size of the population (Cole and Mcglade 1998). These fish species usually show high variability in the recruitment process related to environmental conditions (Bakun 1997).

In this paper, we describe a framework that demonstrates the utility of GIS to support fisheries management in the context of an ecosystem approach. It implements a GIS-based MCDM method combined with broad spatial analysis using the Iberian sardine as a case study. The presented framework has the capability to facilitate EAFM by identifying areas that: (1) are of the highest importance for conservation; (2) are the most crucial for fisheries; (3) imply trade-offs between conservation and fisheries objectives. Based on this information, the most appropriate choices for conservation were presented.

2.2. Material and methods

2.2.1. Study area

Located on the western tip of Europe and with an extension of approximately 25,000 km², the Portuguese continental shelf (0–200 m; Figure 2.1) is in a biogeographic transition zone between temperate and subtropical waters (Briggs 1974). Moreover, the western Portugal coast is located alongside the northernmost part of the Canary Current Upwelling System (CCUS), one of the four major eastern boundary upwelling systems of the World Ocean classified as a Class I highly productive ecosystem ($>300 \text{ g Cm}^{-2} \text{ year}^{-1}$) (Carr 2002). In this area, seasonal upwelling occurs during spring and summer as a result of steady northerly winds (Wooster et al. 1976; Fiúza et al. 1982).

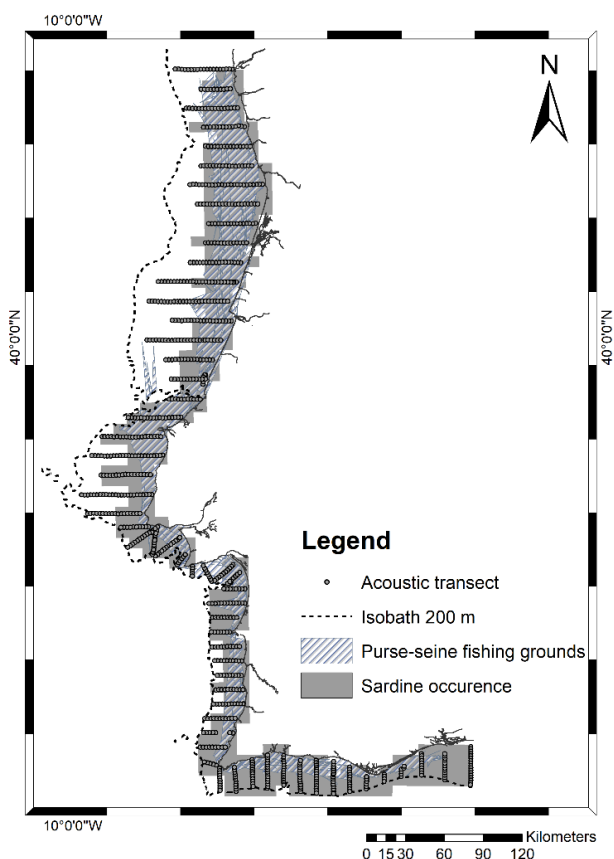


Figure 2.1 Map showing limits of the study area between 200 m isobath and Portuguese coastline, the occurrence of sardine in Portuguese acoustic surveys between 2005 and 2010 (source: IPMA, PELAGO surveys); purse-seine fishing grounds between 2005–2010 (source: DGRM VMS-logbook data) and acoustic transect along which biological data were collected (IPMA, PELAGO surveys).

2.2.2. GIS-MCDM analysis

A combination of GIS and MCDM methodology was used to identify the most suitable sites to preserve essential sardine habitats, while reducing the negative effect on fishing activities. A set of criteria representing a holistic ecosystem approach and considering sardine conservation and fishing industry, was defined. To select the most suitable option from available alternatives, the MCDM technique (decision rule, algorithm), with the weighted linear combination (WLC) (weighted overlay) method, was used. Another widely used method, the Analytical hierarchy process (AHP) was employed to derive the weights associated with attribute map layers used in the WLC method. Applied GIS-based MCDM procedure (Figure 2.2.) consists of five steps: (1) identification of important criteria; (2) data compilation; (3) creation of criteria maps; (4) production of suitability maps; and (5) assessment of suitability maps.

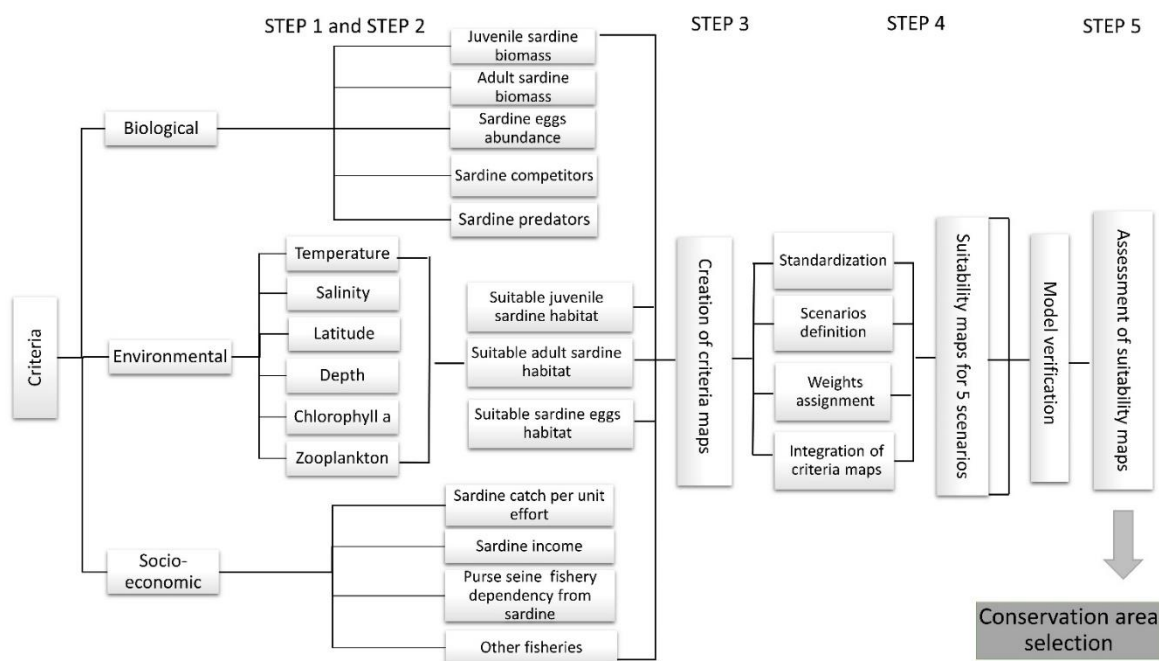


Figure 2.2 Conceptual suitability model showing applied criteria and GIS-based MCDM procedure applied to select conservation areas that aim to protect sardine essential habitat and at the same time attempt to maintain the socio-economic efficiency of purse seine fishery in coastal Portuguese waters.

2.2.2.1. Step 1 - Identification of criteria

The first step of the suitability analysis was a selection of important criteria for sardine essential habitat and purse seine fishery, and the development of a conceptual suitability model accordingly (Figure 2.2). The model consisted of 12 criteria representing three main dimensions of EAFM: biological, environmental and socio-economic (Table 2.1). Criteria selection was based on the best available published literature and expert judgement.

Table 2.1 Description of biological criteria used in the GIS multi-criteria decision-making method. ESDU: elemental sample distance unit that corresponds to 1nm.

Criteria	Reason to include	Assignment of priority values	Type of objective	Years	Data source
Biological					
Juvenile sardine (TL≤16cm) biomass (tonnes ESDU^{-1*})	Sardine recruits (juveniles <1 year) are the proxy for nursery areas which conservation is important for the maintenance of healthy stock.	High juvenile sardine biomass – high conservation priority	Conservation	2005–2010	IPMA, PELAGO survey
Adult sardine (TL>16cm) biomass (tonnes ESDU^{-1*})	High biomass of adult sardine is important for conservation because adult sardine has the maturity to spawn and might be considered important for spawning areas conservation.	High adult sardine biomass – high conservation priority	Conservation	2005–2010	IPMA, PELAGO survey
Sardine eggs abundance (no. m⁻³)	Sardine eggs abundance is an indicator of sardine spawning grounds that are of high importance for conservation.	High sardine eggs abundance – high conservation priority	Conservation	2005–2010	IPMA, PELAGO survey, CUFES
Sardine competitors					
Atlantic chub mackerel	In the study, sardine competitors are considered species that are caught by the same fleet as sardine. A higher number of competitors is an indicator of extra stress for sardine as they compete for space, food etc. Therefore, the areas that have a high number of competitors have a priority for conservation.	High sardine competitors' abundance – high conservation priority	Conservation	2007–2010	IPMA, PELAGO survey
Atlantic mackerel				2005–2010	
Horse mackerel				2005–2010	
Mediterranean horse mackerel				2007–2010	IPMA, PELAGO survey
Blue jack mackerel				2007–2010	
Bogue				2007–2010	

European anchovy	2005–2010			
Sardine predators				
European hake	Sardine predators are indicators of the natural mortality of sardine. The higher number of predators means higher stress (natural withdrawal of sardine from the environment) and therefore, an intensified necessity for conservation. Moreover, these areas indicate locations important to protect to ensure ecological support for other species and the whole marine ecosystem (Pikitch et al. 2012).	High sardine predators' abundance – high conservation priority	Conservation	2005–2010
Squid				2005–2010
Environmental				
Suitable juvenile sardine (TL≤16cm) habitat	Areas that have a high probability of juvenile sardine occurrence are of high priority for conservation as they are indicators of sardine nurseries areas.		Conservation	
West (37-42°N; 9-10°W)				
Temperature (°C)	Juvenile sardine abundance showed a doomed shaped response with temperature, displaying a peak at around 14°C (Rodríguez-Climent et al. 2017).	13.5–14.5°C – high probability of juvenile occurrence – high conservation priority.		2005–2010 MODIS aqua satellite sensor
Salinity (PSU)	Juvenile sardine abundance showed a bimodal shape response with salinity, displaying one peak at ~35.3 PSU and another one at ~33.7 PSU (Rodríguez-Climent et al. 2017).	33.5–34 PSU and 35–35.5 PSU – high probability of juvenile occurrence–high conservation priority.		2005–2010 IPMA, in-situ; PELAGO survey; Sensor associated to CUFES
Latitude	Juvenile sardine abundance showed a bimodal shape response with latitude, displaying one peak at ~38.6°N and another one at ~40.3°N (Rodríguez-Climent et al. 2017).	38.5°–39°N and 40.0°–40.6°N – high probability of juvenile occurrence – high conservation priority.		
Depth (m)	Juvenile sardine depth tolerance is between the coastline and a depth of 100 m.	< 100 m – high probability of juvenile occurrence – high conservation priority.		2005–2010 Portuguese Hydrographic Institute

South (35-37°N; 7-9°W)				
Temperature (°C)	Juvenile sardine abundance is positively correlated with temperature (Rodríguez-Climent et al. 2017).	High temperature – high probability of juvenile occurrence – high conservation priority.	2005–2010	MODIS satellite sensor
Chlorophyll a (mg m ⁻³)	The highest abundance of juvenile sardine occurs in the areas with average chlorophyll concentration (Rodríguez-Climent et al. 2017).	Average chlorophyll – high probability of juvenile occurrence – high conservation priority.	2005–2010	SeaWiFS satellite sensor
Zooplankton (ml 10 m ⁻³)	Juvenile sardine abundance is inversely correlated with zooplankton abundance (Rodríguez-Climent et al. 2017).	Low zooplankton concentration – high probability of juvenile occurrence – high conservation priority.	2005–2010	IPMA, PELAGO survey; CUFES
Depth (m)	Juvenile sardine occurs with the highest probability between the coastline and a depth of 100 m.	<100 m – high probability of juvenile occurrence – high conservation priority.		Portuguese Hydrographic Institute
Suitable adult sardine (TL>16cm) habitat	Areas that have a high probability of adult sardine occurrence are of high importance for conservation as adult sardine has the maturity to spawn and might be considered as important for spawning areas conservation.	Conservation		
Temperature (°C)	Adult sardine abundance is inversely correlated with temperature values (Zwolinski et al. 2010).	Low temperature-high adult sardine biomass – high conservation priority.	2005–2010	MODIS satellite sensor
Chlorophyll a (mg m ⁻³)	Adult sardine abundance is positively correlated with chlorophyll a concentration (Zwolinski et al. 2010).	High chlorophyll – high adult sardine biomass – high conservation priority.	2005–2010	SeaWiFS satellite sensor
Salinity (PSU)	Adult sardine abundance is inversely correlated with salinity values (Zwolinski et al. 2010) that indicate regions of freshwater influence.	Low salinity – high adult sardine biomass – high conservation priority.	2005–2010	IPMA PELAGO survey, sensor associated to CUFES
Depth (m)	Adult sardine occurs with the highest probability between the coastline and a depth of 100 m (Zwolinski et al. 2010).	< 100 m – high probability of sardine occurrence – high		Portuguese Hydrographic Institute

conservation
priority.

Suitable sardine eggs habitat		Conservation			
Temperature (°C)	Areas that have a high probability of sardine eggs occurrence are of high importance for conservation as they are the areas where sardine spawn.	Sardine spawns in the temperature range between 12°C and 17°C, while the temperature preference range is between 13.5°C and 15°C (Bernal et al. 2007).	13.5–15°C – high sardine eggs occurrence probability – high conservation priority; <12 and >17°C – low probability of eggs occurrence – low conservation priority.	2005–2010	MODIS satellite sensor
Depth (m)	Sardine depth tolerance is between the coastline and a depth of 200 m, near the shelf edge, while preferences are found between depths around 10 m to around 150 m (Bernal et al. 2007).	Sardine depth tolerance is between the coastline and a depth of 200 m, near the shelf edge, while preferences are found between depths around 10 m to around 150 m (Bernal et al. 2007).	10–150m – high sardine eggs occurrence probability – high conservation priority; <10 and > 150m – low probability of eggs occurrence – low conservation priority.		Portuguese Hydrographic Institute
Socio-economic					
Sardine catch per unit effort (CPUE)	High sardine landings per unit effort are attributed to the high socio-economic importance, therefore they have low suitability to conservation.	High sardine landings per unit effort –high fishery priority	Fishery	2005–2010	DGRM, landings data DGRM, VMS logbook data
Sardine income (euro/kg)	High sardine income has large socio-economic importance, because it secures fishers well-being.	High sardine income – high fishery priority	Fishery	2005–2010	DGRM, landings data DGRM, VMS logbook data
Purse seine fishery dependency from sardine	High sardine catch relative to total catch is an indicator of dependency of purse seine industry from sardine.	High ratio of sardine catches to total catch – high fishery priority	Fishery	2005–2010	DGRM, landings data DGRM, VMS logbook data
Other fisheries	Fleets other than purse seine (e.g., trawl) were included in the analysis as they are of importance for the socio-economic efficiency of the fishing industry and might be affected by conservation measures.	High value for other fisheries criteria – high fishery priority	Fishery	2005–2010	STECF

2.2.2.2. Step 2 - Data compilation

The second step of the analysis was the compilation of spatial data for each criterion. The spatial data compiled covered a period of 6 years (2005–2010; with few exceptions listed in Table 2.1a). This time scale represents a period with contrasting sardine abundance, high numbers in the years 2005–2007 and low numbers in the years 2008–2010 (ICES 2017a). Data regarding adult (Total length -TL>16 cm) and juvenile (TL≤16 cm) sardine biomass, sardine eggs abundance, and zooplankton concentration were obtained from the acoustic surveys (PELAGO survey series) performed annually by the Portuguese Institute of Sea and Atmosphere (IPMA) in spring (April-May). Surveys were carried out onboard the *R/V Noruega* along predefined parallel transects perpendicular to the coastline covering the whole platform (0–200 m depth) with 8 nautical miles (nm) inter-transect distance (Figure 2.1). Acoustic fish data were obtained following the methodology described in ICES (2016) by performing echo integration along 1 nm Elemental sampling distance unit (ESDU), used as a distance measure in acoustic surveys, and supported by fish samples collection through pelagic and bottom trawling. Estimates of sardine biomass were calculated following the procedures described in Simmonds and MacLennan (2005). For more details about acoustic surveys and sardine biomass estimates refer to publications by ICES (2016) and Rodríguez-Climent et al. (2017).

Sardine eggs and zooplankton data were collected along the acoustic transects every 3 nm at the surface (~3 m), using a Continuous Underway Fish Egg Sampler (CUFES, mesh 335 µm) (Checkley et al. 1997). Sardine eggs abundance (no. m⁻³) was calculated based on the eggs data collected per unit of time and the pump flow rate. Zooplankton biomass expressed as volume of zooplankton (mL 10 m⁻³) was estimated by volumetric method (displacement volume; Ikeda and Omori 1992).

Sardine competitors' species abundance data: atlantic chub mackerel (*Scomber colias*, Gmelin 1789), bogue (*Boops boops*, Linnaeus 1758), anchovy (*Engraulis encrasicolus*, Linnaeus 1758), mediterranean horse mackerel (*Trachurus mediterraneus*, Steindachner, 1868) and blue

jack mackerel (*Trachurus picturatus*, Bowdich, 1825), were assessed by acoustic data (acoustic energy – SA m²/nm²) derived from the PELAGO surveys. The remaining competitors: horse mackerel (*Trachurus trachurus*, Linnaeus 1758) and atlantic mackerel (*Scomber scombrus*, Linnaeus 1758) and sardine predators, hake (*Merluccius merluccius*, Linnaeus 1758) and squid (*Loligo* spp. Lamarck 1798) data were based on abundance data (kg h⁻¹) collected during demersal surveys (2005-2010). Those surveys were carried out in autumn (September - October) onboard the *R/V Noruega* at predefined stations in the Portuguese Exclusive Economic Zone (EEZ) at depths varying from 20 to 500 m depth. For details about abundance estimation based on demersal surveys refer to International bottom trawl surveys (IBTS) protocol published by ICES (2017c). Vessel Monitoring System (VMS) and logbook data from purse seine vessels ≥ 12 m (EU Council 2009) for the years 2006–2010, obtained from the Directorate-General for Natural Resources, Safety and Maritime Services (DGRM), were integrated to produce maps of fishing activity. Purse seine catch distribution maps were developed based on analysing vessel speed patterns from VMS data and linking them to logbook data to identify fishing activity according to Katara and Silva (2017). We reported landings as the sum of tonnes of each species landed per year and per grid cell. VMS and logbook data for the year 2005 were not used because their spatial coverage was not sufficient and representative enough. Instead, the official landing data per main fishing port, registered and obtained from the DGRM, were used for this year. These data were spatially attributed to fishing grounds previously defined according to spatial patterns recorded in 2006-2010 VMS-logbook data (Figure A2.1 in annex 2).

For the criteria ‘other fisheries’ the fleets using the following gear were considered: bottom trawl, longline, gill, trammel and pots. Spatial effort (hours) and landings (tonnes) data (2005-2010) at ICES statistical rectangles level were obtained from the Scientific Technical and Economic Committee for Fisheries (STECF) (annex: WW; country: PRT; <https://stecf.jrc.ec.europa.eu>, 20/05/2017).

Sea surface temperature (°C) and chlorophyll a concentration data (mg m⁻³) were obtained from MODIS aqua (L3; 4 µm) and SeaWiFS satellite sensor respectively (sources: www.opendap.jpl.nasa.gov/opendap/; www.oceancolour.org/portal/, 10/05/2017) and represented the period of the pelagic surveys: March-May. Salinity was collected in situ during the IPMA

acoustic surveys (PELAGO, 2005–2010). Depth (m) data were obtained from the Portuguese Hydrographic Institute website (www.hidrografico.pt/download-gratuito.php, 25/05/2017).

2.2.2.3. Step 3 - Creation of criteria maps

To create surface continuous layers, a similar approach to the one performed in Petitgas et al. (2014) allowing for a reasonable compromise between smoothing and maintaining details, was taken. Data collected along acoustic transects and at the demersal survey's sampling stations were averaged on a common regular grid (8 x 8 km) using the ArcMap neighbourhood point statistic function that allows the creation of cell-based rasters with a smoothing effect. Satellite data was converted to the 8 x 8 km grid to match the resolution of the remaining layers. All analyses were performed using ESRI ArcMap software (version: 10.4.1).

Socio-economic, environmental and some biological criteria - competitors and predators – required processing of initial data in order to be represented as meaningful maps useful for this study.

Generation of socio-economic criteria

The following socio-economic criteria calculated yearly were considered in the present study (1) sardine catch per unit effort (CPUE); (2) sardine income; (3) purse seine fishery dependency from sardine; and (4) other fisheries. Sardine CPUE was calculated by considering the effort to be the duration of a fishing trip times the number of sets per trip (where sardine was caught) except for the year 2005 where the effort was considered to be the number of fishing trips where sardine was caught. For the other fleets, the effort was considered to be the number of fishing hours. Discards were negligible therefore we considered that landings per unit effort (LPUE) were equal to CPUE. Income was calculated by multiplying landings of the species of interest by its price (euro per kg). The prices used were those indicated in the Portuguese National Statistical Institute (INE) annual statistic report (INE 2006–2011). Purse seine fishery dependency from sardine was calculated by dividing sardine landings by total landings. The criterium 'other fisheries' is a combination of CPUE, landings and income for the respective fleet, i.e., bottom trawl, longline, gill, trammel, and pots. In order to combine all these variables, the spatial layers

representing these variables were first reclassified using the Jenks natural breaks method (Jenks 1967) and then averaged using the GIS raster algebra function. Jenks natural breaks method is the default classification method in ArcMap which identifies breakpoints between classes using a statistical formula (Jenks optimization) that minimizes the sum of the variance within each of the classes finding groups and patterns inherent to the data.

Generation of suitable habitat criteria

Maps representing suitable habitat for juvenile sardine, adult sardine and sardine eggs were produced using environmental variables that affect sardine's distribution according to published literature. Environmental variables were reclassified in accordance with Rodríguez-Climent et al. (2017) for sardine juveniles, Zwolinski et al. (2010) for adults and Bernal et al. (2007) for eggs. The reclassified environmental maps were then combined by summing the reclassified layers, corresponding to each variable with raster algebra (raster calculator ArcGis function).

Generation of biotic interactions criteria

In the present analysis, biotic interactions were represented by sardine competitors and predators. Areas with a high number of competitors or predators were treated as a priority for conservation, as they constitute natural stress for sardine. Moreover, these areas were considered as a priority because in these locations sardine seems to play a fundamental role to ecologically support other species and the whole marine ecosystem - as forage species (Pikitch et al. 2012). Species commonly caught along with sardine by the purse seine fleet were considered as sardine competitors namely: *S. colias*, *S. scombrus*, *T. trachurus*, *B. boops*, *E. encrasicolus*, *T. mediterraneus* and *T. picturatus*. Species like *M. merluccius* and *Loligo* spp. were considered as common sardine predators (Coelho et al. 1997; Cabral and Murta 2002; Mahe et al. 2007). Other important sardine predators, such as the common dolphin (*Delphinus delphis* L.1758) (Silva 1999), were not considered in this study as a result of data availability limitations. Note that some of the species considered as sardine competitors (e.g. *S. colias* and *B. boops*) in this study are also predators for sardine eggs (Garrido et al. 2015).

The overlap found between sardine and their competitors/predators, will be referred to as spatial overlap intensity index (O_i) and was estimated using the Jaccard index of similarity (Jaccard 1908) modified as follows:

$$O_i = \sum_{i=1}^n \left(\frac{PIL \& SP_i}{PIL \mid SP_i} \times SP_i \right) \times Af_i \quad \text{Equation 2.1}$$

Where O_i is overlap between sardine and other species considered, PIL is sardine biomass; SP_i is other species abundance; n is the number of other species considered and Af_i is the other species abundance factor. Other species either refers to competitors in *Competitors-sardine overlap* or predators in the *Predators-sardine overlap*.

The Jaccard index is one of the oldest and most widely used similarity indices for assessing compositional similarity of assemblages. It is based on the presence-absence records of species in paired assemblages (Chao et al. 2005). To reflect species abundance in the output of the binary index, the index was modified by adding multiplication by two variables: First, variable SP_i that corresponds to species abundance in the used dataset and then by variable Af that is the general species abundance factor. Available competitors' species data had various units as they were obtained from various surveys. Data regarding sardine predators and competitors, atlantic mackerel and horse mackerel, were available from demersal surveys, while the remaining competitors' data was obtained from the acoustic surveys. This fact made it mathematically impossible to apply equation 2.1. Therefore, in order to address different units in data, each species-sardine overlap raster was reclassified into 10 classes using Jenks natural breaks. Nevertheless, the outputs of the procedure of reclassification made it impossible to differentiate between very abundant species, such as horse mackerel, from low abundant species, such as bogue. Therefore, to address the importance of each species abundance relatively to each other, the reclassified rasters were multiplied by an abundance factor Af established for this purpose. This subjective abundance factor was attributed to each competitor species based on its six-years abundance estimates from bottom Portuguese trawl (ICES data 2009–2014) and subjective classification established by author judgement, that aimed to highlight the differences between species abundance (see Table 2.2. for more details). After multiplication by SP_i variable and Af factor, raster layers representing competitors and predators were summed.

Table 2.2 Abundance factor assigned to each competitor species established based on its abundance in bottom Portuguese trawl data (source: ICES 2009–2014).

Species	Total abundance in 2009-2014 (x1000 no. of species in trawl)	Abundance factor
<i>Trachurus trachurus</i>	396.50	10
<i>Scomber scombrus</i>	168.90	8
<i>Trachurus picturatus</i>	111.45	6
<i>Engraulis encrasicolus</i>	65.91	4
<i>Scomber colias</i>	19.39	2
<i>Boops boops</i>	15.14	2
<i>Trachurus mediterraneus</i>	0.12	1

2.2.2.4. Step 4 - Production of suitability maps

The final suitability maps for sardine conservation without compromising fisheries activities were produced using the weighted linear combination (WLC) method. This method is one of the most widely used GIS-based decision-making methods for land suitability analysis (Hopkins 1977; Malczewski 2000). It was chosen because it is accessible, intuitively appealing to decision-makers (Massam 1988) and easy to implement in GIS (Tomlin 1990). The WLC method involves the standardization of the attribute maps, assigning the weights of relative importance and combining the weighted criteria to obtain an overall suitability score. Therefore, all criterion maps were standardized, weighted and combined to produce the final suitability map as explained below.

Standardization

Criteria were standardized to a uniform scale with values ranging from one to five (1: no suitability; 5: high suitability for conservation; Table 2.1). The applied classification method was Jenks natural breaks (Jenks 1967).

Scenario definition

The analysis was performed for five scenarios that varied depending on the priority objectives. The first scenario balanced conservation and fisheries objectives. The second and third

scenario focused on conservation objectives, while the fourth and fifth scenario focused on fisheries objectives. Scenario 1, the *baseline* scenario, considered all criteria to have the same importance. Scenario 2, *nurseries protection*, aimed to protect sardine nursery areas. This scenario applied increased weight for the following criteria: juvenile biomass and suitable juvenile habitat. Scenario 3, *spawning areas protection*, aimed to protect sardine spawning grounds. It applied increased weight for criteria: sardine eggs abundance, adult sardine biomass (considered potential spawners) and suitable sardine eggs and adult sardine habitat. Biological criteria were obtained from observed values, while habitat criteria were the output of modelling studies (for details see subsection 2.2.2.3 *Generation of suitable habitat criteria*). Therefore, as a result of a higher uncertainty of the latter, they were assigned lower priority compared with the biological criteria. Scenario 4, *fishery profit driven*, aimed to protect sardine fishery revenue. Here increased weight was applied to sardine income criteria. Scenario 5, *safeguarding dependent fishing communities*, aimed to exclude from protection areas where fishers are highly dependent on sardine catches. It applied increased weight to areas where purse seine fishery is highly dependent on sardine.

Weight assignment

The Analytical Hierarchy Process (AHP) method (Saaty 1980) was used to assign weights to criteria, which differ depending on the applied scenario. This mathematical method is the most frequently used in spatial MCDM studies (Phua and Minowa 2005; Bottero et al. 2013; Rahman et al. 2013) and it establishes weights among criteria by making a series of judgements based on pairwise comparisons of the criteria. The relative importance of each criterion is measured according to a numerical scale from one to nine (Table 2.3).

Table 2.3 Scale for Analytical Hierarchy Process (AHP) pairwise comparisons and a description how scales were attributed to criteria in each scenario.

Intensity of importance	Description	Scenarios				
	Importance	Baseline	Nurseries protection	Spawning areas protection	Fishery profit driven	Safeguarding dependent fishing communities
1	Equal	All criteria	Remaining criteria	Remaining criteria	Remaining criteria	Remaining criteria
5	Moderate		Suitable juvenile sardine habitat	Suitable eggs and adult sardine habitat		
9	Essential		Juvenile sardine biomass	Adult sardine biomass and sardine eggs abundance	Sardine income	Purse seine fishery dependency from sardine

In this study, weights were chosen to represent potential differences in the probable stakeholders' objectives. Even though, stakeholders were not directly engaged, as it was out of the scope of the study, the framework design and a choice of methods ensure their inclusion when necessary. Once a pairwise comparison matrix was built, each criterion weight was calculated by computing the eigenvector of each column. Secondly, the matrix components were normalized by averaging the values across the rows (Table 2.4).

Table 2.4 Weight values for each criterion in each scenario derived by the Analytical Hierarchy Process (AHP) method

Criteria	Scenarios				
	Baseline	Nurseries protection	Spawning areas protection	Fishery profit driven	Safeguarding dependent fishing communities
Biological					
Juvenile sardine biomass	0.083	0.401	0.027	0.05	0.05
Adult sardine biomass	0.083	0.041	0.279	0.05	0.05
Sardine eggs abundance	0.083	0.041	0.279	0.05	0.05
Sardine competitors	0.083	0.041	0.027	0.05	0.05
Sardine predators	0.083	0.041	0.027	0.05	0.05
Habitat					
Suitable juvenile sardine habitat	0.083	0.191	0.027	0.05	0.05
Suitable adult sardine habitat	0.083	0.041	0.115	0.05	0.05
Suitable sardine eggs habitat	0.083	0.041	0.115	0.05	0.05
Socio-economic					
Sardine catch per unit effort	0.083	0.041	0.027	0.05	0.05
Sardine income	0.083	0.041	0.027	0.45	0.05
Purse seine fishery dependency from sardine	0.083	0.041	0.027	0.05	0.45
Other fisheries	0.083	0.041	0.027	0.05	0.05

Integration of criteria maps

Each criterion map (Figure 2.3) is composed of i pixels. Each i pixel is characterised by attributes that describe the location (coordinate data) and value x_{ij} , representing a standardised

score of i -th pixel with respect to the j -th criterion (attribute value is associated with the location). The suitability of each i -th pixel is evaluated using the following equation:

$$S_i = \sum_{j=1}^n w_j x_{ij} \quad \text{Equation 2.2}$$

where: S is suitability of the i -th pixel in the final map; n is a number of criteria ($n=12$); w_j is a weight of j -th criterion and x_{ij} is the standardised score for the i -th pixel with respect to the j -th criterion.

Firstly, in order to identify the conflicting areas, biological and environmental criteria and socio-economic criteria were combined separately. Then combination of all criteria was performed for five different scenarios.

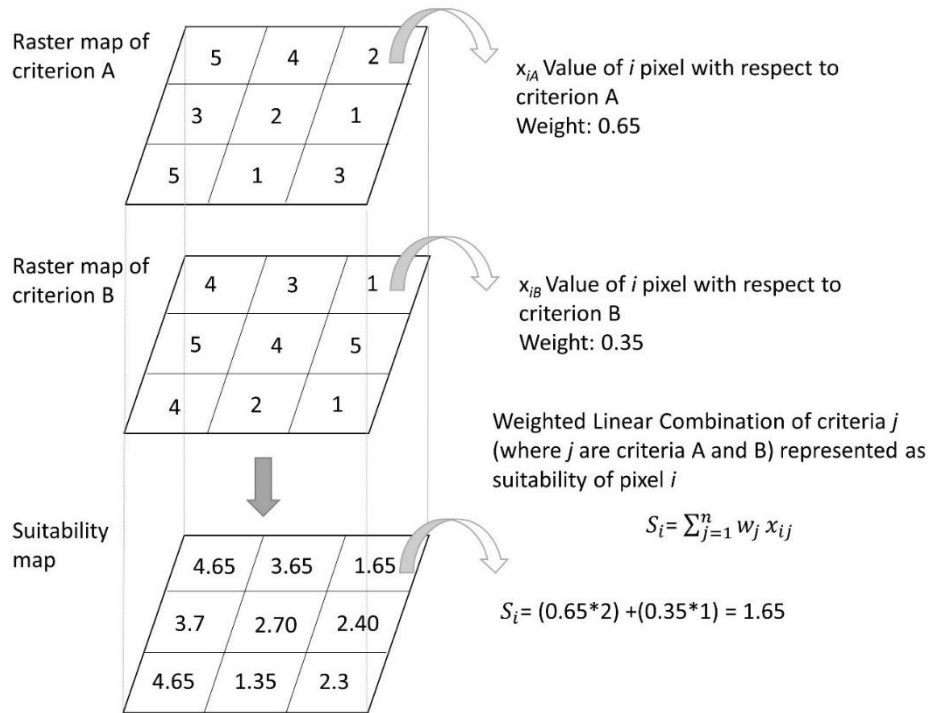


Figure 2.3 Example of the weighted linear combination method of criteria raster maps (redrawn from Pérez et al. 2005; Daputo et al. 2015). The suitability map is a result of the linear combination of j criteria (in the figure j refers to the A and B criteria maps, with weights 0.65 and 0.35 respectively). Each pixel i on criteria map j is represented by a standardised value x_{ij} .

Model verification – sensitivity analysis

Sensitivity analysis (SA) with a one-at-a-time (OAT) method (Daniel 1973; Chen et al. 2010) was performed to evaluate how weights influenced criteria and the spatial patterns on the suitability maps. This method introduces changes in one factor (weight) at a time, while all the other factors remain fixed, and detects how this change might influence the output. A range of percent change (RPC) of $\pm 100\%$ and increment of percent range (IPC) of $\pm 1\%$ were applied to the complete set of criteria used in this study. Therefore, the SA consisted of 200 simulation runs for each criterion. It was performed by using Model Builder module of ArcMap that enables semi-automatic processing of a large data set and options.

2.2.2.5. Step 5 - Assessment of suitability maps

For each scenario, areas with high and very high suitability conservation score (4 and 5 respectively) were selected (Figure A2.3 in annex 2) in order to be analysed in terms of costs to the fishing industry and benefits for sardine conservation (Table 2.5). Among them, only areas with at least two grid cells (minimum of 128 km²) were considered. As costs the following aspects were considered: (1) loss in sardine fishery profit and (2) loss in profit from the other fisheries. As benefits, the protection of sardine was considered for: (1) juvenile; (2) spawning areas and (3) adults.

2.3. Results

2.3.1. Sensitivity analysis

The sensitivity analysis showed that all criteria have a relatively similar sensitivity to change in weights. Effects were first observed after approx. $\pm 20\%$ change from the baseline. Further changes were observed after each additional ± 10 or $\pm 5\%$ changes in the input. Changes higher than $\pm 80\%$ from a base did not cause any further changes in the output. This pattern was similar for most of the criteria (For details refer to Figure A2.2 in annex 2).

2.3.2. Sardine conservation and socio-economic related criteria

Areas with the highest scores for the biological and environmental criteria occurred in the following areas: south of Aveiro (Area 1), near Figueira de Foz (Area 2), Ericeira (Area 3), near the Tejo estuary, between Cabo Raso and Cabo Espichel (Area 4) and near Setúbal (Area 5) (Figure 2.4 a). Area 1 had high scores for juvenile, adult sardine biomass and sardine eggs abundance (Figure 2.4 bcd). Area 2, had a high level of juvenile biomass whereas Area 3, had medium levels of adult biomass, predators, and competitors (Figure 2.4 bcef). Also, Area 4 had high levels of competitors and predators but here high, not adult, but juvenile sardine biomass obtained higher scores (Figure 2.4 bce). Finally, Area 5 had high competitors levels and moderate eggs abundance (Figure 2.4 de). All areas had medium to high levels of suitable juvenile, adult and eggs habitat (Figure 2.4 ghi) with the exception of Area 5, which showed low levels of suitable adult sardine habitat (Figure 2.4 h).

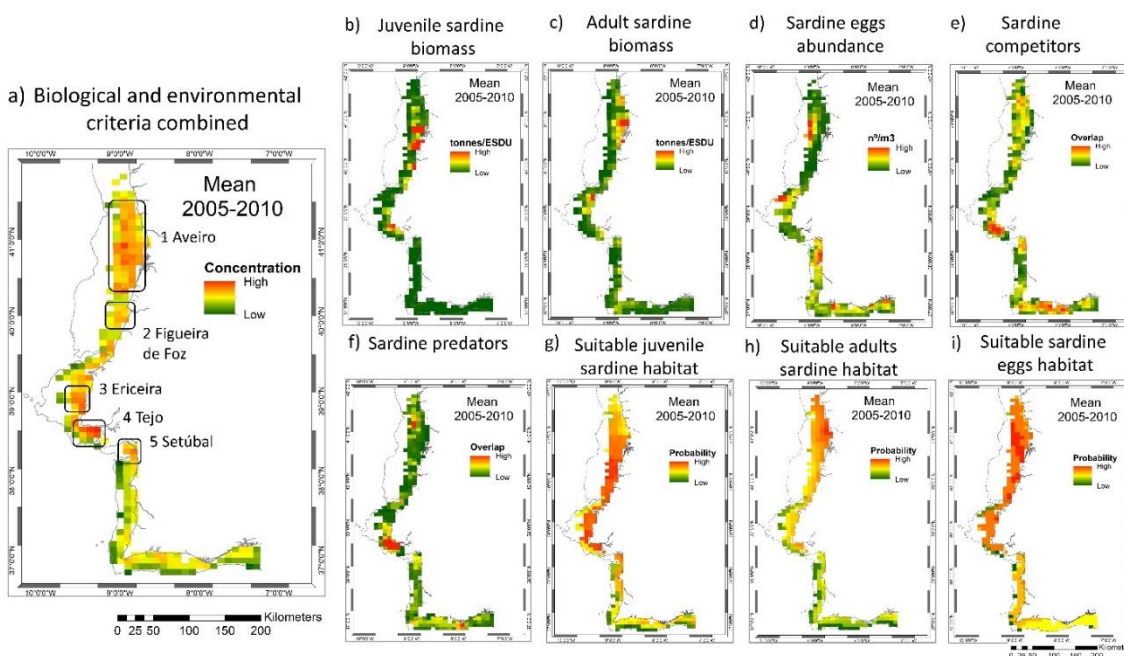


Figure 2.4 Map showing all biological and environmental criteria combined. Areas that obtained their highest scores were highlighted (a); Maps showing means of each biological and environmental criterion separately (b–i).

On the other hand, if we considered the socio-economic criteria (Figure 2.5 a), areas 1, 2 and 3 had high levels of socio-economic features (Figure 2.5 a). Therefore, those areas were identified as conflicting areas. On the other hand, areas 4 and 5 (Figure 2.4 a) had a low level of almost all socio-economic criteria (Figure 2.5 abcd) except for other fisheries feature that showed medium levels (Figure 2.5 e).

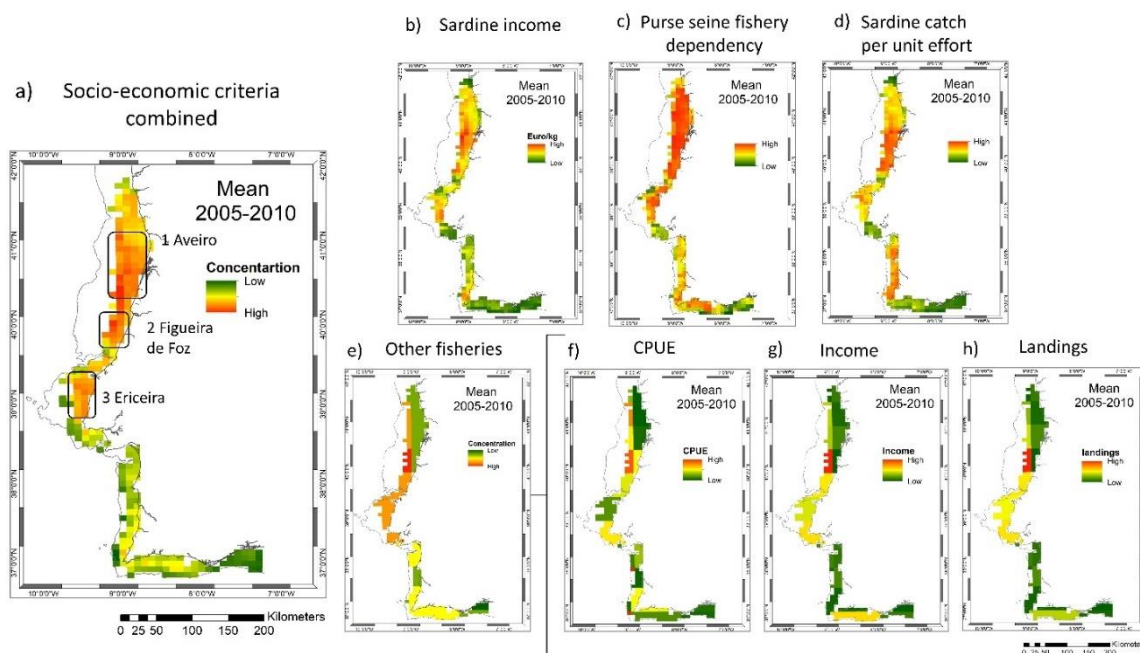


Figure 2.5 Map showing all socio-economic criteria combined. Areas that obtained the highest scores were highlighted (a); Maps showing means of each socio-economic criterion separately (b–h).

2.3.3. Overlay of all criteria for various scenarios

The suitability for sardine conservation varied across scenarios (Figure 2.6). The *baseline* scenario had the highest number of areas (min 128 km² - two pixels) with moderate suitability for conservation (Figure 2.6a - yellow grid cells) and small and fragmented areas of high or very high suitability for conservation (Figure 2.6 a - orange and red grid cells, Table 2.5). Those areas were situated nearby Aveiro and Nazaré and the larger ones near Ericeira, Tejo, and Setúbal. In the south of Portugal, there were also a few regions with high suitability for conservation (Figure 2.6 a). In the remaining scenarios, the high and very highly suitable areas were more aggregated and constrained to specific regions. In the *nurseries protection* scenario, the main suitable areas were

situated near Aveiro, Ericeira, and Tejo (Figure 2.6b). Similarly, in the *spawning areas protection* scenario, these areas were also situated near Aveiro and Ericeira and additionally near Setúbal (Figure 2.6 c). In the scenarios that focused on socio-economic features, the suitable areas for conservation were mainly situated in the area near Tejo, Setúbal for *fishery profit driven* scenario and near Ericeira, Tejo and Setúbal for *safeguarding dependent fishing communities'* scenario. Moreover, for both scenarios, the areas situated in the south of Portugal were identified as suitable (Figure 2.6 de).

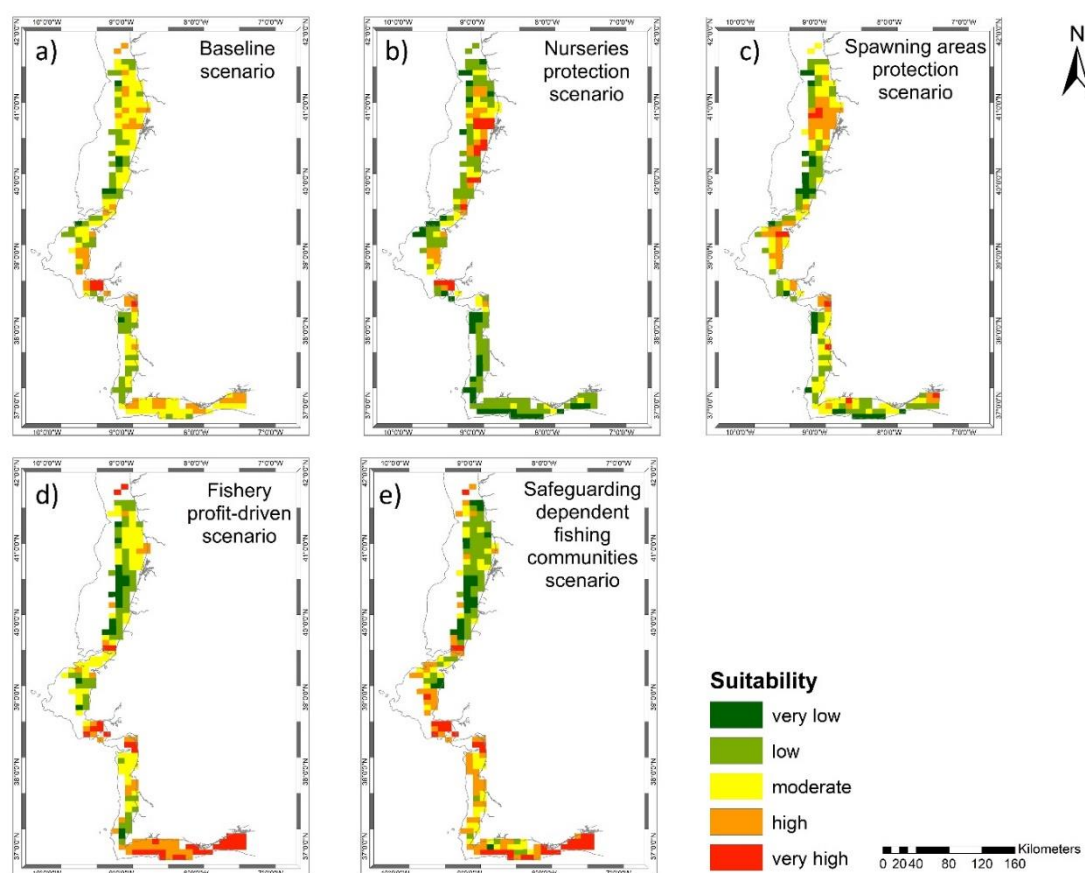


Figure 2.6 Suitability classification for the Iberian sardine stock conservation areas for the different scenarios (a–e).

2.3.4. Assessment of selected areas - Cost-benefit analysis

Cost and benefits in scenarios varied depending on selected areas and prioritized objectives (Table 2.5). If considered scenarios and areas they encompass as total, it is difficult to select the

scenario that best balanced conflicting objectives. For example, *nurseries protection* scenario provided protection for the highest quantity of juvenile 85% and high quantity of adult sardine 31%. However, these conservation benefits were associated with the high cost in fisheries income that was estimated for 16% and 9% of total income for purse seine and other fisheries. On the other hand, the *baseline* scenario provided protection for the second-highest quantity of juvenile (51%) and adult (50%.) sardine. However, in this scenario, the impact on the fisheries income was comparable to the impact observed in *nurseries protection* scenario and was estimated for 15% and 10% for purse seine and other fisheries, respectively.

Table 2.5 Summary of potential costs and benefits estimated for each selected area in the five tested scenarios. Data are shown as the yearly summary in terms of yearly loss in fisheries income and amount of protected sardine biomass and eggs.

Potential costs for industry								Potential benefits for sardine stock					
Affected income								Protected					
	No. area	Area name	Area	Purse seine		Other fisheries		Juvenile sardine biomass		Sardine eggs abundance		Adult sardine biomass	
Scenario			(km ²)	(x 1000 euro year ⁻¹)	%	(x 1000 euro year ⁻¹)	%	(tonnes)	%	(No. m ⁻³ / grid cell)	Deviation from average (%)	(tonnes)	%
Baseline	1	North	768	65.4	6.1	3637	1.0	4456	31.5	13	-31	9719	27.8
	2	Nazare	128	5.5	0.51	2666	0.74	184	1.30	8.4	-54.6	839	2.40
	3	Ericeira	448	35.3	3.32	8380	2.32	757	5.35	18.0	-2.8	1571	4.50
	4	Tejo	448	14.2	1.33	9702	2.69	1674	11.8	41.5	124.6	1563	4.48
	5	Setubal	320	10.0	0.94	1074	0.30	121	0.85	51.2	176.9	1367	3.91
	6	South	1088	26.5	2.49	10321	2.86	47	0.34	31.1	67.9	2440	7.0
	Sum/Average*		3200	156.8	15	35781	10	7239	51	27	47	17500	50
Nurseries protection	1	North	1664	127.3	12	14785	4	8732	61.7	10	-44.7	7619	21.8
	2	Nazare	192	7.5	0.70	4000	1.11	487	3.44	3.57	-80.7	745	2.13
	3	Ericeira	320	25.0	2.34	5608	1.55	455	3.22	22.6	22.0	1331	3.81
	4	Tejo	320	11.3	1.07	6930	1.92	2362	16.7	12.7	-31.2	982	2.81
	Sum/Average*		2496	171.1	16	31323	9	12036	85	12	-34	10676	31
Spawning areas protection	1	Aveiro	1600	120.2	11.3	10477	2.90	4334	30.6	26	43	10022	28.7
	2	Ericeira	960	62.0	5.83	16495	4.57	766	5.41	33	81	6109	17.5
	3	Tejo	128	3.0	0.28	2772	0.77	209	1.48	13.8	-25.4	1094	3.13
	4	Setubal	320	10.0	0.94	1074	0.30	121	0.85	51.2	176.9	1347	3.86
	5	South	384	8.5	0.80	1464.01	0.41	18.09	0.13	18.2	98.4	1037	3.0
	Sum/Average*		3392	203.6	19.1	32282	8.9	5448.8	38.5	28.6	74.6	19608	56.1
Fishery profit driven	1	North	320	10.9	1.02	1054	0.29	102	0.72	1.85	-90.0	4677	13.39
	2	Nazare	192	4.8	0.45	4000	1.11	561	3.96	6.1	-66.9	312	0.89
	3	Tejo	576	14.0	1.32	11389	3.15	1674	11.8	32	76	1600	4.58

	4	Setubal	320	10.0	0.94	1074	0.30	121	0.85	51.2	176.9	1367	3.91
	5	South	3328	74.7	7.0	41789	11.6	100.5	0.7	28.0	51	6620	19.0
	Sum/Average*		4736	114.4	11	59306	16	2559	18	24	29	14576	42
Safeguarding dependent fishing communities	1	Nazare	128	14.0	1.31	7999	2.21	568	4.01	5.5	-70.4	312	0.89
	2	Ericeira	704	56.1	5.27	16100	4.46	810.65	5.73	21.3	15.1	2643	7.6
	3	Tejo	576	17.9	1.69	12775	3.54	1674	11.8	28.4	53.6	1600	4.58
	4	Setubal	384	12.8	1.20	1289	0.36	121	0.85	41.5	124.6	1367	3.91
	5	South	3328	85.1	8.00	33253	9.21	66.03	0.47	27	43	6006	17.2
	Sum/Average*		5120	185.9	17	71416	20	3240	22.9	25	33.3	11929	34.2

The analysis of the main areas within scenarios individually makes the interpretation of the compromise between fisheries and conservation easier. For example, areas situated in the north were the most suitable for juvenile and adult sardine protection. Their highest numbers were observed in: *nurseries protection*, *baseline* and *spawning areas protection* scenarios. However, protection of these areas would be associated with the high cost for the fishery that would vary from 6% in the *baseline* scenario and about 12% of affected income, in *nurseries protection* and *spawning areas protection* scenarios. Moreover, protection of north areas would not benefit spawning areas that are mainly situated in the area near Setubal. On the other hand, protection of the area near Setubal would benefit considerably protection of sardine eggs (areas with high eggs density – 180% higher than the observed mean) but would have a negligible effect on juvenile (<1% of protected juvenile biomass) and adult (~4% of protected adult biomass) sardine protection. This area would also have minimal impact on fisheries, affecting only 1% of purse seine and less than 0.5% of other fisheries income. On the other hand, the area near Tejo, excluding *spawning areas protection* scenario, was the area that protected the second-highest biomass of juvenile sardine (between 12–17% of total biomass) and between 3–5% of total adult sardine. It also had a relatively low impact on the fisheries income (1–2% on purse seine fishery and 2–4% on other fisheries). Therefore, when comparing the cost and benefits of protecting the Tejo area to the North area, it can be stated that with the first a higher percentage of juvenile sardine would be protected, with a lower economic impact on the purse seine fishery.

2.4. Discussion

This study describes a framework that combines GIS and MCDM methodology to advance EAFM. The most important aspect of this approach is its ability to address multiple conflicting objectives and at the same time integrate and synthesize large amounts of information relevant to EAFM into a single analysis. This is essential in EAFM (Garcia and Cochrane 2005) and has been highlighted to have the potential to significantly facilitate the management process (Leslie and McLeod 2007). Nowadays, GIS and spatial analysis are frequently applied in fisheries management (Witt and Godley 2007; Maxwell et al 2009; Moore et al. 2009) but there is still a lack of a more direct, integrative application of GIS in EAFM, as the one presented in this study.

Carocci et al. (2009) stressed the importance of GIS application in EAFM and suggest that it can be especially useful as a first step of a decision support framework for an EAFM, namely in issue identification. Therefore, GIS can be useful in identification of areas which: (1) require conservation; (2) are particularly important to fishing industry and/or (3) are in conflict depending on stakeholders' objectives. Moreover, the adoption and visualization of alternative scenarios and assessment of their trade-offs is particularly important in the management processes of any complex system (Costanza 1998). The approach described in this study deal with both these tasks. Adoption of five exploratory scenarios enabled us to identify: (1) important areas for specific objectives; (2) conflicting areas between fisheries and conservation objectives and (3) suitable areas for sardine conservation. The area near Aveiro was identified as suitable for both nurseries and spawning protection scenarios but was also identified as one of the most conflicting due to its crucial role in fisheries. In this area, the income from sardine fishery is high as well as the dependence of purse seine fishery on sardine. Thus, permanent closure of fishing in this area seems unlikely, as would not be economically and socially accepted, even though the conservation benefits might be high. To rebuild the sardine stock, temporary closures during spawning season and in areas with high juvenile abundance might be an important management solution. In this study, the spatial analysis repeatedly highlighted the area near the Tejo estuary to be appropriate for conservation. This area is an important spot for sardine recruitment, but not as important for the fishing sector. Its closure has the potential to protect between 12% to 17% of total mean juvenile biomass (observed between 2005 and 2010) barely compromising economic objectives, as the affected purse seine income was estimated to be 1% of the total income. The design of marine reserves is a process in which some economic losses are inevitable therefore the analysis and discussion of trade-offs is very important (Stewart and Possingham 2005). Exploratory scenarios such as the ones presented in this study can make a valuable contribution to the marine reserve design process through the indication of the magnitude of trade-offs assumed. In our case study, the most important trade-offs were between protecting juvenile sardine and minimizing the negative economic impacts. The analysis also revealed the two conservation objectives, eggs abundance and juvenile biomass, to be not totally compatible. Thus, the protection of one of them does not imply the protection of the other, suggesting the difficulty of setting one area able to protect sardine in all its vital life stages (egg, juvenile and adult). Moreover, the application of spatial closures as a conservation measure in fisheries is difficult (Jones 2006) and if not properly

performed might end in frustration and failure (Fiske 1992). The effectiveness of such closures has not always been successful (Abbott and Haynie 2012). There are some examples where the implementation of an MPA resulted in higher aggregation of fishing vessels around the protected areas, a phenomenon called ‘fishing the line’ (Kellner et al. 2007; Stelzenmüller et al. 2008). On the other hand, there are also numerous success stories of spatial closures applied as management measure (Halpern and Warner 2002). The potential benefits include increased species richness, biomass and size of organisms within the reserve (Lester et al. 2009). Another important enquiry when considering spatial closures, is the extent to which they should or can be applied in practice. The duration of the protection and the size of the no-take areas have shown to play an important role in MPA effectiveness (Vandeperre et al. 2011). Should the spatial closures encompass only the fishery that targets sardine or be a total closure of fishing activities in the area? What about other sectors such as tourism or recreational fishing? And how do they affect other species and trophic interactions? These are examples of some questions emerging when talking about spatial closures in EAFM (Halpern et al. 2010). In this study, an attempt was made to deal with those questions by including criteria such as ‘other fisheries’ and biotic interactions (sardine competitors and predators). As shown in this study closure of all fishing activities might considerably affect the fishing industry. Biotic interactions are very difficult to represent in this kind of analysis and their involvement was limited to mapping their distribution and indicating the areas overlapping with sardine. To obtain information about how spatial closures might affect trophic interactions and the ecosystem, the application of more sophisticated methods, such as ecosystem models (Polovina 1984; Christensen and Pauly 1992; Walters et al. 1997, 1999, Fulton et al. 2004a, 2004b) might be required. For example, Colléter et al. (2014), used food web models of Mediterranean and Senegalese ecosystems and found out the benefits of an MPA, such as increased biomass and catch yields, to be dependent on the MPA size.

One of the limitations of the performed analysis was data availability. Lack of long time-series impeded the inclusion of statistical predictive modelling which have the capability to reduce uncertainty related to variability in tested variables. GIS environment support integration of spatial analysis with other tools in order to represent the temporal domain (Sahin and Mohamed 2013; Chen et al. 2015), but these approaches are extremely data demanding, and in our case study, spatio-temporal data, especially related to VMS fishery data, were not available. In our study, 6 years of data, were averaged and subjected to the analysis to reduce the uncertainty in the spatial

distribution. The period considered is a good representation of our case study because it covers a time when both, high and low sardine biomass, was observed (ICES 2017). Another important data limitation is the lack of seasonality. Variables included in the analysis, such as productivity patterns, zooplankton, sardine eggs and sardine distribution, tend to vary with season (Bernal et al. 2007; Moita et al. 2010; Zwolinski et al. 2010; Sobrinho-Gonçalves et al. 2013). However, Portuguese surveys do not collect seasonal data for these variables. This limitation might increase the uncertainty of the results and consequently impede the implementation of temporal and permanent conservation areas, thus more studies should be done to analyse the temporal variation of those variables and their effect on sardine biomass.

One of the study's strengths was the application of the AHP process to select weights. Although, it is a common practice in MCDM studies (Phua and Minowa 2005; Chen et al. 2010; Gdoura et al. 2015) sometimes it is criticized (Dyer 1990). Nevertheless, this process is appropriate for this type of analysis because it enables the inclusion of multiple stakeholders (Phua and Minowa 2005; De Feo and De Gisi 2010). Stakeholder involvement in EAFM decision support frameworks is essential and a highly recommended practice (Varjopuro et al. 2008; Kincaid et al. 2017). Even though, stakeholders were not included in the weights selection in this study, the design and methodology applied easily enables their inclusion in the future.

In spatial analysis, uncertainty is introduced at its various stages (Refsgaard et al. 2007; Mosadeghi et al. 2013). In our case, uncertainty can arise from satellite data resolution conversion, creation of raster maps from point observations, identification of criteria and weights selection. In the case of criteria weights estimation, uncertainty was addressed through the performance of a sensitivity analysis which revealed that the majority of variables are quite stable to the changes introduced by the weights (Figure A2.2). Uncertainty was not quantitatively assessed in other stages, but its presence is acknowledged and therefore results should be interpreted with caution. Furthermore, it should be kept in mind that an array of other available statistical approaches, which could substitute the methods used in the present work (e.g., WLC method, AHP, Jenks natural breaks reclassification method), exist and their selection might considerably influence the results.

The biggest difficulty in the application of this type of methodologies is the integration of the various data, disciplines, and institutions together (Leslie and McLeod 2007). The united effort, collaboration and data sharing between scientific institutions, governments, fisheries institutions

and non-governmental organizations (NGOs) is extremely important to the successful development of this and other data-hungry, integrative methods. In this study, scientists specialized in distinctive fields were involved. Moreover, various type of data, e.g., fisheries, satellite, landings and biological were compiled and processed.

2.5. Conclusion

The proposed framework presents a useful tool to support an EAFM implementation. The analysis performed with Portuguese sardine fishery as a study case proved that a combination of GIS and MCDM methodology could synthesise existing information in a fishery system, aid in the visualization of spatial existing problems and pinpoint areas that require special attention. This tool stands out as an efficient first step in an EAFM decision support framework. Further development of the method should start by performing seasonal analysis that will reflect annual variation in species distribution. Other aspects that should be addressed in the future is the involvement of stakeholders in the weights selection process and quantitative assessment of uncertainty in the other stages of the analysis, especially surface maps production and method selection.

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Chapter 3

First representation of the trophic structure and functioning of the Portuguese continental shelf ecosystem: insights into the role of sardine

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Chapter 3 – First representation of the trophic structure and functioning of the Portuguese continental shelf ecosystem: insights into the role of sardine

Abstract

In this study, we analysed the structure and functioning of the Portuguese continental shelf ecosystem and investigated the role of sardine (*Sardina pilchardus*) using the Ecopath mass-balance approach. An Ecopath model was configured to represent the continental shelf waters in the period 2006–2009. The model showed that biomass was concentrated in low and intermediate trophic levels as in other upwelling areas. Several low- and medium-trophic level groups are identified as dominant groups in the ecosystem (e.g., zooplankton, macrozoobenthos, sardine, chub mackerel (*Scomber colias*), and demersal and benthopelagic invertivorous fish). Furthermore, low trophic level groups were responsible for the main energy flows, and overall higher impact on the ecosystem, emphasizing the importance of bottom-up control of the ecosystem structure. Our results are relevant to understand the structure and functioning of this ecosystem and constitute an important step towards an ecosystem approach to fisheries management in the study area.

Keywords: Sardine, Small pelagic fish, Upwelling ecosystem, Trophic interaction, Ecopath

3.1. Introduction

The Portuguese coastal waters are at the northern limit of the Canary Current Upwelling System (Santos et al. 2007; Arístegui et al. 2009). As in other upwelling areas, Portuguese waters have high primary and secondary productivity and are dominated by small and medium pelagic species as sardine (*Sardina pilchardus*), chub mackerel (*Scomber colias*) and horse mackerel (*Trachurus trachurus*; Arístegui et al. 2009; Santos et al. 2013). Sardine is the dominant fish species in the ecosystem down to depths around 120 m (Gomes et al. 2001). Between 150 and 400 m, the ecosystem shifts to the dominance of benthopelagic and demersal species, such as blue whiting (*Micromesistius poutassou*), snipefish (*Macroramphosus* spp.) and boarfish (*Capros aper*). Other species, such as hake (*Merluccius merluccius*), horse mackerel, and chub mackerel have a ubiquitous distribution, with higher densities of younger individuals in shallower waters and older individuals in deeper waters (Sousa et al. 2005). Sardine is an important fishing resource in Portugal being the target species of the purse-seine fleet and the main product of the fish canning industry (Silva et al. 2015). However, since 2006, sardine stock biomass decreased 75% and is currently around the lowest historical level in 30 years (ICES 2016). The causes underlying this decrease are not clear and possibly result from a complex interplay between environmental variability, species interactions and fishing pressure (Malta et al. 2016). Improving the knowledge of the trophic relationships and trophic structure of the coastal western Iberian ecosystem is an important first step to assess the role of sardine in the ecosystem.

Ecosystem models are useful tools to identify the main energy flows within an ecosystem and to quantify the relative magnitude of such flows, providing insight into ecosystem structure and functioning (Murawski 2007; Plagányi 2007). Among such models, Ecopath with Ecosim (EwE), a mass-balance model of trophic interactions (Christensen and Pauly 1993; Christensen and Walters 2004), is one of the most common and widely used (Colléter et al. 2015). The ability to integrate fisheries in the analysis, evaluate their impacts on the ecosystem (Coll and Libralato 2012), and provide a set of ecological indicators are the important strengths of the EwE modelling approach (Fulton et al. 2003).

The mass-balance modelling has been widely used to quantitatively describe aquatic systems and to assess the role of small pelagic fish (SPF) in the upwelling regions around the world

(Shannon et al. 2003; Moloney et al. 2005). However, there are still few examples of ecological modelling applied to the Portuguese coastal ecosystems, limited to modelling of the nearby estuaries of Ria Formosa (Gamito and Erzini 2005), Mondego (Patricio and Marques 2006; Baeta et al. 2011) and Aveiro (Bueno-Pardo et al. 2018). The present application is the first effort to study the Portuguese continental shelf upwelling ecosystem using a mass-balance model. In this study, we examine the structure and functioning of the Portuguese continental shelf ecosystem and investigate the role of sardine using the Ecopath mass-balance approach.

3.2. Materials and Methods

3.2.1. Study area

The Portuguese continental shelf ecosystem (hereafter referred to PCSE) food web model was developed for the area located in the northeast Atlantic between 36.5° and 42°N latitude and 10.5° and 7.5°W longitude (Figure 3.1). It covers an area of around 22,000 km² between the 30 and 200 m isobaths. The continental shelf width varies along the coast, ranging from approximately 5 km to 70 km, being wider on the north-west coast (Figure 3.1), and having an average of 45 km (Arístegui et al. 2009; Martins et al. 2012). The Portuguese shelf sea surface temperature ranges from 18°C in the south and 16.5°C in the north with an overall average of 17°C.

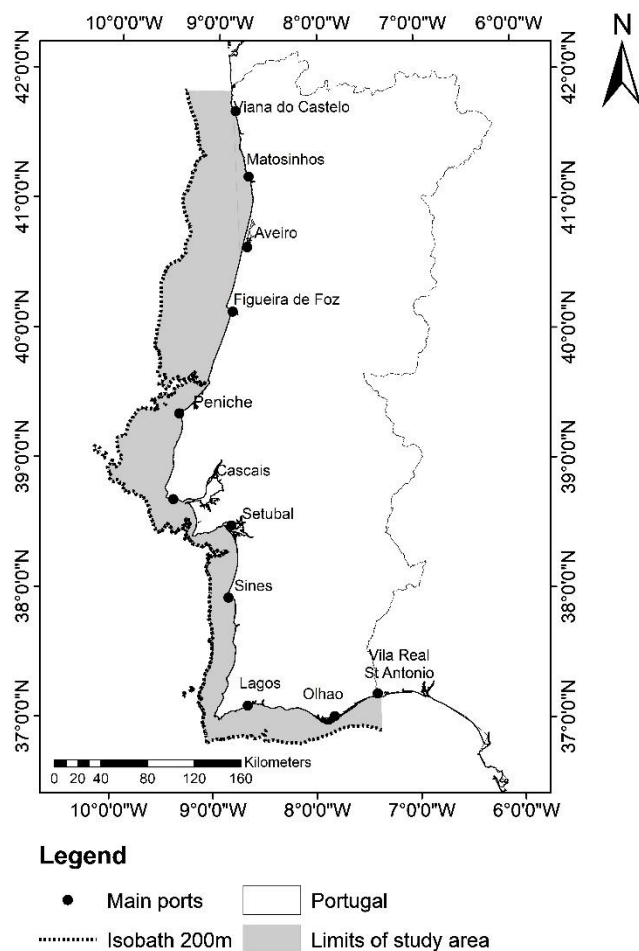


Figure 3.1 Map of the Portuguese continental shelf showing limits of the study area and main fishing ports.

3.2.2. Model structure

A mass-balance model was constructed using Ecopath with Ecosim version 6.5 (Christensen and Walters 2004, Christensen et al. 2008, www.ecopath.org). The static Ecopath model was applied to the period 2006–2009. The model had 33 functional groups including seabirds, cetaceans, fish, macro-invertebrates, zooplankton, phytoplankton (Table 3.1) and two types of detritus: discards and detritus. Groups were formed based on criteria such as the similarity of ecological and/or biological features (e.g., habitat, feeding), amount of data available for the study area and period and potential relationships with the sardine. The most abundant pelagic fish species and their main predators were modelled as single species groups (e.g., sardine, anchovy,

horse mackerel, blue jack mackerel, chub mackerel, Atlantic mackerel (*Scomber scombrus*), hake and 5 species of marine mammals). This was not possible for tuna and cephalopods because of insufficient data. The fish species considered in the model were selected based on the results of monitoring surveys undertaken in the study area over the modelled period and include species that constituted 99% of the total survey's biomass.

Table 3.1. List of functional groups and species within each group included in the Portuguese continental shelf model. The relative abundance/biomass for each species within the respective functional group is shown in parentheses. When no relative abundance is given, such information was not available or was deemed unreliable (see explanation in Materials and Methods section).

Functional group	Species
1. Seabirds	<i>Morus bassanus</i> (86.8%); <i>Calonectris borealis</i> (7.9%); <i>Alca torda</i> (2.7%); <i>Puffinus mauretanicus</i> (1.6%); <i>Uria aalge</i> (0.9%)
2. Minke whale	<i>Balaenoptera acutorostrata</i> (100%)
3. Common dolphin	<i>Delphinus delphis</i> (100%)
4. Striped dolphin	<i>Stenella coeruleoalba</i> (100%)
5. Bottlenose dolphin	<i>Tursiops truncatus</i> (100%)
6. Harbor porpoise	<i>Phocoena phocoena</i> (100%)
7. Tunas	<i>Sarda sarda</i> ; <i>Auxis rochei</i> ; <i>Thunnus thynnus</i>
8. Rays	<i>Raja clavata</i> ; <i>Raja brachyura</i> ; <i>Leucoraja naevus</i> ; <i>Raja montagui</i>
9. Hake	<i>Merluccius merluccius</i> (100%)
10. Squids	<i>Loligo vulgaris</i> ; <i>Illex coindetii</i> ; <i>Todaropsis eblanae</i> ; <i>Alloteuthis subulata</i> ; <i>Alloteuthis media</i>
11. Benthic cephalopods	<i>Octopus vulgaris</i> ; <i>Eledone cirrhosa</i> ; <i>Sepia officinalis</i> ; <i>Sepiola</i> spp.
12. Horse mackerel	<i>Trachurus trachurus</i> (100%)
13. Blue jack mackerel	<i>Trachurus picturatus</i> (100%)
14. Chub mackerel	<i>Scomber colias</i> (100%)
15. Mackerel	<i>Scomber scombrus</i> (100%)
16. Demersal piscivorous fish	<i>Conger conger</i> ; <i>Chelidonichthys lucernus</i> ; <i>Helicolenus dactylopterus</i> ; <i>Dicentrarchus labrax</i> ; <i>Lophius budegassa</i> ; <i>Lophius piscatorius</i>
17. Demersal invertivorous fish	<i>Trigla lyra</i> ; <i>Serranus hepatus</i> ; <i>Callionymus lyra</i> ; <i>Chelidonichthys cuculus</i> ; <i>Synchiropus phaeton</i> ; <i>Lepidotrigla cavillone</i> ; <i>Callanthias ruber</i> ; <i>Mullus surmuletus</i> ; <i>Mullus barbatus</i> ; <i>Cepola macrophthalma</i> ; <i>Ammodytidae</i> ; <i>Gobiidae</i>
18. Benthopelagic piscivorous fish	<i>Zeus faber</i> ; <i>Lepidopus caudatus</i> ; <i>Belone belone</i> ; <i>Phycis blennoides</i> ; <i>Phycis phycis</i>
19. Benthopelagic invertivorous fish	<i>Trisopterus luscus</i> ; <i>Micromesistius poutassou</i> ; <i>Argentina sphyraena</i> ; <i>Macroramphosus</i> spp.; <i>Capros aper</i> ; <i>Gadiculus argenteus</i> ; <i>Anthias anthias</i>
20. Flatfish	<i>Solea solea</i> ; <i>Solea senegalensis</i> ; <i>Pegusa lascaris</i> ; <i>Microchirus azevia</i> ; <i>Microchirus variegatus</i> ; <i>Platichthys flesus</i> ; <i>Citharus linguatula</i> ; <i>Dicologlossa cuneata</i> ; <i>Scophthalmus maximus</i> ; <i>Scophthalmus rhombus</i> ; <i>Lepidorhombus boscii</i> ; <i>Lepidorhombus whiffiagonis</i> ; <i>Arnoglossus laterna</i>
21. Sparids	<i>Pagellus acarne</i> (55.9%); <i>Pagellus erythrinus</i> (3%); <i>Pagellus bogaraveo</i> (0.7%); <i>Spondyliosoma cantharus</i> (12.5%); <i>Diplodus vulgaris</i> (26.4%); <i>Diplodus bellottii</i>

	(0.1%); <i>Diplodus annularis</i> (0.1%); <i>Diplodus sargus</i> (0.1%); <i>Pagrus pagrus</i> (1.1%); <i>Pagrus auriga</i> (0.2%)
22. Anchovy	<i>Engraulis encrasicolus</i> (100%)
23. Sardine	<i>Sardina pilchardus</i> (100%)
24. Bogue	<i>Boops boops</i> (100%)
25. Henslow's crab	<i>Polybius henslowii</i> (100%)
26. Shrimps	Unspecified Crustacea natantia
27. Macrozoobenthos	Starfishes; Annelids; Sea urchins; Sea cucumbers; Bivalves; Crustaceans; Sea anemone; other benthic invertebrates
28. Suprabenthic invertebrates	Euphausiids, Mysids, Isopods and Amphipods
29. Macrozooplankton	Macrozooplankton (Zooplankton length > 3 mm, width > 1 mm)
30. Meso and microzooplankton	Mesozooplankton and microzooplankton (Zooplankton length ≤ 3 mm, width ≤ 1 mm; including fish eggs)
31. Phytoplankton	Phytoplankton

Benthopelagic and demersal fish were split into piscivorous and invertivorous based on the diet composition (Table A3.2 in annex 3). Species with diets composed of more than 25% of weight or volume of fish were allocated to piscivorous groups, while the rest was allocated to invertivorous groups. Due to lack of data at the species or genus level, invertebrates were aggregated into more broad functional groups (e.g., squids, benthic cephalopods, shrimps, suprabenthic invertebrates, and macrozoobenthos). Henslow's swimming crab (*Polybius henslowii*) was modelled as an individual group owing to its high abundance and frequency of occurrence in the purse seine fishery.

3.2.3. Parameter estimation

Data from the study period and area were given priority in the calculation of all input parameters stated in the following 5 subsections. If such data were not available, priority was given to data from the same species in nearby areas (Cantabrian Sea, Bay of Biscay and Gulf of Cadiz) followed by data from the same species or functional groups in a different ecosystem and, finally, data compiled from FishBase (www.fishbase.org). In the cases where, for a given functional group, the information available in nearby areas' models was different, the source of the information for each value was taken into account, and priority given to values that were obtained from experimental data and how similar the species within the functional groups were. If the uncertainty

around those values was similar (e.g., same source type or values assumed), an average value was used. For functional groups that consisted of more than one species, input data (e.g., diet, production/biomass ratio, and consumption/biomass ratio) were calculated as weighted averages of the species data using relative biomasses as weighting factors. When biomass data were not available, group data were simple averages of component species data (Table 3.2 and Table A3.1 in annex 3). Input parameters are presented in Table 3.2 and detailed information on data sources and estimation methods for each functional group are in Table A3.1 in annex 3.

Table 3.2. Main inputs of the Portuguese continental shelf Ecopath model. Functional groups that include commercially exploited species are shown in bold. Biomass and ecotrophic efficiency values estimated by the model are shown underlined. B: Biomass; P: Production; Q: Consumption; EE: Ecotrophic Efficiency; BA: Biomass Accumulation.

	Functional group	B (t km ⁻²)	EE	P/B (year ⁻¹)	Q/B (year ⁻¹)	BA Rate (year ⁻¹)	Landings (t km ⁻²)	Discards (t km ⁻²)
1	Seabirds	0.01	<u>0.00</u>	0.10	57.64	-	-	-
2	Minke whale	0.06	<u>0.37</u>	0.03	35.11	-	0.001	-
3	Common dolphin	0.04	<u>0.20</u>	0.08	31.29	-	0.001	-
4	Striped dolphin	0.01	<u>0.11</u>	0.08	30.98	-	4.0E-05	-
5	Bottlenose dolphin	0.01	<u>0.03</u>	0.08	32.06	-	4.0E-04	-
6	Harbour porpoise	0.00	<u>0.33</u>	0.08	14.17	-	4.5E-06	-
7	Tunas	0.20	<u>0.10</u>	0.42	4.21	-	0.008	-
8	Rays	<u>0.14</u>	0.85	0.73	4.83	-	0.067	0.017
9	Hake	0.39	<u>0.93</u>	1.30	6.07	-	0.090	0.050
10	Squids	<u>0.96</u>	0.95	2.80	8.00	-	0.012	0.006
11	Benthic cephalopods	<u>1.15</u>	0.95	2.30	6.50	-	0.340	0.081
12	Horse mackerel	2.84	<u>0.93</u>	0.51	7.61	-	0.508	0.001
13	Blue jack mackerel	0.78	<u>0.90</u>	0.54	7.21	-	0.115	0.012
14	Chub mackerel	6.58	<u>0.92</u>	0.65	6.82	-	0.601	0.470
15	Mackerel	0.45	<u>0.94</u>	0.80	7.14	-	0.105	0.013
16	Demersal piscivorous fish	<u>0.53</u>	0.95	0.64	3.57	-	0.106	0.024
17	Demersal invertivorous fish	<u>5.77</u>	0.95	1.22	6.68	-	0.027	0.005
18	Benthopelagic piscivorous fish	<u>0.34</u>	0.95	0.83	4.10	-	0.033	0.007
19	Benthopelagic invertivorous fish	<u>6.62</u>	0.95	0.95	7.10	-	0.268	0.107
20	Flatfish	<u>0.91</u>	0.95	0.94	5.69	-	0.046	0.009
21	Sparids	0.60	<u>0.86</u>	0.73	5.42	-	0.104	0.021
22	Anchovy	0.31	<u>0.92</u>	1.17	12.22	-	0.016	-
23	Sardine	14.76	<u>0.72</u>	0.89	9.68	-0.21	2.838	0.156
24	Bogue	<u>0.79</u>	0.95	1.25	6.20	-	0.009	0.019
25	Henslow's crab	<u>0.53</u>	0.95	2.10	10.64	-	0.001	-
26	Shrimps	<u>3.62</u>	0.95	4.20	11.67	-	-	-

27	Macrozoobenthos	14.54	<u>0.84</u>	3.55	9.73	-	0.023	0.005
28	Suprabenthic inv.	<u>3.60</u>	0.95	16.00	42.00	-	-	-
29	Macrozooplankton	5.25	<u>0.78</u>	17.00	44.00	-	-	-
30	Meso- and Microzoo	25.29	<u>0.47</u>	30.10	152.52	-	-	-
31	Phytoplankton	18.72	<u>0.58</u>	350.78	-	-	-	-
32	Discards	1.00	<u>0.93</u>	-	-	0.13	-	-
33	Detritus	45.23	<u>0.08</u>	-	-	-	-	-

3.2.4. Biomass data

Only biomasses within the coastal zone to 200 meters depth were included in the model and were considered to be representative of the average biomass available throughout the year for each functional group. Abundance and density estimates for seabirds and marine mammals were obtained in aerial surveys covering the Portuguese continental shelf and adjacent oceanic waters (Araújo et al. 2014). For each species, density data were used to estimate total abundance and then biomass using mean weight (Table A3.1 in annex 3).

Biomass estimates for fish groups (pelagic, benthopelagic and demersal) were compiled from acoustic (AC) and bottom trawl (BT) surveys carried out annually in the Portuguese waters in spring and autumn, respectively (ICES 2012, 2013). Biomasses from BT surveys were estimated by the swept-area method. The fishing gear used in the BT survey is not in full contact with the ground because the ground-rope has rollers and it is not suitable for rocky bottoms. Thus, some species, such as flatfish (which can escape under the gear), demersal species that stay near the bottom and species that prefer rocky areas, may be highly underestimated. Therefore, catchability rates of 0.8 for Hake (Huse et al. 2001) and 0.25 for other demersal and benthopelagic species (Harley and Myers 2001; Trenkel and Skaug 2005) were assumed. The model initial inputs did not include the biomasses of 12 functional groups due to insufficient data (e.g., suprabenthic invertebrates, shrimps, and benthic cephalopods) or because the estimated biomasses based on the BT surveys were too low even when assuming very low catchability rates (e.g., flatfish, squids, and the aggregated groups of benthopelagic and demersal fishes). Catchability rates lower than the recommended rates in the literature were tried for all species of these functional groups and the obtained biomasses for each species compared with the respective catches in the area. For the majority of the species, the catches were higher than the estimated biomasses, therefore they were

considered unrealistically low. Furthermore, the abundance estimates were considered to be acceptable when considering each species individually, but when considering them within a functional group the relative abundances within each group were not considered to be representative. For all these 12 functional groups, the biomasses were estimated by the Ecopath model and for those groups, ecotrophic efficiency (EE) was assumed to be 0.95, except for rays for which EE was assumed to be 0.85 based on EE values for the same group in nearby areas (Sanchez and Olaso 2004; Torres et al. 2013). Biomass estimates from AC surveys were assumed to be absolute (i.e., catchability=1; ICES 2011).

Macro- and mesozooplankton biomass estimations were based on samples collected with a continuous underway fish eggs sampler (CUFES) (mesh size of 335 μm) during AC surveys chosen because of their high spatial resolution along a large geographical coverage. To approximate near-surface (3 m depth) zooplankton biomass estimates sampled by CUFES to the whole water column and correct for the effect of the comparatively larger mesh size (335 μm), extensive research of localized paired comparisons between CUFES samples and net-hauled vertically integrated samples (Bongo 200 and 335 μm , Wp2 200 μm , Calvet 150 μm) was performed (L. Sobrinho-Gonçalves unpubl. data). As a result, a factor of 3.5 was found and biomass values, obtained from CUFES samples, were multiplied by this factor. Microzooplankton biomass data were available for coastal waters and for offshore waters it was corrected by a factor of 2 in the productive season (April-October) based on the study in the nearby region of the Bay of Biscay (Marquis et al. 2011).

Phytoplankton biomass was estimated using chlorophyll a satellite data from the Globcolour project (www.globcolour.info; Table A3.1 in annex 3). Detritus biomass was estimated based on the empirical equation proposed by Pauly et al. (1993):

$$\text{Log}(D) = -2.41 + 0.954 \times \log(PP) + 0.863 \times \log(E) \quad \text{Equation 3.1}$$

where D is the detritus biomass in g m^{-2} , PP is the annual primary production of the area in $\text{g C m}^{-2} \text{ year}^{-1}$ and E is the average euphotic depth in meters.

Due to the well-documented decreasing trend in sardine biomass observed in the recent decades, and significant change in its biomass between years 2006 and 2009 for which the model was parameterized, a negative annual average rate of sardine biomass accumulation (BA) of

0.21%, was applied. This value was calculated based on the acoustic data. As not clear changes in biomass were observed for the other functional groups, in their case, BA and other export terms were assumed equal to zero.

3.2.5. Diet composition

For a vast majority of the species considered in the model, diet composition was compiled from studies on stomach content analysis of individuals caught within the PCSE. Cetacean stomach content analyses were performed on stranded dead animals; thus, the identified prey likely comes from within the PCSE. More detailed information regarding the sources for the different species' diet composition can be found Table A3.1 in annex 3.

The diet composition matrix (Table A3.2 in annex 3) was constructed taking into account the following steps: (1) in case unidentified species were present in the diet, data were re-scaled to 100% for the respective taxonomic groups; (2) when diet composition from areas other than the PCSE was used, the proportion of the elements in the diet was adapted to the species composition of the PCSE (e.g. species from the same genus or family and similar function in the ecosystem); (3) for mackerels (*Scomber* spp.) and horse mackerels (*Trachurus* spp.) whose older individuals are distributed beyond the shelf and show ontogenetic variation in the feeding habits, diets were adjusted to the continental shelf life stage based on the literature (e.g. Garrido et al. 2015), and to the average length size caught within the shelf for each species; (4) species' migratory behaviour (e.g. seabirds and minke whale (*Balaenoptera acutorostrata*) was taken into account by adjusting a portion of their diet as import to the ecosystem proportionally to the time they spent outside the area (Christensen and Walters 2004; Coll et al. 2006) and (5) for the four small cetaceans species considered in the model, prey that is distributed outside the continental shelf or estuaries were considered as import.

3.2.6. Production/biomass ratio (P/B)

Production/biomass (P/B) data for seabirds and marine mammals were compiled from Christensen et al. (2009) since these values were an average of similar groups in exploited areas

around the world. Considering no active fishery for marine mammals, fishing mortality was replaced by by-catch mortality from 2010 to 2012. For fish groups, P/B was estimated using the assumption, that in steady-state conditions, it is equivalent to total mortality (Z) where Z equals to natural mortality (M) plus fishing mortality (F) according to Allen (1971). To calculate M the empirical equation by Pauly (1980) (annex A3) was used while F was calculated as catch/biomass. When no biomass estimates were available, a mean F for the group was assumed based on literature and expert knowledge. For invertebrates and zooplankton groups, values were compiled from the literature (e.g., squids, meso- and microzooplankton) or adapted based on data from models of nearby areas (e.g., benthic cephalopods, Henlow's crab, shrimps, macrozoobenthos, suprabenthic invertebrates; Table A3.1). Phytoplankton P/B was calculated by dividing the annual primary production by the annual mean biomass. Phytoplankton primary production was estimated using vertically generalized production model (VGPM; Behrenfeld and Falkowski 1997; Table A3.1 in annex 3) that based their product on the sea-viewing wide field-of-view sensor (SeaWiFS) and moderate resolution imaging spectroradiometer (MODIS) satellite sensors.

3.2.7. Consumption/biomass ratio (Q/B)

Daily ration for seabirds (DR) in g d^{-1} was calculated using the empirical equation from Nilsson and Nilsson (1976; annex 3). Values for marine mammals were calculated using daily food consumption estimates (kg d^{-1}) in Iberian Atlantic waters (Santos et al. 2014), except for minke whale estimates, which were for the Northeast Atlantic (Markussen et al. 1992). For fish groups, Q/B was calculated with the empirical equation from Pauly et al. (1990) (annex 3).

For Henlow's swimming crab, Q/B was calculated using the empirical equation for the daily consumption rate of invertebrates (Cammen 1980) (annex 3):

For other groups of invertebrates and zooplankton, Q/B values were compiled from literature or Ecopath models from nearby areas (Table A3.2).

3.2.8. Fisheries data

Average landings in 2006–2009 were calculated for purse seine, BT, and polyvalent fleets, the last of these referring to the (artisanal) multi-gear fleet. BT and purse seine discards were compiled from the literature (Feijó 2013; Fernandes et al. 2015). For the purse-seine fleet, slipping estimates were also included assuming mortality of one-third of the slipped biomass for all species and included as discards in the model (Huse and Vold 2010; Marçalo et al. 2010, Tenningen et al. 2012). Similar assumptions were made for discards of SPF in the polyvalent fleet since those species are mainly caught using purse seine. For all other groups caught by the polyvalent fleet, 20% of the catch was assumed to be discarded based on local studies (Borges et al. 2008; Batista et al. 2009). Marine mammal by-catch estimates were derived from unpublished data of the MarPro strandings and bycatch evaluations databases (Ferreira et al. 2012).

3.2.9. Pre-balance, model balancing and analysis

To ensure that the model parameters followed the general ecological principles, a pre-balance (PREBAL) diagnostic (Link 2010) was performed, including the slopes of biomass ratios, vital rates, total production and consumption based on trophic levels. The results of this diagnostic were used as a guide for balancing procedure and to check the integrity of the input data. Furthermore, the pedigree level (Christensen and Walters 2004; Christensen et al. 2008) was attributed to input data and used as a guideline to select the parameters more suitable for adjustment during model balancing. Pedigree values vary between zero for highly uncertain inputs, such as guesstimates, and one for precise estimates, well-sampled and high-precision local data (Christensen and Walters 2004). The process of model balancing was carried out following the best practice guidelines provided in the literature (Christensen et al. 2008; Heymans et al. 2016). The model was considered balanced when the following requirements were met: (1) EE estimates were lower than one; (2) estimated values of gross food conversion efficiency (GE or P/Q) were within the range of 0.05–0.35 considered physiologically realistic for most species; top predators and fast-growing species can have lower and higher values, respectively; (3) estimates of net efficiency of food conversion were below 1 for all functional groups.

The sensitivity of the model input parameters was examined by changing each parameter from -50% to 50% of its original value in 10% steps and re-running the model. This was carried out for either B or EE, P/B and Q/B per functional group. The impact that each step change caused on the output parameters was recorded for all functional groups. An index of sensitivity was calculated as the number of impacts, of one given functional group, equal to or above 30% on the output parameters of other functional groups (Olson and Watters 2003).

Ecopath built-in ecological indices and network analysis tools were used to summarise the ecosystem status in terms of biomasses, flows, maturity and resistance to external perturbations (Christensen et al. 2008). Trophic level (TL) and transfer efficiency (TE) were calculated for each functional group. Flows and biomasses were aggregated by TL to provide a quantitative description of the ecosystem structure (Lindeman spine analysis; Lindeman 1942; Libralato et al. 2002). Keystone groups, relatively low biomass groups with high overall effect in the trophic network, and dominant groups, with both relatively high biomass and high overall effect, were identified (Libralato et al. 2006). The quantification of total trophic impacts (direct and indirect, positive and negative) of a hypothetical increase in biomass of one group in all other groups in the ecosystem was carried out using mixed trophic impact (MTI) analysis (Ulanowicz and Puccia 1990).

3.3. Results

3.3.1. PREBAL, pedigree and uncertainty routines

PREBAL procedure revealed that for some functional groups B, P/B and Q/B values were low (underestimated, below slope line) or high (overestimated, above slope line). These values were checked for data integrity before initiating the mass-balance of the model.

The pedigree index obtained for the PCSE model was 0.54, placing the model in the upper range (0.16–0.68) of 50 balanced Ecopath models analysed by Morissette (2007). This value implies a reasonable quality of data but also highlights room for improvement.

The sensitivity analysis routine showed that by altering the input parameters of a functional group, the model is mainly sensitive to both cephalopods groups and, to a lesser extent, demersal

piscivorous and invertivorous fish, benthopelagic invertivorous fish, flatfish and meso- and microzooplankton groups (Table 3.3).

Table 3.3. Main outputs of the Portuguese continental shelf Ecopath model. Functional groups that include commercially exploited species are shown in bold. TL: Trophic level; B: Biomass; P: Production; Q: Consumption; F: Fishing mortality; M2: Predation mortality; M0: Other mortality; Z: Total mortality; NE: Net efficiency; OI: Omnivory Index; SI: Sensitivity Index.

	Functional group	TL	F (year ⁻¹)	M2 (year ⁻¹)	M0 (year ⁻¹)	F/Z	P/Q	NE	OI	SI
1	Seabirds	4.3	0.000	0.00	0.10	0.00	0.002	0.002	0.224	0
2	Minke whale	4.2	0.011	0.00	0.02	0.37	0.001	0.001	0.125	0
3	Common dolphin	4.3	0.016	0.00	0.06	0.20	0.003	0.003	0.176	0
4	Striped dolphin	4.5	0.008	0.00	0.07	0.11	0.003	0.003	0.278	0
5	Bottlenose dolphin	5.3	0.003	0.00	0.08	0.03	0.002	0.003	0.489	0
6	Harbor porpoise	4.9	0.027	0.00	0.05	0.33	0.006	0.007	2.064	0
7	Tunas	4.0	0.040	0.00	0.38	0.10	0.100	0.125	1.165	0
8	Rays	4.2	0.619	0.00	0.11	0.85	0.151	0.189	0.309	0
9	Hake	4.3	0.360	0.85	0.09	0.28	0.214	0.268	0.129	0
10	Squids	4.2	0.018	2.64	0.14	0.01	0.350	0.438	0.212	24
11	Benthic cephalopods	4.1	0.364	1.82	0.11	0.16	0.354	0.442	0.220	24
12	Horse mackerel	3.5	0.179	0.30	0.03	0.35	0.067	0.084	0.069	0
13	Blue jack mackerel	3.3	0.162	0.32	0.05	0.30	0.074	0.093	0.118	0
14	Chub mackerel	3.4	0.163	0.44	0.06	0.25	0.096	0.120	0.290	4
15	Mackerel	3.3	0.264	0.49	0.05	0.33	0.113	0.141	0.248	0
16	Demersal piscivorous fish	4.3	0.245	0.37	0.03	0.38	0.180	0.225	0.248	8
17	Demersal invertivorous fish	3.4	0.005	1.15	0.06	0.00	0.183	0.229	0.125	15
18	Benthopelagic piscivorous fish	4.1	0.120	0.67	0.04	0.14	0.203	0.254	0.303	0
19	Benthopelagic invertivorous fish	3.4	0.057	0.85	0.05	0.06	0.134	0.168	0.111	10
20	Flatfish	3.9	0.061	0.83	0.05	0.06	0.165	0.207	0.430	6
21	Sparids	3.6	0.210	0.41	0.10	0.29	0.134	0.167	0.334	0
22	Anchovy	3.0	0.051	1.02	0.09	0.04	0.096	0.120	0.013	0
23	Sardine	2.8	0.203	0.65	0.04	0.05	0.092	0.115	0.139	0
24	Bogue	3.5	0.035	1.15	0.06	0.03	0.201	0.251	0.051	0
25	Henslow's crab	3.3	0.002	1.99	0.11	0.00	0.197	0.329	0.361	0
26	Shrimps	2.7	-	3.99	0.21	-	0.360	0.600	0.421	0
27	Macrozoobenthos	2.3	-	2.99	0.56	-	0.365	0.609	0.355	0
28	Suprabenthic inv.	2.3	-	15.20	0.80	-	0.381	0.635	0.244	0
29	Macrozooplankton	2.7	-	13.27	3.73	-	0.386	0.644	0.210	0
30	Meso- and Microzoo	2.0	-	14.16	15.94	-	0.197	0.329	-	8
31	Phytoplankton	1.0	-	202.10	148.70	-	-	-	-	0
32	Discards	1.0	-	-	-	-	-	-	-	-
33	Detritus	1.0	-	-	-	-	-	-	0.334	-

3.3.2. Model balancing

The initial model presented EE values higher than one for horse mackerel, mackerel, macrozoobenthos, and hake. For horse mackerel and mackerel, the balance was achieved by a small adjustment (less than 5%) of the predatory pressure, redirecting it to similar small pelagic groups. For macrozoobenthos, the initial percentage of cannibalism was high (around 10%) and the balance was achieved by setting cannibalism to 2%. Hake had an EE over 1.5 in the initial model. Since the assumed catchability (0.8) had a higher pedigree score than P/B, the latter was adjusted. The value obtained from empirical equations (Allen 1971; Pauly 1980) was replaced by total mortality estimated in stock assessment for the age groups predominant in the Portuguese continental shelf (1–3 years). The final output parameters for the 33 functional groups are shown in Table 3.3.

3.3.3. Summary statistics

The summary statistics and ecological network analysis indicators (for more details see Heymans et al. 2014) describing PCSE are presented in Table 3.4. The total flow of detritus and total exports represented about one-third of the total system throughput (TST – defined as total ecosystem size), total consumption represented around 25% of TST and the remaining fraction of the TST was total respiration. Furthermore, ecosystem indices that describe ecosystem's maturity state *sensu* Odum (1968), such as total primary production/total respiration, connectance index, system omnivory Index, Finn's mean path length, ascendancy and overhead (for more details see Heymans et al. 2014; Table 3.4) suggested that PCSE was an immature ecosystem.

Table 3.4 Comparisons of Portuguese continental shelf with models of the global large upwelling ecosystems. TL: trophic level; TST: total system throughput; na: data not available; *: dimensionless indices.

Characteristics of the model	Portuguese continental shelf ecosystem	Southern Benguela current		Northern Benguela current			Northwest Africa Canary current	Northern Humboldt current			Northern California current
Modelled period	2006-2009	1980	1990	1971-1977	1980-1989	1990-1995	1987	1953	1960	1973	1990
Area (km ²)	22209	220000	220000	179000	179000	179000	3561029	780000	780000	780000	70000
Nr of groups	33	31	31	17	17	17	27	20	20	20	65
Depth range (m)	15-200	0-500	0-500	0-500	0-500	0-500	na	0-2000	0-2001	0-2002	0-1280
Longitude range	7.5° 10.5°W	15°- 28°E	15°- 28°E	11°- 17°E	11°- 17°E	11°- 17°E	6.5°- 30°W	67° - 83°W	67 °- 83°W	67° - 83°W	123° - 127°W
Latitude range	36.6°- 42°N	29°- 35°S	29°- 35°S	15°- 29°S	15° - 29°S	15° - 29°S	8.5° - 36°N	3°- 18°S	3°- 18° S	3° - 18°S	40°- 47°N
Ecosystem theory indices (t km ⁻² year ⁻¹)											
Total system throughput	16412	37975	39304	17443	23495	16252	26556	59638	59677	53101	15993
Sum of all consumption	4776	17230	18831	3214	11743	4477	10617	23127	23601	19661	4331
Sum of all exports	4654	2559	1698	6124	1221	4452	1	12754	11985	10186	4180
Sum of all respiratory flows	1917	9416	10279	1550	6070	1731	6526	9774	10075	9895	2442
Sum of all flows into detritus	5066	8771	8496	8264	4461	5591	9413	13982	14016	13359	5040
Sum of all production	7585	16233	16638	8264	10036	7479	14433	26996	26606	49540	7636
Calculated total net primary production	6566	11974	11977	7675	7319	6183	12461	22528	22060	47235	6620
Total primary production/total respiration *	3.4	1.3	1.0	5.0	1.2	3.6	1.9	2.3	2.2	4.8	2.7
Net system production	4649	2559	1698	6124	1249	4452	5935	12754	11985	37340	4178
Total primary production/total biomass *	56.7	54.1	51.8	27.0	20.0	16.0	43.2	76.3	69.2	117.0	25.6
Total biomass/total throughput *	0.01	0.01	0.01	0.02	0.02	0.02	0.01	0.00	0.01	0.01	0.02
Total biomass (excluding detritus)	116	221	231	282	361	381	288	295	319	404	259
Connectance index *	0.29	0.23	0.24	0.26	0.29	0.30	0.15	0.25	0.25	0.26	0.19
System omnivory index *	0.22	0.23	0.24	0.15	0.17	0.12	0.15	0.12	0.11	0.14	0.16

Fishery status indices											
Total catch (t km ⁻² year ⁻¹)	6.3	3.0	2.5	6.6	6.7	3.4	0.5	6.5	91.7	32.2	4.7
Mean trophic level of the catch	3.25	4.74	4.80	2.85	3.25	3.10	2.80	2.35	2.22	2.61	3.52
Gross efficiency (catch/net PP)	0.001	0.0003	0.0002	0.0009	0.0009	0.0006	0.0000	0.0003	0.0042	0.0007	0.0007
PPR (%)	17.0	4.4	4.5	5.0	5.9	4.3	0.4	5.2	7.2	17.8	18.1
Transfer efficiencies - all flows (%)											
TL II	11.0	6.5	6.5	7.8	3.0	6.8	8.2	2.6	2.9	5.1	19.5
TL III	20.1	24.3	24.3	6.0	6.5	3.5	6.2	9.8	10.6	11.5	16.1
TL IV	16.4	22.0	22.0	2.5	4.5	1.5	4.0	1.8	1.9	5.6	13.3
TL V	15.5	11.3	11.2	0.5	1.5	1.0	0.9	0.9	0.1	1.9	9.4
TL VI	14.4	12.1	11.9	na	na	na	0.1	0.6	0.0	1.1	6.7
Mean TL II-IV	15.3	15.1	15.1	ns	na	na	5.9	3.6	3.9	6.9	16.1
Proportion of flow originated from detritus	18.3	45.0	45.0	na	na	na	4.3	0.3	0.3	0.3	0.4
Keystone index											
Librarato et al. (2006) (first 6 with the highest relative total impact > 0.5)	Phyto-plankton, benthic cephalopods, meso- and micro-zooplankton, sardine, chub mackerel, minke whale	na	na	na	na	na	Cephalopods, coastal demersal fish, phyto-plankton, zoo-plankton, clupeids, meso-pelagic predators	Anchovy, horse mackerel, phyto-plankton	Anchovy, phyto-plankton, cormorant, zoo-plankton, horse mackerel	Horse mackerel, anchoveta, phyto-plankton, sardine, zoo-plankton, hake	Orcas, euphisidis, forage fish, phyto-plankton, copepods, gulls
Role of small pelagics											

Biomass	High sardine but decreasing	High anchovy, low sardine	Low anchovy, sardine increasing	High sardine, moderate anchovy	Low sardine, low anchovy, increase in other small pelagics	Low sardine, low anchovy	High clupeids	High anchovy, smaller sardine	High anchovy, small sardine	High anchovy and sardine	Low sardine, forage fish high
Presence in keystone index	Yes - sardine and chub mackerel	na	na	na	na	na	Yes - clupeids	Yes - anchovy	Yes - anchovy	Yes - anchovy and sardine	Yes - forage fish
Cycling indices											
Predatory cycling index (PCI, % of TST without detritus)	0.07	na	na	6.3	12.1	11.2	0.60	3.42	3.41	0.62	na
Throughput cycled (excluding detritus)	5.82	na	na	na	na	na	81.5	1082	1080	164.7	na
Finn's cycling index (FCI, % of TST)	1.94	na	na	2.8	22.1	9.5	7.65	4.35	6.13	6.67	1.13
Finn's mean path length (MPL)	3.58	3.17	3.28	2.3	3.2	2.6	4.07	2.65	2.71	2.64	2.42
Information indices											
Ascendency (%)	27.2	21.0	20.0	41.7	23.9	31.7	32.4	44.4	40.6	36.4	31.6
Overhead (%)	72.8	79.0	80.0	58.3	76.1	68.3	67.6	55.6	59.4	63.6	68.4
Publication											
	Present study	Shannon et al. (2003)		Heymans et al. (2004)			Morissette et al. (2010)	Jarre-Teichmann and Pauly (1993)		Field (2004)	

Total ecosystem biomass was 162.0 t km^{-2} . Producers, consumers, and detritus represented 11.6%, 59.9% and 27.9% of the total biomass, respectively. Discards represented a negligible parcel of the total biomass (0.6%). In terms of consumers' biomass (i.e., excluding detritus, discards, and phytoplankton), the ecosystem was dominated by SPF (27.3%), invertebrates (23.0%) and zooplankton (31.5%). Marine mammals and seabirds represented a negligible fraction of consumers' biomass (0.1%). Sardine presented the second highest fraction of consumers' biomass (15.2%), after the group of meso- and microzooplankton, and 35.1% of the total biomass of the fish groups. Moreover, sardine was the dominant small pelagic species in the PCSE, representing 55.7% of their biomass, followed by chub mackerel (24.8%).

3.3.4. Mortalities

EE values estimated for fish and macroinvertebrate groups showed a broad range, from 0.10 (tunas) to 0.96 (sardine) but were generally high ($\text{mean} \pm \text{SD} = 0.78 \pm 0.33$; Table 3.2). The exploitation rates (F/Z) where F is fishing mortality and Z is the total mortality (Table 3.2) suggest that fishing mortality was not the main cause of mortality in the PCSE, except for rays. Among commercially exploited groups, the highest F estimates were registered for rays, benthic cephalopods and hake (0.62 , 0.36 and 0.36 year^{-1} , respectively) and the lowest for demersal invertivorous fish and squids (0.005 and 0.01 year^{-1} , respectively). Sardine fishing mortality (0.20 year^{-1}) was slightly above the average for the commercially exploited groups (0.18 year^{-1}). Accidental mortality of cetaceans in fisheries ranged from 0.003 year^{-1} for bottlenose dolphin to 0.027 year^{-1} for harbour porpoise. There was no obvious relationship between TL and either fishing mortality or exploitation rate.

3.3.5. Trophic levels and flows

The mean TL of the PCSE was 3.5 (Table 3.3). Trophic levels ranged from 1.0 (phytoplankton) to 5.3 (bottlenose dolphin). Mean trophic levels of catch (mTLc) for the purse seine fleet was 2.97, while for BT and polyvalent fleets, mTLc were 3.53 and 3.56, respectively. Among fish groups, demersal piscivorous fish and hake showed the highest TL (both 4.3), while sardine showed the lowest, 2.8. Among invertebrates, cephalopods showed the highest TL (higher

than four for both groups). The trophic flows diagram of the PCSE reveals the complexity of trophic connections between and within the pelagic and benthic domains (Figure 3.2).

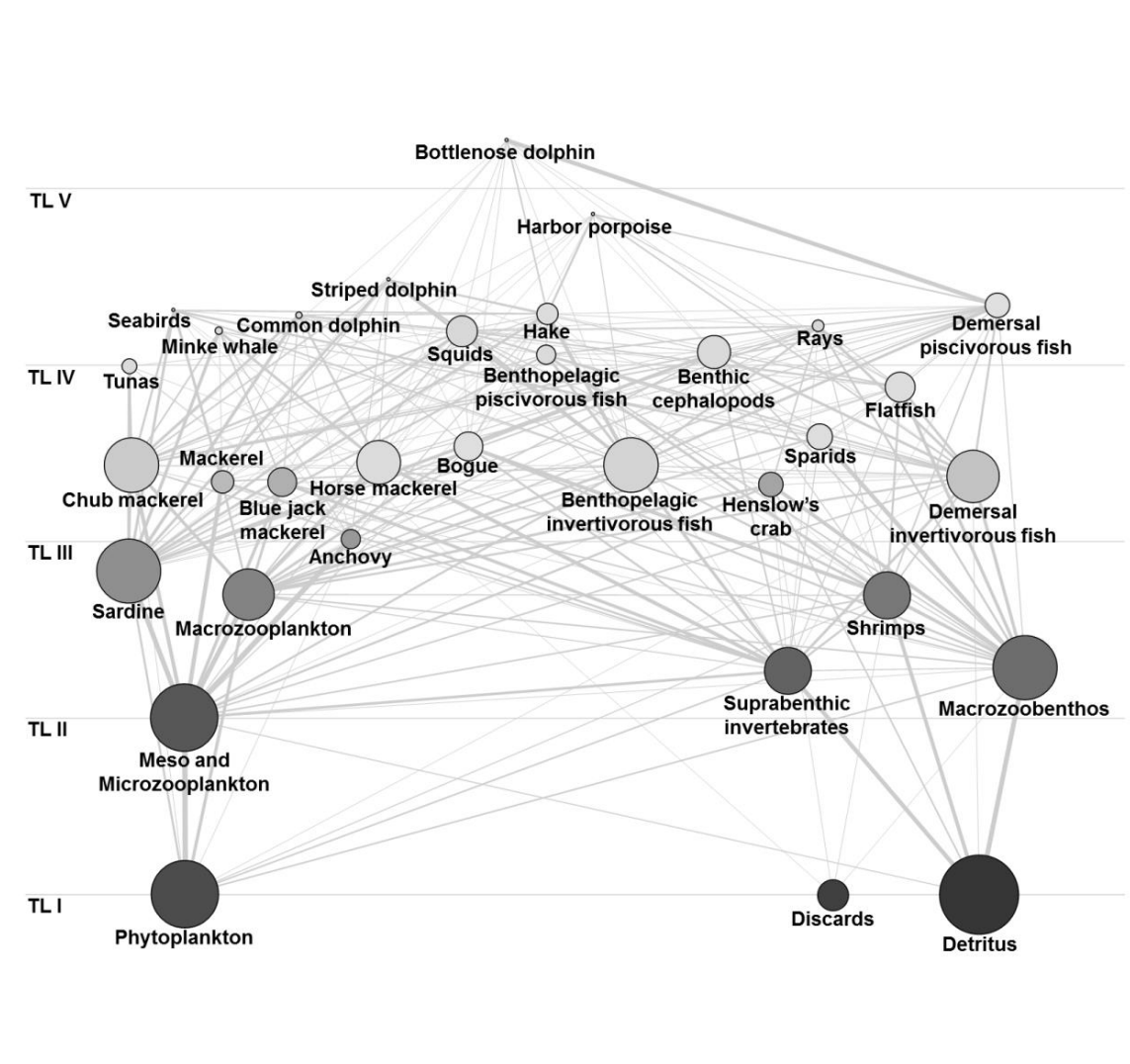


Figure 3.2 Flow diagram of the food web of the Portuguese continental shelf in 2006-2009. The size of each circle is proportional to the biomass of the functional group. All the functional groups are represented according to their trophic levels on the y axis (TL). Light grey lines connecting the groups represent prey-predator relationships. The thickness of the lines indicates the proportion of the prey in the predator diet (thicker lines, higher proportion).

The link between the two domains appears to be made through dolphins, hake and squid groups. The Lindeman spine analysis shows an ecosystem divided into 11 TLs, which may be represented by only the first five levels due to the low biomasses and flow values in the other levels (Figure 3.3). TEs were similar between trophic levels, being the highest from TL III to TL IV

(0.20). The majority of the flows in the ecosystem (99%) originate from TL I to TL III. The integration of results from the diet and the trophic flows diagram showed that a high proportion of catches, consumption, and predation originate from TL III, where SPF, particularly sardine, are the main components.

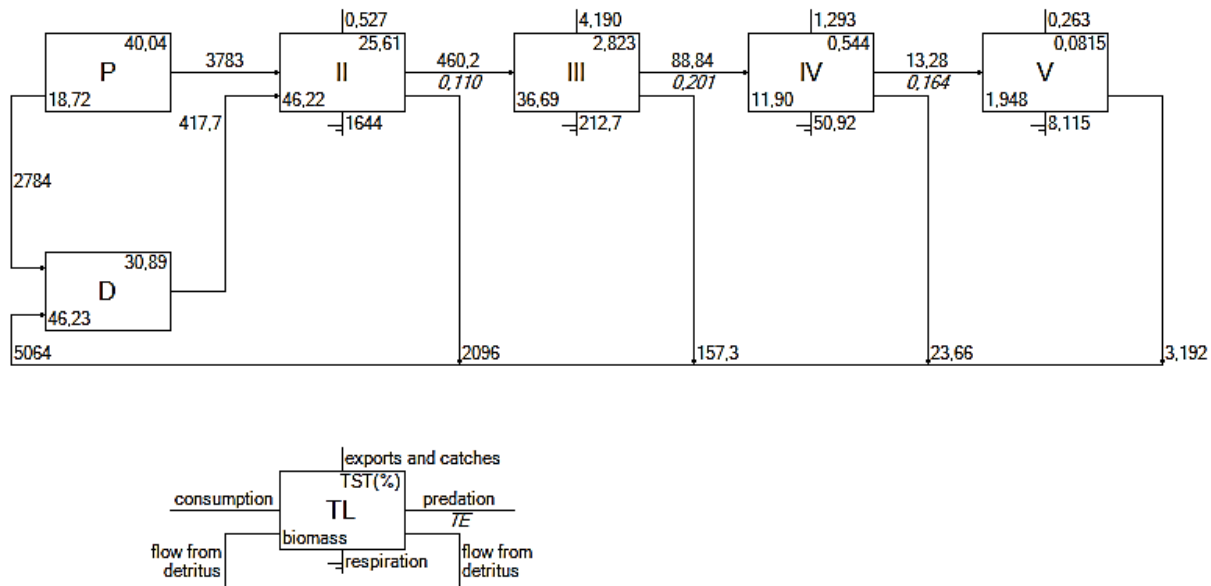


Figure 3.3 A Lindeman spine representation of trophic flows in the ecosystem of the Portuguese continental shelf in 2006–2009. The flows are represented in $\text{t km}^{-2} \text{ year}^{-1}$. P: primary producers component; D: detritus component; TL: trophic level; TE: trophic efficiency.

3.3.6. Consumption

Fisheries consumed 22.8% of sardine annual production and 19 of the 30 consumer groups consumed 72.8% within the PCSE, the most important being fish (31.5%) and cephalopods (30.9%) whilst, cetaceans and seabirds had comparatively lower importance, 9.4% and 1%, respectively. Furthermore, sardine is an exclusive planktivorous preying on meso- and microzooplankton and phytoplankton (83% and 17% of the diet composition, respectively). Among fish groups, sardine consumed the highest fraction of phytoplankton and meso- and microzooplankton production (0.4% and 21.1%, respectively).

3.3.7. Mixed trophic impact

The mixed trophic impact (MTI) analysis (Figure 3.4) showed that in general fishing fleets have a negative impact on their target species with the substantially stronger and more widespread impact of the polyvalent fleet. As expected, predator groups have negative impacts on their prey while lower trophic level groups had generally positive effects on corresponding predators. Sardine showed the second-highest overall impact on the ecosystem after the polyvalent fleet, owing both to the positive and the negative overall impacts and the number of functional groups that were impacted (Figure 3.4). As expected, an increase of sardine biomass positively affects some of its main predators (seabirds, minke whale, cephalopods, and hake), and negatively impacts its main prey (meso- and microzooplankton), (Figure 3.4). However, sardine also had a positive impact on its other prey, phytoplankton, while having negative impacts on some top predators, such as the common dolphin, striped dolphin and tunas. Moreover, a negative effect of sardine biomass increase on other small pelagic species was observed (Figure 3.4).

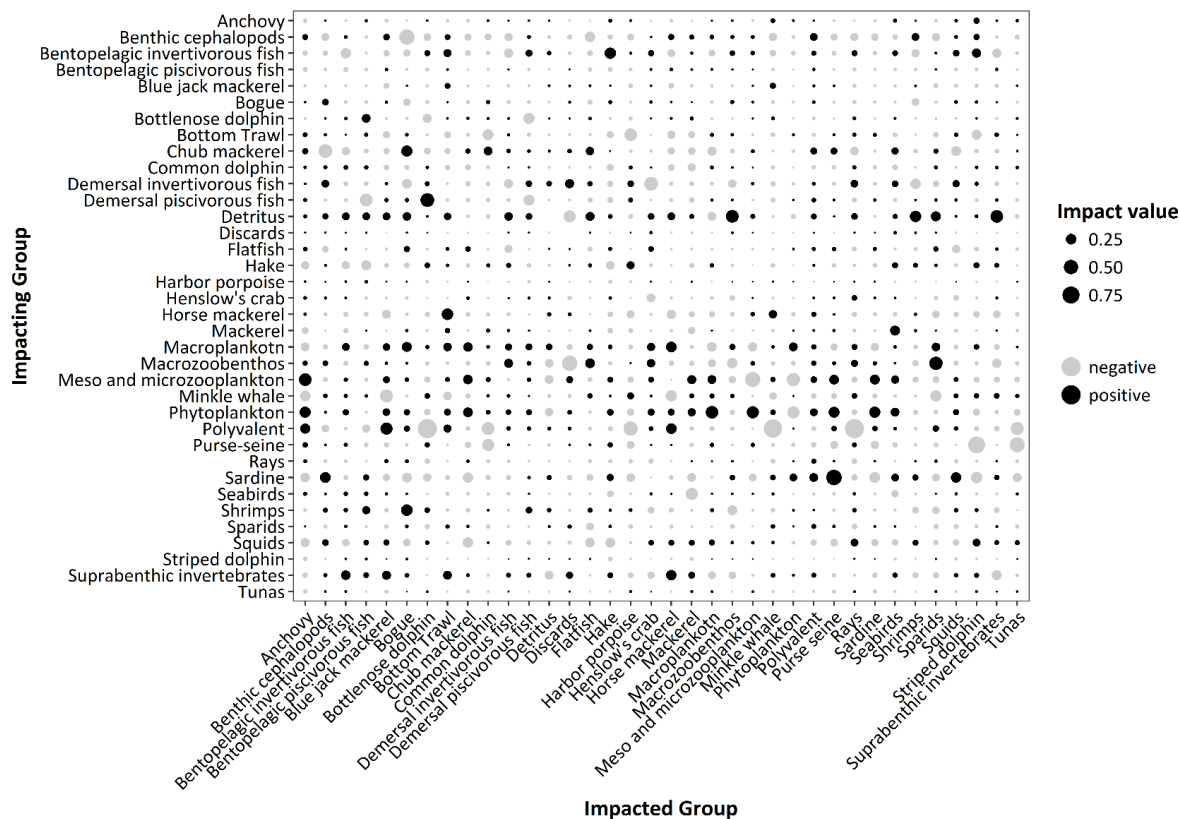


Figure 3.4 Mixed trophic impact analysis of the Portuguese continental shelf Ecopath model in 2006–2009.

3.3.8. Keystone and dominant species

Minke whale, demersal piscivorous fish, squids, and benthic cephalopods were identified as keystone groups in the ecosystem (Figure 3.5). Moreover, eight functional groups were pointed out as dominant: phytoplankton, meso- and microzooplankton, macrozooplankton, macrozoobenthos, sardine, chub mackerel, benthopelagic invertivorous fish, and demersal invertivorous fish. Groups that showed little or no impact on the ecosystem in the MTI analysis were also identified as low impact functional groups by the keystone analysis.

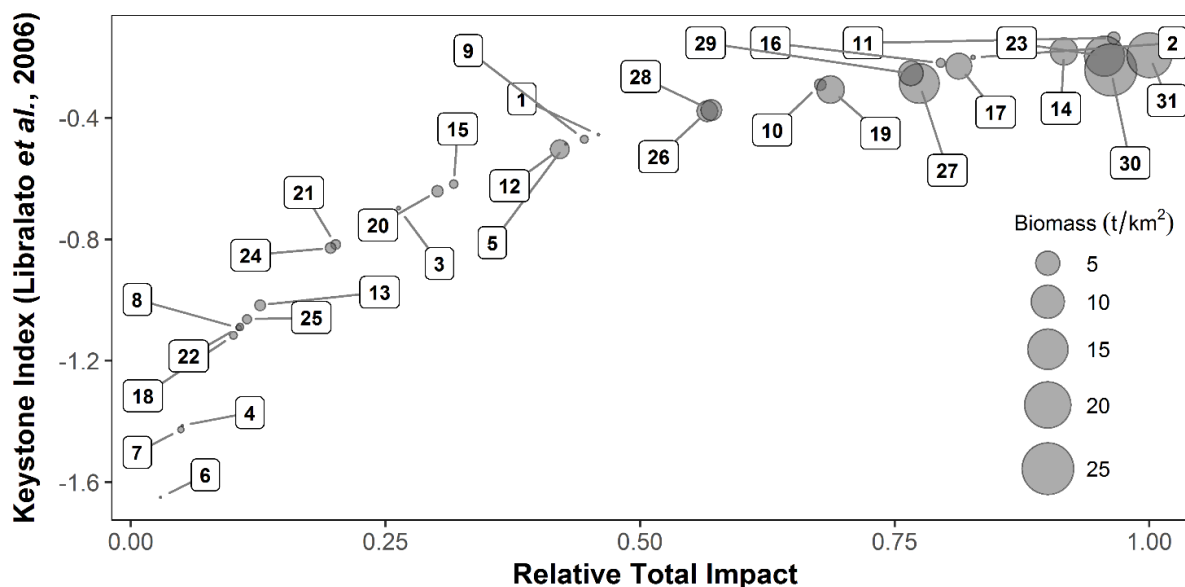


Figure 3.5 Keystone index (Libralato et al. 2006) and relative total impact of each of the functional groups in the ecosystem of the Portuguese continental shelf in 2006–2009. The number in labels represent the different functional groups in the model (see Table 3.1 for identification).

3.4. Discussion

The present study indicated that the ecosystem of the Portuguese continental shelf is regulated by low- and intermediate-trophic-level species, mainly plankton and SPF. These groups made up the bulk of the biomass, generated most of the flows, and had the highest relative impact on other groups, including fisheries, pointing to the importance of bottom-up control in the ecosystem. Similar bottom-up structures have been described for other areas of the Atlantic Iberian Peninsula (Lassalle et al. 2011; Santos et al. 2013). Moreover, SPF were shown to be a key link between lower and higher trophic levels, as in nearby ecosystems: the Bay of Biscay and the Cantabrian Sea located north, and the Gulf of Cadiz located south of the Portuguese coast (Sánchez and Olaso 2004; Lassalle et al. 2011; Torres et al. 2013). Also, in terms of system maturity, the PCSE ecosystem resembles nearby ecosystems: the Cantabrian Sea and the Gulf of Cadiz, which were also described as immature ecosystems (Sánchez and Olaso 2004; Torres et al. 2013). Although, in contrast to the other nearby areas, the French Bay of Biscay was described as a mature ecosystem (Lassalle et al. 2011).

The Portuguese fisheries showed higher catches of lower trophic level species than fisheries in other areas of the Iberian Peninsula, particularly the Cantabrian Sea (Sánchez and Olaso 2004), as reflected by the mean trophic level of the catches obtained in the present study. This is due to the high contribution of the purse seine fishery to the total catches. The high overall impact of the polyvalent fleet in the ecosystem is due to targeting high-trophic-level species, which are highly sensitive to increases in fishing effort, such as rays and benthopelagic and demersal piscivorous (Gascuel et al. 2008; Shannon et al. 2014). The higher bycatch rates of marine mammals in this fishery compared with other fisheries may have also contributed to the overall high impact in the PCSE.

Sardine was identified as a dominant species in the PCSE, with particularly strong dominance of the pelagic component of the ecosystem. This was due to its high biomass, the second highest after multi-specific zooplankton groups, and more than two times the biomass of any other consumer group, and due to showing one of the highest relative impacts on the ecosystem. Furthermore, the large number of functional groups preying on sardine and the fact that sardine was one of the main predators of the lower-trophic-levels groups highlights its importance as a link between the lower and the higher trophic levels. This role of sardine in the ecosystem has also been described for other areas of the Iberian Peninsula (Sánchez and Olaso 2004; Torres et al. 2013). The proportion of sardine total biomass production captured in the fishery concurs with the mean exploitation level estimated in the assessment of the Iberian stock during the study period (0.30 year^{-1} ; ICES 2016). Furthermore, the high percentage of sardine caught by the purse-seine fleet emphasizes the dependency of this fleet on the sardine. The polyvalent fleet also showed a considerable portion of sardine in its catches. This is mainly because some of the vessels in this fleet use purse seine and target sardine in some periods of the year.

The low EE of sardine suggests that other mortality, besides predation and fisheries, is important in explaining sardine consumption within the ecosystem. High sardine other mortality might be related to environmental variability, as SPF are documented to be considerably affected by environmental changes (Fréon 2005).

Direct and indirect interactions within the PCSE were observed. As expected, the MTI analysis showed that most of the groups had a negative impact on their prey and on themselves. Also, indirect impacts within the system could be detected, for example, the negative effect of

sardine on the common dolphin, the striped dolphin, and the tunas. This may be a result of the overall negative impact that sardine has on the other small pelagic species, which are also prey for top predator groups. Another example of indirect impacts was the negative effect of sardine on anchovy and other SPF that can be explained by an overlap between their niches and consequently increased competition for food (Garrido et al. 2015). However, the negative impact of sardine on the other SPF may be overestimated due to the aggregation of meso- and microzooplankton into one functional group. Garrido et al. (2015) showed that sardine prey on considerably smaller prey sizes than the other small pelagic species.

The PCSE has several structural features in common with the main large upwelling ecosystems (the Northern Humboldt current, the Northern Benguela current, the southern Benguela current, the southern Canary current and the California current). These shared characteristics are: (1) general species composition; (2) major flow patterns; (3) important role of small pelagics as a basis of the food web; (4) total fraction of primary production required to sustain fish groups in the ecosystem, and (5) overall low system maturity (Jarre-Teichmann and Christensen 1998). In terms of the system's size (TST, catch, biomass and net primary production), the PCSE is similar to the Northern California current upwelling system (Field 2004; Jarre-Teichmann and Christensen 1998). The productivity of small pelagics in the PCSE (anchovy and sardine) falls in the range of other upwelling systems and also their natural mortality appears to be considerably higher than their fishing mortality, the same as in other upwelling systems (Jarre-Teichmann and Christensen 1998). In addition, the primary production required to sustain the fishery (PPR) in the Portuguese upwelling system is similar to large global upwelling systems, especially those of Northern Benguela (Jarre-Teichmann and Christensen 1998) and the Northern Humboldt (Jarre-Teichmann and Pauly 1993) currents. In terms of TEs, the PCSE is similar to the Southern Benguela ecosystem (Shannon et al. 2003). However, these values are generally higher than in the majority of upwelling systems (Pauly and Christensen 1995, Jarre-Teichmann and Christensen 1998). This indicates that the PCSE system may be food limited much like the Southern Benguela (Shannon et al. 2003) or Northwest Mediterranean (Coll et al. 2006) systems. Another common characteristic shared by upwelling ecosystems is large decadal fluctuations in abundance and species replacement between small pelagics (Cury et al. 2000). Based on the modelling studies of upwelling systems where this fluctuation has been observed (Cury and Shannon 2004; Heymans et al. 2004), it can be concluded that changes in SPF might inflict

significant changes in the ecosystem structure and function, defined as regime shifts, as was the case for the Northern Benguela system (Heymans et al. 2004). However, it is not a rule and replacement between 2 pelagic species in upwelling ecosystems might occur, without causing a shift to a new ecosystem state (Cury and Shannon 2004). The Ecopath model, developed in this study provides a basis to further develop dynamic simulations to understand the cause and impact of sardine decrease on the ecosystem.

3.4.1. Model quality, uncertainties and knowledge gaps

The pedigree index obtained for this Ecopath model implies moderate data quality, although lower than similar models on nearby areas (Sánchez and Olaso 2004; Bănaru et al. 2013, Torres et al. 2013). If the production/biomass and consumption/biomass ratios were based on local estimates (since local data is incorporated in the empirical formula) instead of estimated from empirical equations, the model pedigree would improve to 0.65 and consequently show values similar to those of the models mentioned above. Nevertheless, the present model pedigree points to a need to improve knowledge within the PCSE. In particular, the information required for several input parameters of the model was not available for some of the cephalopods, most invertebrate species and local microzooplankton offshore biomass data. Moreover, the top five functional groups indicated by the sensitivity analysis are groups where two or more of the input parameters showed data deficiency. This adds uncertainty to the model as the outputs from these groups can considerably affect the outputs of other groups where the data were available. However, it also can be used as a guide for the allocation of future research effort. Furthermore, biomass information on demersal and benthic fish species obtained from BT surveys is usually in the form of relative biomass indices, highlighting the importance of future studies on research surveys catchability for the different species. Also, even though data regarding diet composition, came mainly from the analysed ecosystem, the time period when it was obtained was highly variable.

3.5. Conclusion

The present model is to our knowledge, the first representation of the trophic structure and functioning of the ecosystem of the Portuguese continental shelf. A large effort was required to

compile, standardize and adapt the best available data and information for a large number of functional groups within the ecosystem. We believe that our results provide a broad understanding of the ecosystem functioning and deepen the knowledge of inter-specific trophic interactions despite the uncertainties. Knowledge gaps were identified for important components of the ecosystem. This information is important to direct future studies in the area. The next step for future research should be the application of dynamic models such as Ecosim and Ecospace to better understand the cause and impact of sardine abundance decline (Walters et al. 1997, 1999). Moreover, the dynamic model would allow simulations of different ecological and management scenarios (Heymans et al. 2016) that will support an advance to an ecosystem approach to fisheries management in the Portuguese coastal shelf ecosystem.

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Chapter 4

Food-web dynamics in the Portuguese continental shelf ecosystem between 1986 and 2017: unravelling drivers of sardine decline

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Chapter 4 – Food-web dynamics in the Portuguese continental shelf ecosystem between 1986 and 2017: unravelling drivers of sardine decline

Abstract

The Ecopath food web model that describes the Portuguese continental shelf ecosystem was fitted to available time series to investigate the ecosystem dynamics and decline of the Portuguese sardine stock. Our results showed that the Portuguese continental shelf ecosystem model is a good predictor of biomass and catch time-series trends for many species. Moreover, our results suggested that the main factors that drove the ecosystem dynamics were trophic interactions, fishing and environmental forcing (sea surface temperature). The same drivers were important in explaining sardine decline among which the largest contribution was observed when incorporating sea surface temperature forcing on adult sardine, followed by fishing. Moreover, sardine eggs predators (i.e., chub mackerel, horse mackerel and bogue) were emphasised as the most important among trophic interactions in explaining sardine trend between 1986 and 2017. Furthermore, a flow control hypothesis test, showed that model parametrization allows explaining sardine behaviour through wasp-waist control mechanism, characteristic for upwelling systems. This study represents an important step forward in understanding the changes that occurred in the Portuguese continental shelf ecosystem and provides helpful insights to explain Portuguese sardine decline.

Keywords: Sardine fisheries; Ecopath with Ecosim; Hindcast analysis; Food webs; Ecosystem modelling, Portuguese shelf

4.1. Introduction

Marine resources should be managed by considering a broad perspective including all trophic interactions and external drivers since both human activities and environmental conditions influence ecosystems and their productivity (Halpern et al. 2008; Doney et al. 2012). Understanding trophic interactions and the drivers that contribute to changes in ecosystems have become a key step in the integrated and ecosystem approach to fisheries management (EAFM) (Pikitch et al. 2004). Important characteristics of this approach include multispecies considerations, trophic interactions, impact on ecosystems and the socio-economic dimension (Garcia et al., 2003). A better understanding of ecosystem functioning and complex food-web interactions is crucial in fisheries management in the context of the ecosystem approach. In recent decades plenty of new tools that address the EAFM have been developed and explored including (1) ecosystem models (Plagányi 2007; Fulton 2010); (2) statistical methods that support an Integrated Ecosystem Assessment (Link et al. 2002), and (3) spatial methods, such as the use of geographic information systems (GISs) (Olson 2011; chapter 2; Szalaj et al. 2018). Due to its widespread application, ecosystem models deserve special attention, in the context of EAFM (Plagányi 2007). One of the most used ecosystem models is the Ecopath with Ecosim (EwE) modelling framework (Colléter et al. 2015). Due to its continuous development, it is able to explore a variety of research questions concerning fishing activities, spatial closures (Dichmont et al. 2013), socioeconomics (Christensen et al. 2014) and even the fate of marine pollutants in food webs (Walters and Christensen 2018). Moreover, a dynamic module of EwE software, Ecosim (Walters et al. 1997) has been widely used to hindcast and forecast how pressures, such as fishing (Coll et al. 2008; Shannon et al. 2004), climate change (Serpetti et al. 2017) and invasive species (Corrales et al. 2017) impact marine food webs.

Among Portuguese Exclusive Economic Zone (EEZ), Ecopath mass balanced food webs models were developed for estuaries/coastal lagoons (Patrício and Marques 2006; Gamito and Erzini 2005; Bueno-Pardo et al. 2018), open ocean and deep-sea environments (Morato et al. 2016) and continental shelf (chapter 3; Veiga-Malta et al. 2019). To our knowledge, no prior studies have examined the dynamics of trophic interactions using Ecosystem models in the Portuguese waters.

The Portuguese fishing industry is important for the national economy, food security and cultural identity. In 2017, the Portuguese fleet landed 179,437 tonnes of seafood that

amounted to a total of 272 million euros (INE 2018). Moreover, Portugal is the highest consumer of fish per capita annually in the European Union (57 kg in 2016) (EUMOFA 2018), which demonstrates that fishing products are an important part of Portuguese culture. Due to Portugal's proximity to the open ocean and long naval tradition, fish products have been considered as a staple food throughout history and this importance and tradition are maintained till the present day.

Sardine (*Sardina pilchardus*) along with horse mackerel (*Trachurus trachurus*) and chub mackerel (*Scomber colias*) were the most landed species in Portugal in 2017 with around 15,000, 19,000 and 19,500 tonnes respectively (INE 2018). However, during the last decade, there has been significant decrease in the Portuguese sardine stock biomass and in 2016, the biomass and sardine recruitment reached a critical level, the lowest in 40 years (ICES 2017a). Sardine recruitment has been associated with sea surface temperature (SST), chlorophyll concentration (Chla) (Garrido et al. 2017), North Atlantic Oscillation (NAO), Atlantic multidecadal oscillation (AMO) and coastal upwelling (Malta et al. 2016). Complex inter-trophic dynamics between several species was also suggested to be related to sardine decline (Martins et al. 2013). Some authors have observed an increase in other coastal pelagic species that compete and prey upon sardine eggs and larvae. For example, an increase in biomass was recently observed for chub mackerel (*Scomber colias*), horse mackerel (*Trachurus trachurus*), blue jack mackerel (*Trachurus picturatus*) and anchovy (*Engraulis encrasicolous*) (Martins et al. 2013; ICES 2017a; Garrido et al. 2015). On the other hand, it is also possible that the sardine stock may just be unable to sustain the fishing pressure it has been subjected in recent decades. According to the latest stock assessment evaluations, ICES advised that when the Maximum Sustainable Yield (MSY) approach was about to be applied, there should be zero catches in 2018 and 2019 (ICES 2017b, 2018b). However, due to its socio-economic importance, ICES advice was not applied, and sardine fishery (with substantially reduced quotas) was operated.

In this paper, we further developed the static Portuguese continental shelf ecosystem (PCSE) food-web model described by Veiga-Malta et al. (2019) (chapter 3) and examined the drivers that explain the ecosystem food-web dynamics between 1986 and 2017. The following research questions have been formulated: (1) which factors drove PCSE change? (2) which factors contributed the most to sardine biomass decline? (3) which were the key sardine trophic interactions that drove sardine change?

4.2. Material and methods

4.2.1. Study area

The Portuguese continental shelf ecosystem (PCSE) is situated in the northeast Atlantic between 36.5° and 42° N and between 10.5° and 7.5° W (Figure 4.1) and covers an area of around 25,000 km². The Portuguese shelf waters have an overall average surface temperature of 17°C. The western Portuguese coast is affected by seasonal upwelling that occurs during spring and summer due to steady northerly winds (Wooster et al. 1976; Fiúza et al. 1982). Also, the Iberian Peninsula is influenced by mid-term atmospheric phenomena such as Atlantic multidecadal oscillation (AMO) and North Atlantic Oscillation (NAO) (Trigo et al. 2004; Santos et al. 2011).

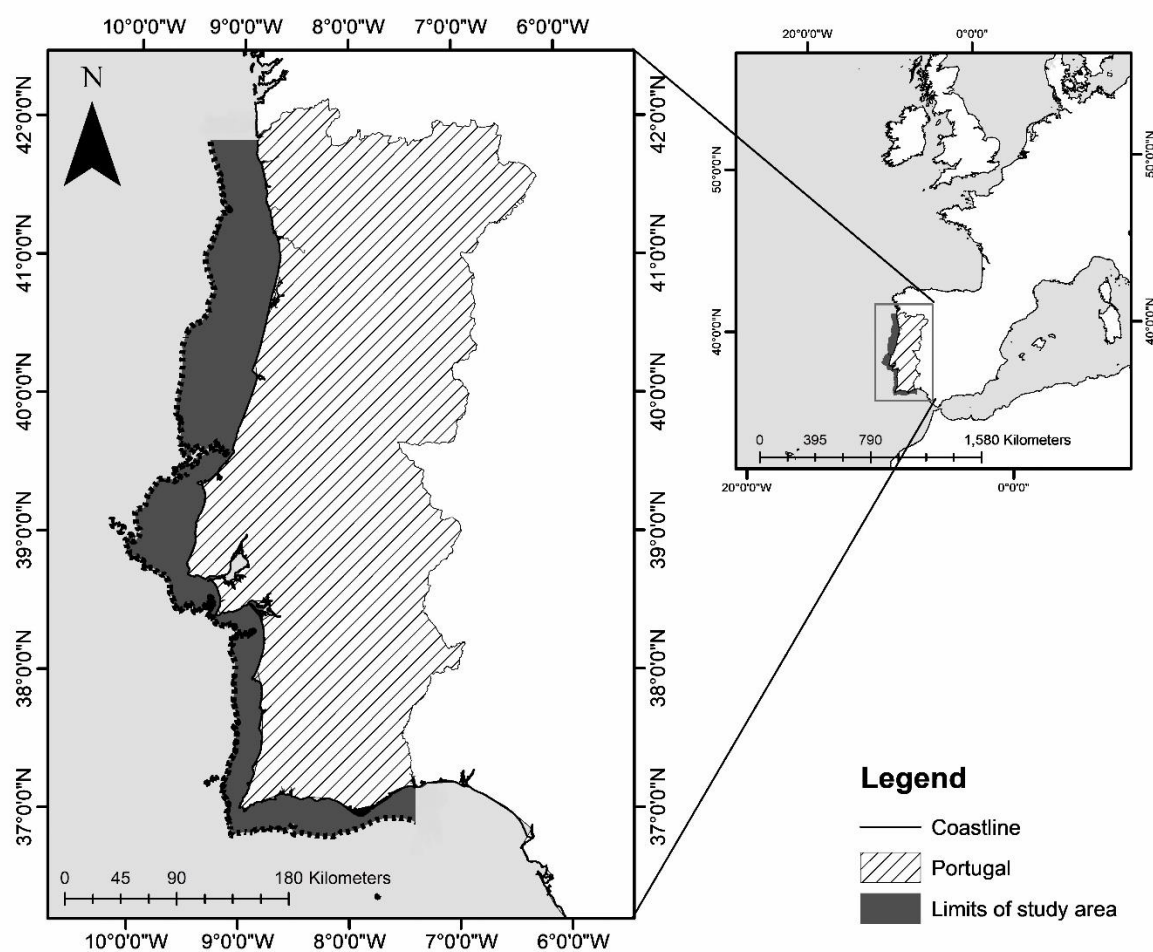


Figure 4.1 Map showing study area (limits of the Portuguese continental shelf ecosystem).

4.2.2. The baseline food web model of the Portuguese continental shelf

A food web model previously developed by Veiga-Malta et al. (2019) (chapter 3), representing the Portuguese continental shelf ecosystem (PCSE) in 2006–2009, was used in this study. The model was constructed using the Ecopath mass balanced module (Christensen and Pauly 1992; Christensen and Walters 2004; www.ecopath.org). For practical reasons we are going to refer to it as the “initial model”.

In the present study, the initial model was used as a baseline to perform hindcast (1986–2017) analyses. To do so, the initial model was adapted to the year 1986. This year was chosen as it is the most recent year for which quality time series data for sardine exist in the PCSE. To better represent the ecosystem structure in the model’s new version, a few structural changes were performed. Firstly, sardine was split into two multi-stanza groups (juvenile and adult). A detailed description of the multi-stanza group and adapted multi-stanza parameters are presented in the following subsection 2.3. and Table A4.1 in annex 4. Moreover, in the new model version, a new functional group representing sharks was added. The species that comprise this group are shown in Table A4.2 in annex 4. The adapted PSCE Ecopath model in 1986 consists of 33 functional groups ranging from phytoplankton and invertebrates to birds and marine mammals. The list of species and functional groups included in the model is described in Veiga-Malta et al. (2019) (chapter 3). Biomass data, for which information from 1986 existed, were updated and detailed information about their data sources are provided in Table 4.1. The production/biomass ratio (P/B) from the initial Ecopath model was updated based on 1986 catch data. Landings from 1986 for all commercial groups were obtained from the Portuguese national statistical institute (INE 1987–2018) while discards were adopted from the initial model and scaled in accordance with landings in 1986. Also, consumption per unit of biomass (Q/B) was taken from the initial model. For most species, 1986 biomass data were collected during demersal surveys, carried out in autumn (September–October) at predefined stations in the Portuguese Exclusive Economic Zone at depths varying from 20 m to 500 m depth (ICES 2017c). Only biomass data, that referred to the continental shelf (depth <200 m) was considered. Bottom trawl survey biomass estimates were calculated using the swept area method. For most species, the diet composition was adapted from Veiga-Malta et al. (2019) (chapter 3). Modifications were only performed when needed to represent the diets and consumptions of new groups introduced (sharks and juvenile sardine stanza) and to balance the model (macrozoobenthos and discards groups, explained below). Updated diet composition

table is presented in Table A4.3 in annex 4. After the adaptation of the Ecopath model to 1986, the output of the model was unbalanced for six fish species (hake, demersal piscivorous fish, rays, sparids, mackerel, and blue jack mackerel) as well as macrozoobenthos and discards groups. To balance the model, various levels of catchability, varying from 0.15 to 0.65, were assumed and applied to fish species caught by bottom trawl surveys (for a detailed description see Table 4.1). Assumed catchability rates were chosen to fall in the ranges of the catchability observed around the world for demersal and benthopelagic species (Harley and Myers 2001; Trenkel and Skaug 2005). Macrozoobenthos and discards were balanced by redirecting a small proportion (less than 1%) of its main predators' diet (Demersal invertivorous fish and shrimps), to other species (preys).

Table 4.1 Input and output parameters of the Portuguese continental shelf ecosystem 1986 model with data sources. Output parameters are underlined. Zooplankton and Phytoplankton biomass estimates considered carbon to wet weight conversion factors from Cushing et al. (1958) and mean depth 50 m. Catchability* refers to bottom trawl biomass estimate; Invertivorous refers to invertebrate feeders.

No.	Functional group	Trophic level (TL)	Biomass (B) t km ⁻²	Production to biomass ratio (P/B)	Consumption to biomass ratio (Q/B)	Ecotrophic efficiency (EE)	Biomass data source	Catchability *
1	Bottlenose dolphin	<u>5.107</u>	0.006	0.080	32.06	<u>0.03</u>	Veiga-Malta et al. 2019,	
2	Harbour porpoise	<u>4.701</u>	0.004	0.080	14.17	<u>0.33</u>	Veiga-Malta et al. 2019	
3	Striped dolphin	<u>4.353</u>	0.005	0.080	30.98	<u>0.11</u>	Veiga-Malta et al. 2019	
4	Seabirds	<u>4.184</u>	0.009	0.100	57.64	<u>0.00</u>	Veiga-Malta et al. 2019	
5	Demersal piscivorous fish	<u>4.167</u>	0.516	0.840	3.921	<u>0.98</u>	1986 BT survey	0.15
6	Hake	<u>4.144</u>	1.380	0.597	6.070	<u>0.99</u>	1986 BT survey	0.30
7	Common dolphin	<u>4.142</u>	0.038	0.080	31.29	<u>0.20</u>	Veiga-Malta et al. 2019	
8	Rays	<u>4.068</u>	0.365	0.508	3.622	<u>0.44</u>	1986 BT survey	0.30
9	Minkie whale	<u>4.066</u>	0.061	0.030	35.11	<u>0.37</u>	Veiga-Malta et al. 2019	
10	Squids	<u>4.054</u>	<u>1.416</u>	2.800	8.000	0.95	Estimated by Ecopath	
11	Benthopelagic piscivorous fish	<u>3.965</u>	<u>0.700</u>	1.016	4.098	0.95	Estimated by Ecopath	
12	Benthic cephalopods	<u>3.944</u>	<u>1.285</u>	2.400	6.500	0.95	Estimated by Ecopath	

13	Tunas	<u>3.912</u>	0.200	0.460	4.211	<u>0.30</u>	Veiga-Malta et al. 2019	
14	Sharks	<u>3.896</u>	0.107	0.600	4.450	<u>0.90</u>	1986 BT survey	0.25
15	Flatfish	<u>3.815</u>	<u>1.716</u>	0.655	5.615	0.95	Estimated by Ecopath	
16	Sparids	<u>3.451</u>	0.619	0.724	4.918	<u>0.89</u>	1986 BT survey	0.65
17	Bogue	<u>3.386</u>	<u>1.759</u>	0.844	6.201	0.95	Estimated by Ecopath	
18	Benthopelagic invertivorous fish	<u>3.249</u>	<u>12.62</u>	0.946	7.096	0.95	Estimated by Ecopath	
19	Demersal invertivorous fish	<u>3.234</u>	<u>11.83</u>	0.919	6.677	0.95	Estimated by Ecopath	
20	Mackerel	<u>3.220</u>	0.393	1.250	7.137	<u>0.99</u>	1986 BT survey	0.25
21	Horse mackerel	<u>3.197</u>	6.100	0.512	7.607	<u>0.69</u>	1986 BT survey	1.00
22	Chub mackerel	<u>3.190</u>	<u>7.526</u>	0.655	6.816	0.95	Estimated by Ecopath	
23	Blue jack mackerel	<u>3.175</u>	1.032	0.405	7.208	<u>0.94</u>	1989 BT survey	0.20
24	Henslow's crab	<u>3.135</u>	<u>0.997</u>	2.100	10.64	0.95	Estimated by Ecopath	
25	Anchovy	<u>3.000</u>	<u>0.394</u>	1.170	12.22	0.95	Estimated by Ecopath	
26	Sardine adult	<u>2.840</u>	31.30	0.830	8.780	<u>0.63</u>	Stock assessment output	
27	Shrimps	<u>2.645</u>	<u>6.869</u>	4.200	11.67	0.95	Estimated by Ecopath	
28	Sardine juvenile	<u>2.606</u>	3.066	3.00	25.95	<u>0.98</u>	Estimated by Ecopath	
29	Suprabenthic invertebrates	<u>2.244</u>	<u>6.814</u>	16.00	42.00	0.95	Estimated by Ecopath	
30	Macrozoobenthos	<u>2.234</u>	21.80	3.573	9.727	<u>0.95</u>	López-Jamar et al. 1992	
31	Macrozooplankton	<u>2.100</u>	6.310	17.00	44.00	0.95	Estimated by Ecopath	
32	Meso and Microzooplankton	<u>2.000</u>	18.75	30.10	152.5	<u>0.79</u>	Veiga-Malta et al. 2019	
33	Phytoplankton	<u>1.000</u>	59.20	150.0		<u>0.28</u>	Cunha 2001	

4.2.3. Sardine multi-stanza group

In the adapted model sardine was represented as multistanza and divided into two groups adult and juvenile. To address the recently documented important predation on sardine eggs (Garrido et al. 2008; Garrido et al. 2015), we assumed that the juvenile sardine stanza includes predation directed towards sardine eggs. This was done as juvenile sardine constitute

the group from 0 to 12 months and therefore included the eggs stage. Multiple stanzas parameters estimated by the model, biomass (B) and consumption per unit of biomass (Q/B), are calculated based on the B of leading stanza using the Deriso-Schnute delay-difference model (Deriso 1980; Schnute 1987) and following a von Bertalanffy (1938) growth curve (K) (for more details see Christensen et al. 2008). Parameters that have to be introduced, the von Bertalanffy (1938) growth parameter (K) and P/B (that equal to the instantaneous rate of total mortality (Z) in steady-state systems) were adapted from Silva et al. (2008) and ICES (2018a) respectively. Juvenile stanza was modelled to support the consumption of predators on eggs, therefore the production/biomass ratio obtained from ICES (2018a) was increased by a fraction that would correspond to P/B of eggs. We were not able to find the P/B for eggs stages, therefore, we assumed its value by increased P/B until the model produced sufficient biomass of juvenile stanza (eggs) to support the dietary needs of its predators (eggs predators). To assess if the assumptions are reasonable, we tested Stock-Recruitment (S-R) curve to assess if introduced parameters produced plausible S-R relationship (for more details see Figure A4.1 in annex 4).

Sardine diet and its consumption was adapted from the initial model (Veiga-Matla et al. 2019) (chapter 3) with few modifications related to the juvenile stanza. Share of sardine eggs in diets of pelagic fish was adapted from Garrido et al. (2008) for adult sardine and from Garrido et al. (2015) for other predators (chub mackerel, bogue, and horse mackerel). In order to account for seasonality and uncertainty in diet composition, the total annual predation on sardine eggs was reduced by 4-fold. This assumption was justified by the fact that the peak in sardine spawning in Portugal lasts three months a year - between December and February (Bernal et al. 2007). We assume that out of the spawning period sardine eggs are not as abundant and therefore their contribution in diets of other species is considerably reduced. Moreover, this reduction was necessary to balance the model and to obtain a more plausible relationship for sardine population biomass with age.

Adult sardine diet composition was introduced based on the regional stomach content analysis data obtained for the Portuguese continental shelf (Garrido et al. 2008, 2015). Based on these sources it turns out that the most important prey of sardine was zooplankton comprising crustacean eggs, copepods, decapods, cirripedes and fish eggs that belongs to meso/microzooplankton functional group in the present model, and to lesser extent phytoplankton species dinoflagellates and diatoms (Figure 4.2 ab).

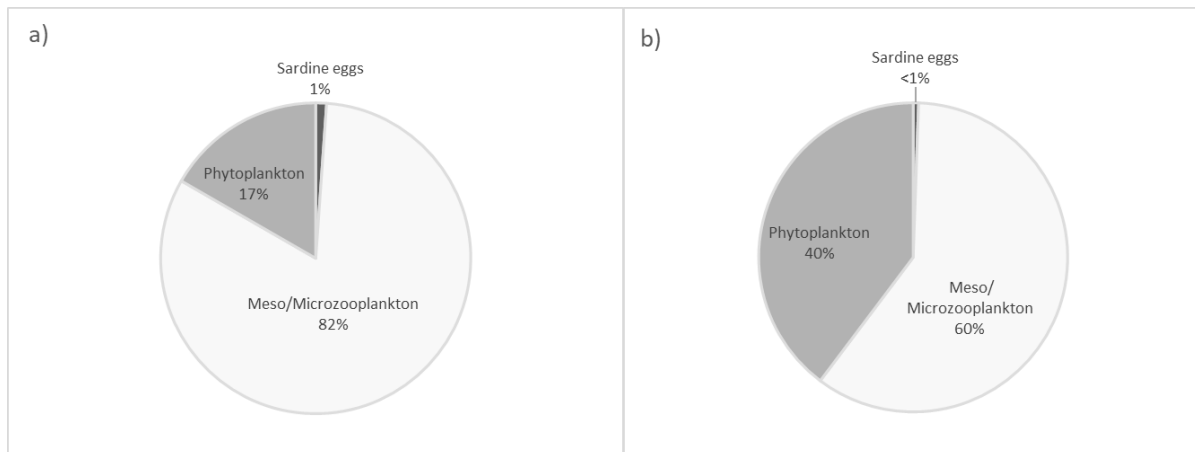


Figure 4.2 Diet composition for adult (a) and juvenile (b) sardine used in the model assessed based on regional stomach content analysis performed in the Portuguese continental shelf ecosystem by Garrido et al. (2008) and Garrido et al. (2015).

Sardine predators and its consumption was identified based on in-depth analysis of the stomach data of fish species occurring in PCSE (for more details see Table A3.1 in annex 3). When it was possible, the data from regional studies were used, however, for species for which regional data did not exist, the data from the areas located closest to the study site was adapted. Based on this analysis, we find out that the main adult sardine predators were cephalopods, hake, benthopelagic invertivorous fish, flatfish and minke whale (Figure 4.3 a), while small pelagic fish (SPF) such as adult sardine, chub mackerel, horse mackerel and bogue prey on sardine eggs that in this model were represented as juvenile sardine stanza (Figure 4.3 b). Main predators of juvenile sardine (no eggs) were squids, hake, common dolphin, and tunas (Figure 4.3 b).

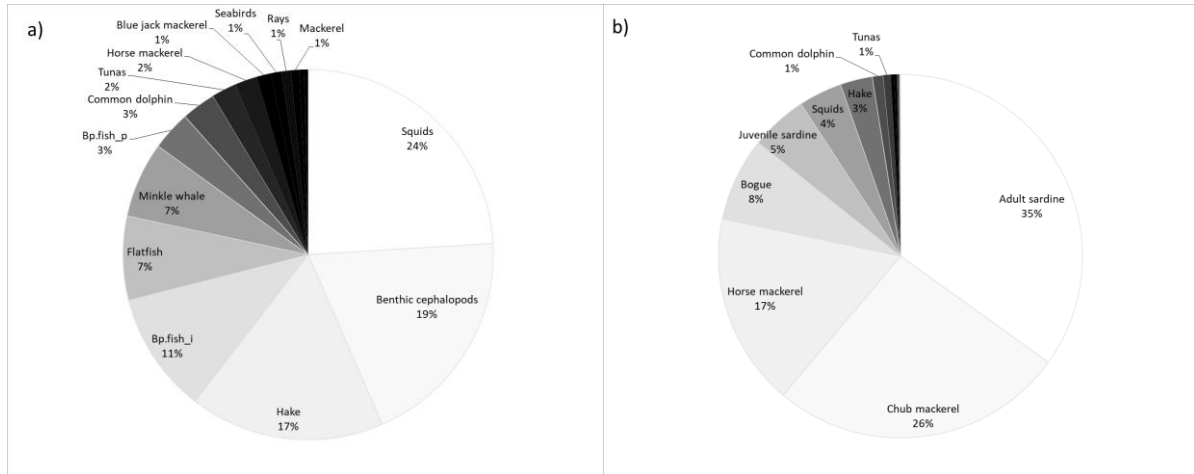


Figure 4.3 The most important predators identified for adult (a) and juvenile (b) sardine stanza identified based on the analysis of the best available literature.

4.2.4. Ecopath and Ecosim diagnostics

To ensure that the 1986 model version met the general ecological principles, a pre-balance (PREBAL) diagnostic (Link et al. 2010) was performed (Figure A4.2 in annex 4). Moreover, the credibility of model behaviour was ascertained by applying criteria proposed by the Working Group on Multispecies Assessment Methods (WGSAM, ICES 2016, 2017d) that include assessment of (1) fit to historical data; (2) stock-recruitment and F-catch relationships, and (3) model stability. For more details, please see annex 4 (Table A4.4; Table A4.5)

4.2.5. Temporal dynamic modelling

The dynamic module Ecosim of the EwE software (Walters et al. 1997), was used to run the hindcast temporal (1986–2017) analysis of the PCSE. It uses a set of differential equations to estimate biomass fluxes for each functional group of the ecosystem, as follows:

$$\frac{dB_i}{dt} = g_i \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - (M_i + F_i + e_i) B_i \quad \text{Equation 4.1}$$

where $\frac{dB_i}{dt}$ is the biomass growth rate of group i during the period dt , g_i is the net growth efficiency (production/consumption ratio), I_i is the immigration rate, M_i and F_i is the natural and fishing mortality rates respectively, e_i is emigration rate and B_i is the biomass.

Consumption rates (Q_{ij}) are calculated based on the foraging arena theory (Ahrens et al. 2012), where the biomass of prey is represented by a vulnerable and non-vulnerable fraction, as follows:

$$Q_{ij} = \frac{v_{ij} a_{ij} B_i B_j T_i T_j S_{ij} M_{ij} / D_j}{v_{ij} + v'_{ij} T_i M_{ij} + a_{ij} M_{ij} B_j S_{ij} T_j / D_j} \cdot f(Env_{function}, t) \quad \text{Equation 4.2}$$

where v_i and v'_i are vulnerabilities that express the transfer rate between vulnerable and invulnerable state; a_{ij} is effective search rate for i (prey) by j (predator); B_i and B_j are biomass of prey and predator, T_i and T_j are relative feeding time for prey and predator, S_{ij} is seasonal or long term effects, M_{ij} is the mediation forcing effects and D_j represents the effect of prey handling time by a predator as a limit to consumption rate. Environmental response function ($f(Env_{function}, t)$) accounts for external drivers that change over time. The intercept between the environmental driver and environmental response function is used to determine a multiplier factor, that modifies the consumption rate of the functional group when the environmental driver deviates from the optimum values (Corrales et al. 2017). Environmental response function was used to incorporate the impact of climate change (SST) overtime on sardine recruitment (see below section 4.2.6 for details).

In Ecosim, vulnerability parameters (v_{ij}) describe the interaction between each predator and prey in the model. Low vulnerabilities ($v_{ij}=1$) indicate the bottom-up control, prey controls predator mortality, while high vulnerabilities ($v_{ij}>>1$) describe top-down control, predator determines how much prey is consumed. In other words, when predator biomass doubles then it will cause close to a doubling effect on its prey mortality in case of high vulnerabilities, while almost no effect when prey vulnerabilities are low. Default values of vulnerabilities ($v_{ij}=2$) represent a mixed flow control.

4.2.6. Calibration procedure and time-series used

The model calibration process was performed by applying the hypothesis testing procedure proposed by Mackinson et al. (2009) and appended by introducing environmental forcing on sardine in form of recruitment forcing patterns (also referred to as “egg production” anomalies) and through environmental response function as performed frequently in previous studies (e.g., Harvey et al. 2003; Ainsworth et al. 2008; Tomczak et al. 2012) (for more details see Table A4.6 in annex 4). In this method, a reduction in the weighted sum of squared deviations (SS) between log observed biomass and log predicted biomass values and the

Akaike Information Criterion (AIC) parameter (Akaike 1974) are used as a metric to assess and select the “best” fit model. Based on the guide on EwE best practices (Heymans et al. 2016) we considered K-1 as a maximum number of parameters to be estimated (vulnerabilities or primary production spline points), where K is the number of catch and biomass time-series used for estimating the SS. Model calibration to the observed time-series was performed by adjusting vulnerability parameters, searching for an environmental anomaly to reduce SS, and applying the environmental effect on sardine reproduction. The importance of different drivers of the final model (“best” fit model) was assessed by running a few scenarios of the final model, in which each time the effect of one driver was minimized. Then the SS of each scenario was compared to the final model fit. The following scenarios were considered: (1) Baseline that does not include any driver; (2) Final model that includes all drivers; (3) Sc_PP that includes all drivers less the effect of PP; (4) Sc_ENV that includes all drivers less the effect of environmental forcing function; (5) Sc_Vs that includes all drivers less the effect of vulnerabilities and (6) Sc_F that includes all drivers less the effect of fishing mortality.

The search for the most sensitive predator-prey interactions (vulnerabilities) was performed in two stages adopting the similar approach as proposed by Bentley et al. (2019). They proposed a new approach for the ecological optimisation of vulnerability multipliers that besides the automatic search (through fit to time series module and automated stepwise fitting routine), includes also manual, systematic search for sensitive predator-prey vulnerabilities that improve the statistical fit of the model. Search for vulnerabilities in this study was performed first, manually by testing every single trophic interaction predator-prey in the model in the following way: (1) vulnerability parameters for each predator-prey interaction were checked for three alternative hypotheses assuming different flow-control between predator-prey interactions: a) $v_{ij}=1$ for bottom-up control; b) $v_{ij}=1000$ for top-down control and c) $v_{ij}=2$ for mixed control-default; (2) after each change in tested hypothesis (and vulnerability parameters), model fit and SS were verified and the vulnerability that resulted in the best fit and considerable reduction in SS was maintained. Secondly, after the manual search, the automatic search for the most sensitive predator-prey interaction was performed using the “Fit to time series” module of Ecosim. Vulnerability parameters identified during the calibration process are presented in Table A4.7 in annex 4.

After adjusting vulnerabilities, a search for the primary production anomaly (PP anomaly) to further improve the fit was performed. PP anomaly is a non-parametric routine

implemented in Ecosim that search for primary productivity historical time series that might impact biomasses through the food web and help in explaining variability in observed time-series. Obtained PP anomaly function may reflect known environmental influences and therefore it was correlated with available climate variables (their names and sources are presented in Table A4.8 in annex 4). All environmental variables were separated in winter (December-March), summer (June-August) and annual averages (January-December). Thus, 15 environmental variables were used during this study (Table A4.8 in annex 4). This approach allowed us to investigate the effect of the environmental variables during different critical life periods of the sardine recruits as proposed in the study by Malta et al. (2016).

Moreover, to test the hypothesis of climate change influence on sardine decline we introduced environmental response function for adult sardine stanza in Ecosim using as a driving force mean Sea Surface Temperature extracted from KNMI Climate Explorer web application (<https://climexp.knmi.nl/about.cgi?id=someone@somewhere>). To demonstrate climate change effects on sardine, we implemented an optimal temperature range of spawning for sardine according to studies performed offshore the Portuguese coast (Coombs et al. 2006; Stratoudakis et al. (2007)). The environmental response function ($f(\text{Env}_{\text{function}}, t)$ in Eq. 2) that link sardine dynamics with the environmental driver was set based on available literature. We used trapezoid response function with an optimum range of 14.55°C–16.35°C (Coombs et al. 2006) and an overall tolerance range between 12°C and 18°C according to Stratoudakis et al. (2007). We tested other available shapes of response function in EwE, but they do not improve sardine fit so much as trapezoid function. Moreover, to further improve a fit of sardine (explain sardine dynamics), we applied the effect of “forcing on egg production” using as a forcing function index of sardine spawning biomass (ICES 2017a). This approach was used previously in Ecosim to represent forcing on recruitment for species which stocks are assessed and recruitment is well studied (e.g., Ainsworth et al. 2008; Tomczak et al. 2012).

During the fitting procedure, we noticed that for most species, biomass data obtained from bottom trawl surveys (B_T) had substantial noise that made the fitting procedure unattainable. Therefore, we subjected B_T to a Stock Reduction Analysis (SRA, Kimura et al. 1984) implemented as a stochastic SRA (Walters et al. 2006) to estimate plausible biomass (B_{SRA}) trends and further calculate fishing mortality (F_{SRA}), as performed in Christensen et al. (2015). A detailed description of SRA methodology and obtained results are provided in annex 4. Fishing mortality (F_{SRA}) was calculated as C/B_{SRA} where C is the catch composed of landings obtained from INE and discard estimates were adopted from the initial Ecopath model and

scaled to time series of landings. Data used as input in SRA consisted of historical catch time-series (from 1950–2014) obtained from the Sea Around Us project (Leitão 2014) complemented with recent catch data (2014–2017), provided by INE. Independent estimates of abundance for all species except anchovy were obtained from Portuguese bottom trawl surveys carried out in autumn (September–October) at predefined stations. For anchovy abundance estimates were obtained from acoustic surveys (PELAGO survey series) performed annually in spring (April–May). Both, acoustic and bottom trawl surveys were performed by the Portuguese Institute of Sea and Atmosphere (IPMA).

Biomass time series for species, which lacked sufficient data to perform SRA, were taken directly from BT surveys (sharks, squids, benthic cephalopods, flatfish, demersal invertivorous fish – feeding on invertebrates), with exception to the biomass of chub mackerel that was taken from acoustic surveys. Adult and juvenile sardine, hake and horse mackerel biomass data were taken from stock assessment estimates. Biomass time-series inputs were used as relative values.

Description of time series used to drive and calibrate the model, with their sources are provided in Table 4.2.

Table 4.2 Time-series data used in Ecosim. Biomass and catch data were used to calibrate the model while fishing mortality (F), average Sea Surface Temperature (SST) and Sardine spawning biomass (SSB) index data was used to drive the model. INE stand for official landings statistics obtained from National Portuguese Statistical Institute (INE); C_{INE} is the catch, composed of landings obtained from INE official statistics, and discards estimates adopted from the initial Ecopath model and scaled to time series of INE landings; B_{SRA} is biomass estimates obtained from stochastic SRA (50th percentile); SRA: Stock reduction analysis; SA: Stock assessment output.

Species	Source of biomass data	Source of catch data	Source of forcing data
Demersal piscivorous fish	SRA output	INE	$F = C_{INE}/B_{SRA}$
Hake	SA output	SA output	F from SA output
Rays	SRA output	INE	$F = C_{INE}/B_{SRA}$
Squids	B _T survey	INE	no data
Benthic cephalopods	B _T survey	INE	no data
Sharks	B _T survey	no data	no data
Benthopelagic piscivorous fish	SRA output	INE	$F = C_{INE}/B_{SRA}$
Flatfish	B _T survey	INE	no data
Sparids	SRA output	INE	$F = C_{INE}/B_{SRA}$
Bogue	SRA output	INE	$F = C_{INE}/B_{SRA}$
Horse mackerel	SA output	INE	$F = C_{INE}/B_{SRA}$

Benthopelagic invertivorous fish	SRA output	INE	$F=C_{INE}/B_{SRA}$
Chub mackerel	Acoustic survey	INE	no data
Demersal invertivorous fish	B _T survey	INE	no data
Mackerel	SRA output	INE	$F=C_{INE}/B_{SRA}$
Blue jack mackerel	SRA output	INE	$F=C_{INE}/B_{SRA}$
Anchovy	SRA output	INE	$F=C_{INE}/B_{SRA}$
Sardine adult	SA output	SA output	F and SSB index to force sardine egg production from SA output, SST to force sardine spawning environmental response from KNMI Climate Explorer web application.
Sardine juvenile	SA output	DGRM	no data

4.2.7. Addressing uncertainty

Monte Carlo routine built-in EwE was applied to Ecosim to assess the sensitivity of outputs to the Ecopath input parameters. We ran 500 simulations using a coefficient of variation obtained from the pedigree routine, which assesses the quality of the input data, in the following input variables: biomass, consumption/biomass, ecotrophic efficiency, production/biomass. Monte Carlo simulations result were used to plot 5th and 95th percentile confidence intervals for the fitted biomass and catch trends.

4.2.8. Sardine key trophic interactions /trophic flow control analysis for sardine

For the species that are directly related to sardine as predators or preys, different hypothesis about flow control (top-down, bottom-up and mixed) were checked in order to see which are the key interactions that help explain sardine variability. Improvement in the fit of adult sardine was assessed by comparing the impact the changes in flow control of both sardine stanza and their predators or preys have on SS. During the hypothesis flow control test, all forcing parameters were maintained the same as in the selected model that represents the best fit.

4.3. Results

4.3.1. Fitting the model to data

The best model fit was obtained when changes in vulnerabilities, fishing, PP anomaly and environmental forcing on sardine were used together to drive and fit the model (Table 4.3). By including these variables together, the model fit improved by 31.4% compared to the baseline model. When assessing the importance of each driver to the final model, the largest

improvement to model fit was obtained by including vulnerabilities (172%), followed by fishing mortality (41%). Including environmental forcing on sardine and PP anomaly improved the model fit by 15% and 3.4% respectively. When considering the contributions of each driver to the fit improvement for the adult sardine functional group separately, we found out that the largest improvement was obtained when environmental forcing on sardine was included (> 400%). The inclusion of changes in PP anomaly and vulnerability parameters contributed to the improvement of adult sardine fit by 45% and 52% respectively. Also, for juvenile sardine stanza, the largest fit improvement of 64% and 40% was observed when environmental forcing on adult sardine and changes in vulnerabilities were added, respectively (Table 4.3).

Table 4.3 Assessment of the contribution of each driver to explain the dynamic of PCSE and sardine biomass trend. *Contribution in the final model scenario was assessed by comparing SS of final model with SS of the baseline model (model without any drivers) while for remaining scenarios, the contribution was assessed by subtracting each driver from the final model in each scenario and assessing its effect by SS improvement in reference to SS of the final model. Scenarios: 1) Baseline - does not include any driver; 2) Final model – includes all drivers, 3) Sc_PP – includes all drivers less the effect of PP anomaly; 4) Sc_ENV – includes all drivers less the effect of environmental forcing function; 5) Sc_Vs – includes all drivers less the effect of vulnerabilities and 6) Sc_F – includes all drivers less the effect of fishing mortality. Vs: number of vulnerabilities estimated; Spp: number of primary productivity spline points estimates; Min SS: reduction in the weighted sum of squared deviations; k: the total number of parameters estimated; AIC: an Akaike Information Criterion (AIC) parameter and % IF_M, %IF_{BS}, %IF_{BS_JUV}: a percentage of SS change when compared SS of baseline scenario/ final model to SS of final model, adult sardine and juvenile sardine biomasses respectively.

No.	Scenario	Considered drivers	Assessed driver	Parameters					Assessed contribution*		
				k	Vs	Spp	minSS	AIC	% IF _M	% IF _{BS}	% IF _{BS_JUV}
1	Baseline						1202	6.277			
2	Final model	F+V+ENV+PP		32	27	5	825.6	-447.4	31.4	53.5	32.6
3	Sc_PP	F+V+ENV	PP	27	27	0	853.6	-406.5	3.4	82.2	4.2
4	Sc_ENV	F+V+PP	ENV	32	27	5	949.1	-304.7	15.0	648.7	70.4
5	Sc_Vs	F+ENV+PP	Vs	5	0	5	2243	743.6	171.7	81.4	20.2
6	Sc_F	V+ENV+PP	F	32	27	5	1168	-47.92	41.5	94.8	34.3

Ecosim predicted the biomass trends satisfactorily (contributions to SS<5; Table A4.4 in annex 4) for horse mackerel, benthopelagic invertivorous fish, sparids, rays, adult sardine, mackerel, benthopelagic piscivorous fish and anchovy (Figure 4.4 a–h). Among species with larger contributions to overall SS, bogue, demersal piscivore fish, hake, blue jack mackerel, and juvenile sardine, trends were reproduced quite well (Figure 4.4 i–m) while fits to time series of remaining species were rather poor (Figure 4.4 n–t).

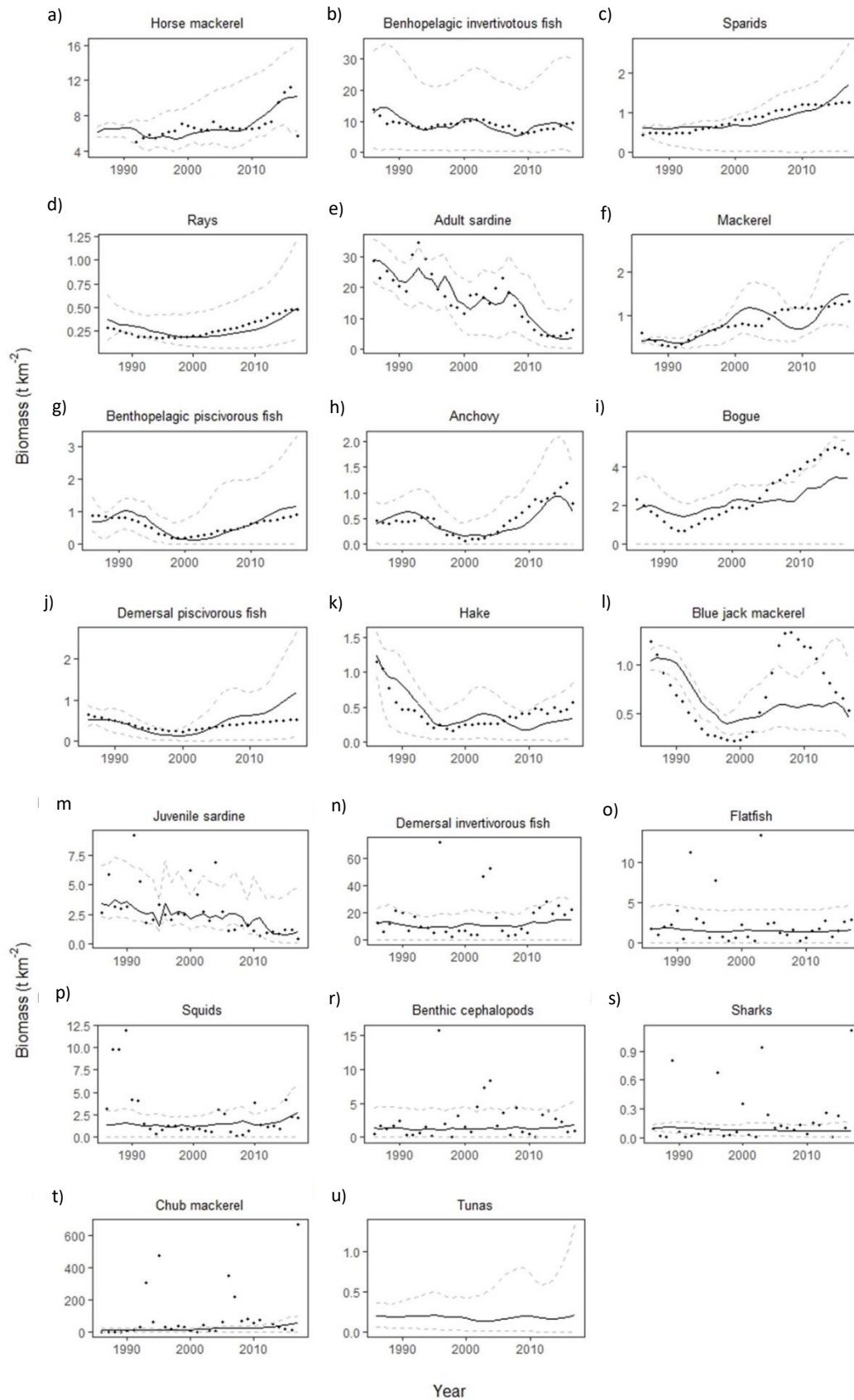


Figure 4.4 Predicted by Ecosim (black line) and observed (points) biomass temporal trends for the fish species in the Portuguese continental shelf ecosystem between 1986–2017. Dashed lines indicate Monte Carlo 5th and 95th percentile. For graphs, a, e and k observed biomass refers to biomass estimated from SA methods by ICES, while for b–d, f–j and l refers to biomass estimated from SRA.

Among the functional groups that lacked historical observations, the model predicted increasing trends for seabirds and meso/microzooplankton and to a lesser extent for bottlenose dolphin, common dolphin and phytoplankton (Figure 4.5 albdm),

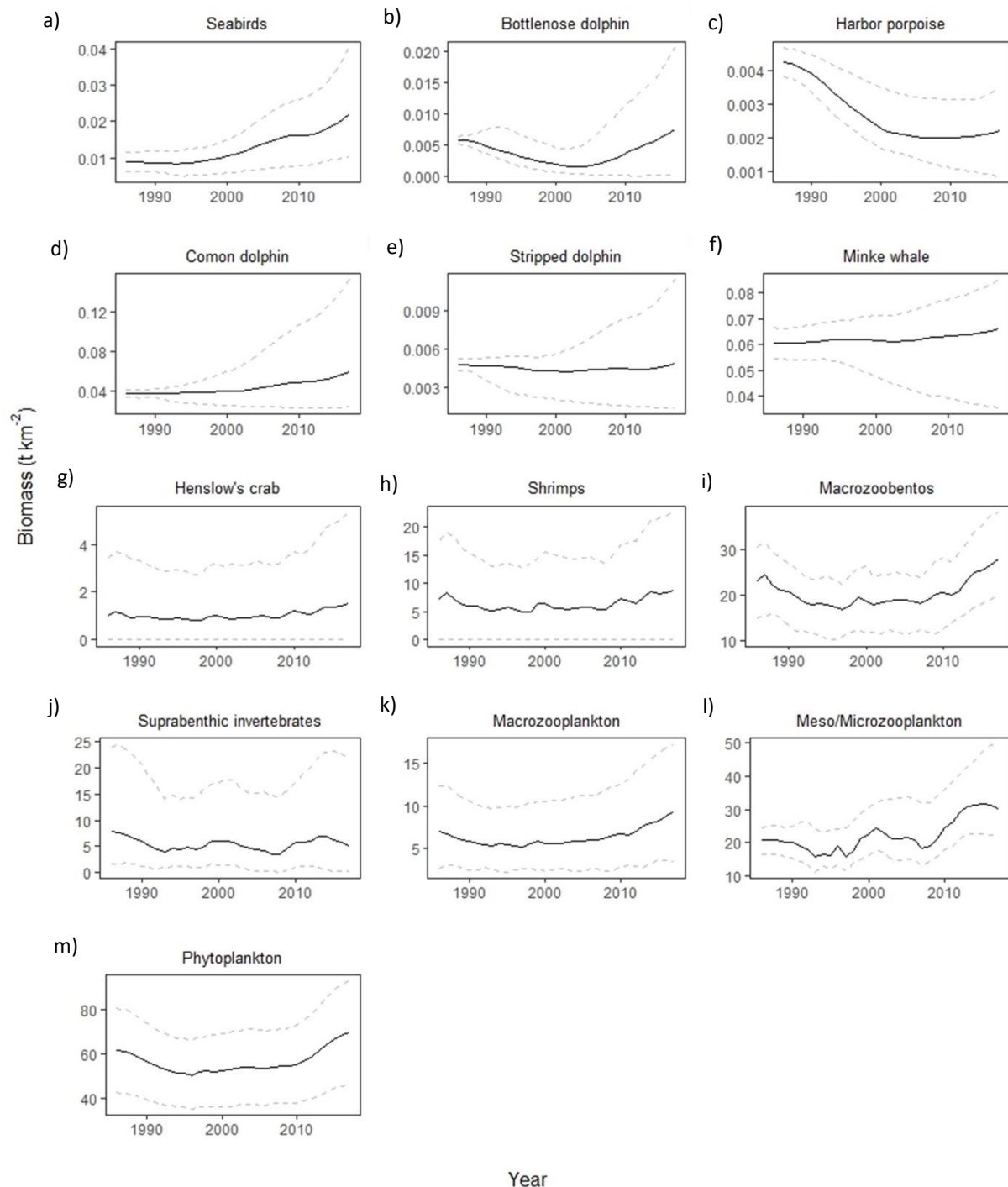


Figure 4.5 Biomass trends predicted by Ecosim (black line) in the Portuguese continental shelf ecosystem between 1986–2017. Dashed lines indicate Monte Carlo 5th and 95th percentile.

On the other hand decreasing trend was observed for harbour porpoise (Figure 4.5 c). There was no clear trend shown for striped dolphin, minke whale and remaining lower trophic level groups (Figure 4.5 e–k).

Catch time-series predictions matched observation data well (the lowest contribution to SS, <5) for benthopelagic invertivorous fish, flatfish, horse mackerel, rays, demersal piscivores fish, sparids, anchovy and benthopelagic piscivores fish (Figure 4.6 a–h). Among the species with a higher contribution to SS, (>5 and <13), catch trends were quite well reproduced for bogue, mackerel, demersal invertivores fish and blue jack mackerel (Figure 4.6 i–l). Modelled catches of hake and adult sardine were overestimated (Figure 4.6 np) while benthic cephalopods catches were underestimated (Figure 4.6 m). The model did not represent the catch trends for squids, juvenile sardine and sharks (Figure 4.6 r–t).

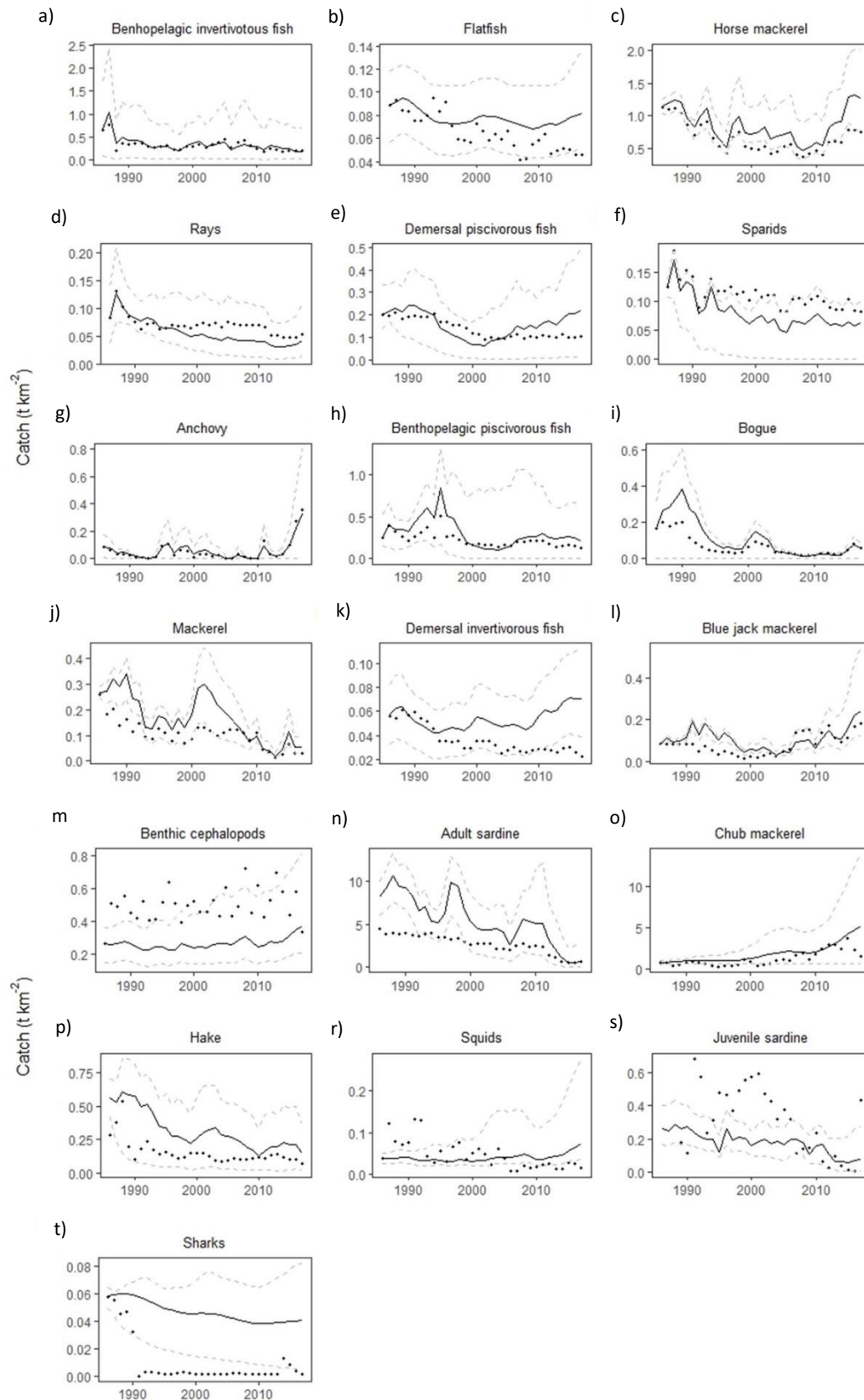


Figure 4.6 Predicted by Ecosim (black line) and observed (points) catch temporal trends for the fish species in the Portuguese continental shelf ecosystem between 1986–2017. Dashed lines indicate Monte Carlo 5th and 95th percentile.

The PP anomaly obtained during the calibration of the model (Figure 4.7 a), improved the fit of the final “best fit” model by 2.4% when compared to the model that considers fishing, changes in vulnerability parameters and environmental forcing (Table 4.3).

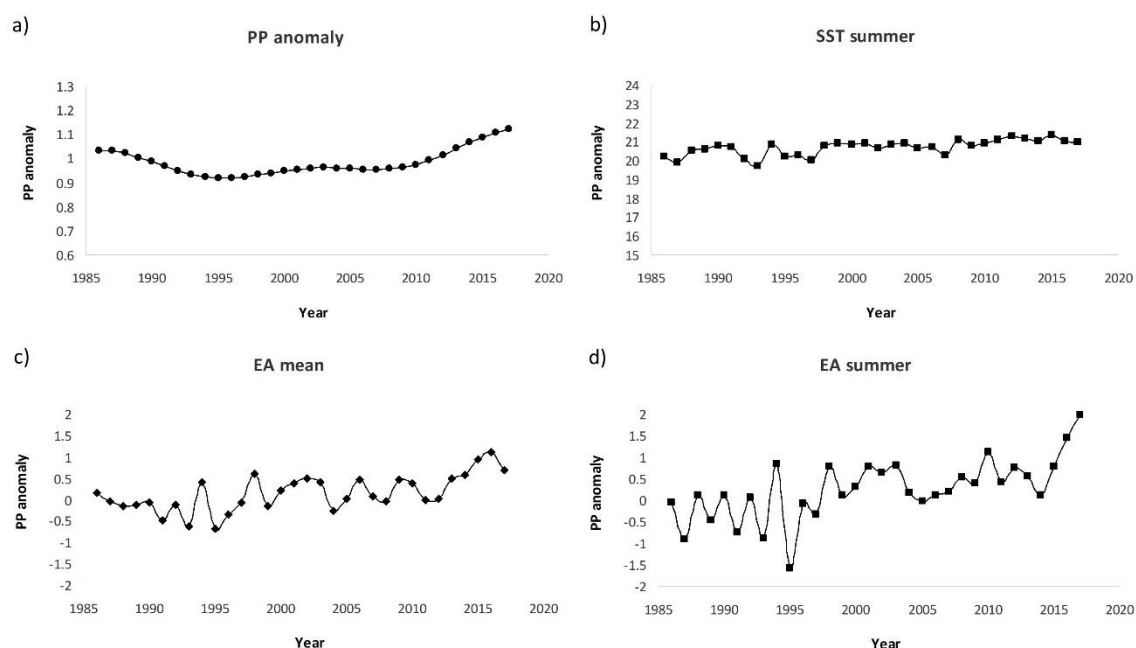


Figure 4.7 PP anomaly trend obtained during the calibration process (a), trends of environmental variables that showed significant correlations with PP anomaly: summer average Sea surface temperature (SST) (b); annual average Eastern Atlantic pattern (c); summer annual average of Eastern Atlantic pattern (d).

The PP anomaly showed a slightly increasing trend with time (Figure 4.7 a) and was linearly and significantly correlated ($p \leq 0.05$) with SST summer average and both summer and annual means of Eastern Atlantic pattern (Figure 4.7 b–d; Table A4.8 in annex 4).

4.3.2. Temporal changes in PCSE between 1987 and 2017

Collation and graphical representation of a large biomass and catch data set for PCSE revealed that the studied system has undergone considerable changes in the last 30 years. Biomass of many species such as horse mackerel, sparids, rays, mackerel, anchovy, bogue and chub mackerel increased noticeably during the studied period (Figure 4.4 acdfhit). On the other hand, the biomass of commercially important sardine and hake displayed a substantial decrease (Figure 4.4 ek). Biomass changes were accompanied by a substantial reduction in catch

observed for the majority of species (Figure 4.6) with the exception of anchovy, blue jack mackerel and chub mackerel for which catch doubled or even quadrupled in the studied period (Figure 4.6 glo).

4.3.3. Sardine key trophic interactions

Cephalopods, benthopelagic fish, minke whale, flatfish and common dolphin were predators that made the largest contribution to the improvement of sardine fit under bottom-up control scenario (Figure 4.8 a). When considering adult sardine preys, the largest improvement was observed for phytoplankton and zooplankton under the top-down scenario (Figure 4.8 a). Among juvenile sardine predators, chub mackerel, horse mackerel and bogue led to the largest sardine fit improvement under the top-down flow control, while among its preys the largest improvement in the fit was caused by meso/microzooplankton group and phytoplankton under bottom-up and top-down flow control scenarios respectively (Figure 4.8 b).

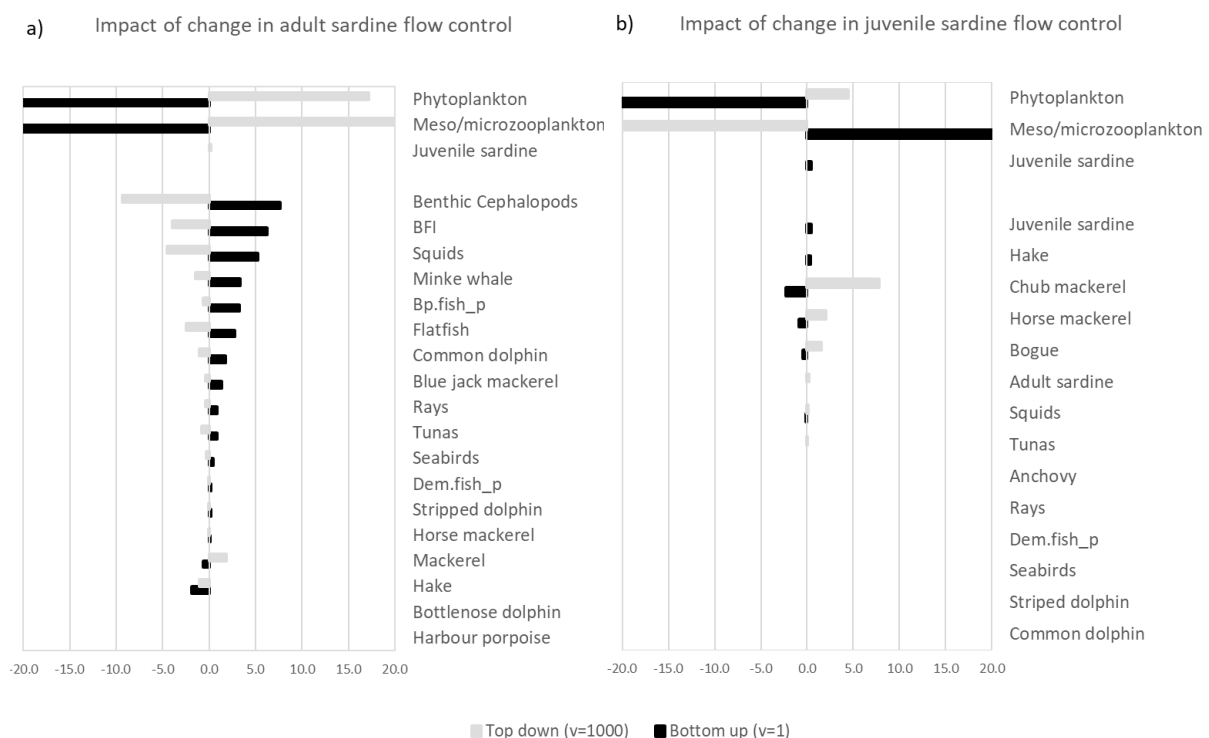


Figure 4.8 Partial contribution each functional group (that have direct trophic relations with sardine) have on the improvement of the adult sardine fit. Improvement in sardine fit was assessed by changing trophic flow control parameters between predators/preys and adult sardine (a) and juvenile sardine (b). Three flow control scenarios were tested: initial conditions that represent mixed ($v_{ij}=2$), bottom-up ($v_{ij}=1$) and top-down ($v_{ij}>>1$) flow control settings. Negative results indicate bad fitting, while positive results indicate an improvement in fit when compared with the initial conditions. To improve the legibility of the figure, the values for phytoplankton and meso/microzooplankton groups (that were very large) were not shown on the horizontal axes.

4.4. Discussion

4.4.1. Model assumptions and limitations

Modelling with EwE software is a very data demanding and time-consuming process. The main challenge of the 1986 Ecopath model parametrization was the difficulty in gathering regional data. The biomass of species surveyed by bottom-up trawl is substantially underrepresented (chapter 3; Veiga-Malta et al. 2019) therefore in the model, of 33 functional groups, the biomass of 12 groups was estimated by the model. Also, cetaceans and birds' biomass data describing the years between 2010 and 2012, were directly adapted from the Ecopath model developed by Veiga-Malta et al. (2019) (chapter 3). Another limitation was related to the lack of diets composition data with a temporal dimension that is an obstacle commonly reported in EwE studies (e.g., Alexander et al. 2015; Piroddi et al. 2017). With regards to the temporal-dynamic simulation, during the modelling procedure, we noticed that the model did not work well with the raw data from the BT surveys. Therefore, the data required prior processing in order to be used. Stock reduction analysis (SRA), as explained in section 4.2.6 and in annex 4 was performed to estimate plausible biomass trends based on the available historical catch data and life history parameters. The introduction of the SRA increased the complexity and uncertainty of the study; however, it greatly improved the modelling outputs (goodness of model fit). This is in line with the study by Christensen et al. (2009) who demonstrated that using long time-series data to drive and calibrate model considerably increases the ability of EwE to explain ecosystem changes. Also, in the studied region, the inclusion of the temporal time series of lower trophic levels biomasses of phytoplankton, zooplankton and marine invertebrates was not possible due to the lack of such data or inconsistencies between data collection methods between older and more recent data. Moreover, many commercial species lacked fishing mortality data that might mislead results by limiting the fishing impact on the ecosystem that has been observed in the study. Despite the limitations described above, the study includes the best available regional data that exists in the studied system. Moreover, the EwE model was highlighted as one of the most appropriate tools to investigate marine ecosystem dynamics (e.g., Coll et al. 2008; Piroddi et al. 2017; Corrales et al. 2017). When applicable, we accounted for the uncertainty in the model input parameters by applying a Monte Carlo routine that allows interpreting the quality of results considering presented confidence intervals. This analysis highlights the importance of

improvement in input data quality for future studies, especially if the results are to be used for management purposes (Heymans et al. 2016).

4.4.2. Drivers of changes in Portuguese continental shelf ecosystem from 1986 to 2017

The model had the capability to explain 31.4% of the variability of available time series from 1986 to 2017 when trophic interactions, fishing, environmental forcing on sardine and primary production anomaly were combined. It is questionable whether 31.4 % is an acceptable reduction in SS as there are no official criteria on how to assess a model's performance. Based on the published literature we can notice that models developed for better-studied systems tend to explain a larger proportion of variability in the time series (e.g., Alexander et al. 2015; Bentley et al. 2017).

The largest impact on the final model fit was observed by including vulnerabilities. The importance of trophic interactions in the management of marine resources has gained more interest and awareness in the last decades with many studies worldwide stressing its relevance in the dynamics of ecosystems (e.g., Coll et al. 2008; Alexander et al. 2015). In EwE modelling one of the ways to represent specific predator-prey interactions is through the vulnerability parameters. In the PCSE, vulnerabilities adjustment revealed to be important in explaining its dynamics. Among 27 interactions, for which the vulnerabilities had the strongest impact on the fit improvement, hake was the predator with the largest number of low vulnerabilities on its preys, suggesting bottom-up flow control (called also “prey control”). These settings mean that an increase in hake biomass will not cause any noticeable increase in the predation mortality of its preys. On the other hand, sparids, bogue, horse mackerel, chub mackerel and mackerel held mainly high vulnerabilities over its preys that indicate top-down flow control and suggest that these groups as predators control their preys (“predator control”). This implies that an increase in their biomass might cause a noticeable increase in the predation mortality of their preys: benthopelagic invertivorous fish, juvenile sardine, macrozoobenthos, suprabenthic invertebrates, sardine, and zooplankton groups. Top-down settings ($v_{ij} > 1$) were also observed for other pelagic species: blue jack mackerel, anchovy, and adult sardine predation on their preys. Moreover, blue jack mackerel, anchovy, bogue and chub mackerel exerted bottom-up control ($v_{ij} = 1$) over their predators: hake, and benthic cephalopods highlighting their

importance as preys in the ecosystem, described as wasp-waist flow control scenario (Bakun 2006), and being consistent with the dynamics of upwelling systems (Cury et al. 2000).

The second-largest impact on the overall model fit was due to the fishing mortality driver. Fishing was highlighted to be an important driver of ecosystems in many areas worldwide (e.g., Coll et al. 2008; Alexander et al. 2015). On the other hand, fishing has not been identified as an important driver in other upwelling ecosystems such as the Southern Benguela model (Shannon et al. 2004). However, in the PCSE model, we only force the fishing mortality of 12 of commercial functional groups (from a total of 20) representing a major limitation in assessing the real impact of fishing in the model.

The environmental forcing, that was introduced through the SST response function and egg production function directed towards sardine, improved overall model fit by 15% when compared to the scenario without this driver. This substantial improvement confirms well-documented evidence that climate change is one of the unquestionable drivers of marine ecosystems affecting fish stocks recruitment worldwide (e.g., Zimmermann et al. 2019; Brunel and Bouchel et al. 2007). Also, in the PCSE, an increase in SST was linked with the changes in the distribution and ecological functions of fish species (Vinagre et al. 2011). Bottom-up forcing expressed as the PP anomaly effect on phytoplankton biomass, revealed to be a minor driver in the PCSE ecosystem, improving the final model fit only by 3.4%. Such a minor bottom-up effect is unexpected for an ecosystem that is characterised by seasonal upwelling. In other upwelling ecosystems, or ecosystems that share structural features with upwelling ecosystems (e.g., NW Mediterranean, Coll et al. 2006), for which the Ecosim models were developed and calibrated, the PP anomaly driver tends to play a more important role. For example, the inclusion of the PP anomaly driver improved the fit by an additional 6% and 16% in Southern Benguela (Shannon et al. 2004) and in the South Catalan Sea (NW Mediterranean) (Coll et al. 2008) respectively. However, the PP anomaly seemed to play an important role in several functional groups especially pelagic ones. This highlighted the complexity of the PCSE dynamics and implies that the ecosystem drivers are affecting various functional groups with varying intensity. A similar observation was registered in the NW Mediterranean Sea where pelagic ecosystem components tend to be more affected by PP anomaly, while the demersal domain by fishing (Coll et al. 2008). PP anomaly driver was correlated with summer SST and Eastern Atlantic pattern. In the Portuguese coast, several authors linked changes in SST with the substitution of temperate species with subtropical/ tropical species (e.g., Henriques et al. 2007; Vinagre et al. 2011). Moreover, some studies have shown that ecological functions of

fish species along the Portuguese coast are affected by the increased SST (e.g., Cabral et al. 2001). The potential relationship of the Eastern Atlantic pattern and PP anomaly and how it can impact the ecosystem through the bottom-up effects, is more complex and less straightforward. A considerable fraction of inter-annual climate variability in the Northern Hemisphere is driven by NAO, the first mode of North Atlantic climate variability that is well studied and well understood (Hurrell 1995; Trigo et al. 2002). However, recent studies have shown that considering the second mode of variability namely the Eastern Atlantic pattern greatly improves understanding of their controlling mechanisms, as well as their impact on climate (Comas-Bru and Hernández 2018). Although EA and NAO indices are computed as independent variables it has been suggested that EA's impact on climate should be investigated in conjunction with the NAO (Moore et al. 2011; Comas-Bru and McDermott 2014; Bastos et al. 2016). So far, it is known that EA modulates NAO strength and location (Moore et al. 2013) and Comas-Bru and McDermott (2014) showed that the combined analysis of NAO and EA more appropriately describes winter climate variability in Europe. In the west coast of the Iberian Peninsula, during a negative phase, NAO is usually associated with weaker northwest winds (i.e., weaker upwelling events), lower precipitation, higher SST, and higher climate instability (Folland et al. 2009). These conditions were linked to impact recruitment of many fish species such as European hake (Sanchez et al. 2003a), megrim (Sanchez et al. 2003b), horse mackerel, sardine (Guisande et al. 2001; Santos et al. 2001; Santos et al. 2012, Malta et al. 2016) and anchovy (Borja et al. 2008).

4.4.3. Sardine changes from 1986 to 2017 and its drivers

In this study, environmental effects introduced through SST forcing on sardine spawning and egg production were identified as the most important drivers of sardine decline. An increase in water temperature observed in the northeast Atlantic (Relvas et al. 2009) might have impacted sardine decline in multiple ways. First, the effect of SST forcing on sardine spawning introduced in the model agrees with the studies that linked SST and sardine productivity (e.g., Santos et al. 2012; Malta et al. 2016; Garrido et al. 2017). Effect of increased temperature on sardine decline can be explained by the fact that optimal and tolerance ranges of sardine spawning in PCSE are quite narrow and varies between 14°C and 16°C (Coombs et al. 2006) and 12°C and 18 °C (Stratoudakis et al. 2007) respectively. Moreover, climate effect can be intensified by the fact that increased temperature might favour other SPF that prey on sardine at some life stage. For example, chub mackerel optimal range for spawning is higher

than sardine and fluctuate between 15°C and 20°C (Vasconcelos et al. 2012), implying that increasing temperature might be positive for chub mackerel and, at the same time, can indirectly intensify predation stress on sardine. Secondly, SST shows a negative relationship with upwelling strength (Peliz and Fiúza 1999; Relvas et al. 2009; Lemos et al. 2010) and stronger upwelling events are linked with nutrient richer waters that favour higher abundance of sardine food (Peliz and Fiúza, 1999; Garrido et al. 2008), thus creating more beneficial conditions for sardine juveniles survival and growth. Also, Zwolinski et al. (2010) demonstrated that sardine distributes along the areas with lower temperatures ($<16^{\circ}\text{C}$) and hypothesizes that higher SST temperatures may be indicators of low food availability for sardine juveniles. Also, the inclusion of PP anomaly substantially improved adult sardine biomass trend and as PP anomaly showed significant correlation with SST, we can assume that discussion of the role of SST forcing on sardine is valid for PP anomaly as well.

In line with the overall model, fishing mortality was the second most important driver that explained sardine biomass trend. From 1986, sardine catches have gradually decreased from about 190,000 tonnes (4 t km^{-2}) to about 22,000 tonnes (0.6 t km^{-2}) in 2017. However, the level of sardine fishing mortality was maintained between 0.2 and 0.4 with a peak of approximately 0.57 in 2011. Since 2006 sardine biomass started to decline sharply, halving in only 3 years, and since 2009 its biomass was around its lowest historical level and below the limit biomass (Blim) (ICES 2018a). As demonstrated in this study, drivers other than fishing had an important role in this quick and considerable decline. However, based on the latest ICES stock assessment evaluation, it seems that the current stock productivity is insufficient to support a sustainable fishery (ICES 2018a). This might suggest that since 2006–2009 fishing pressure on sardine might have aggravated its decline. For example, the highest historical fishing mortality addressed on sardine occurred at the time when the stock was already depleted (in 2011: $B \sim 18,000$ tonnes, $F=0.57$).

Moreover, sardine fit was substantially improved by an adjustment in vulnerability parameters. Testing various hypotheses about flow control between sardine and their direct trophic interactions allows identifying the key trophic interactions between sardine and other species. This analysis showed that model parametrization allows explaining sardine behaviour through a typical wasp-waist control mechanism, characteristic for upwelling systems (Bakun 2006). Even though, this scenario did not contribute largely to overall model fit improvement (and therefore was not selected as the best model fit), adult sardine SS reduced when top-down control over sardine preys (phytoplankton and meso/microzooplankton) and bottom-up control

by sardine predators (benthic cephalopods, benthopelagic fish, minke whale, flatfish and common dolphin) was introduced. Alternative wasp-waist control mechanism scenario between sardine and its predators/preys highlights the importance of sardine in PCSE and implies a dependence of some higher trophic level fish (predators) on their prey (sardine). Collapses of forage fish might negatively impact predatory fish. For example, when Chilean anchoveta (*Engraulis ringens*) population collapsed in 1973, its predator, the snoek (*Thyrssites atun*), collapsed 4 years later (Cury et al. 2000). The prey recovered in 1986 but the catch of snoek remained very low, indicating that the recovery of snoek was delayed. A similar situation occurred to bonito (*Sarda chiliensis*) in the upwelling system off Peru (Pauly et al. 1987) with the difference that for this predator, the recovery occurred almost immediately after biomass of its prey improved. Moreover, predators in upwelling ecosystems may have adapted to long-term changes in their food resources by switching from one prey species to another as their relative abundance changes. Such changes in the diet of predators between anchovy and sardine have been observed off South Africa in Cape gannets (Crawford 1999) as well as in several seabird species in the Gulf of California (Velarde et al. 1994). On the other hand, flow control analysis for juvenile sardine showed top-down control of juvenile sardine by their predators (in contrast to adult sardine): chub mackerel, horse mackerel and bogue controlled juvenile sardine through the top-down scenario and juvenile sardine shows bottom-up control towards its prey meso/microzooplankton. This flow control scenario (in contrary to the wasp waist scenario) helps to improve not only sardine fit but also the overall fit of the model, therefore it was incorporated in the selected best model fit. This scenario implies that an increase in biomass of species that prey on sardine eggs (chub mackerel, horse mackerel and bogue) might negatively impact sardine that under this scenario is vulnerable to its predators. Alternating patterns of abundance between pelagic species have been observed in upwelling systems worldwide (Bakun 1998) and also, in the recent decade, this phenomenon manifested in PCSE when increasing biomass of horse mackerel, chub mackerel, mackerel, anchovy and bogue coincides with sardine decline (Martins et al 2013; ICES 2018a). The mechanism behind fluctuations of SPF in upwelling systems is not fully known, but it is suggested that climatic factors together with intra-specific competition play an important role (Cury et al. 2000; Serra et al. 1998). Garrido et al (2015) demonstrated the existence of a significant dietary overlap between chub mackerel, sardine, and anchovy. Moreover, this study highlighted that cannibalism and intraguild predation between SPF might play a role in egg mortality and recruitment strength of these species. According to Garrido et al. (2015), sardine and chub mackerel juveniles, followed by bogue, were the main predators of fish eggs, particularly those of sardines.

Moreover, sardine was identified as the main predator of its eggs (cannibalism) and eggs of anchovy in the Iberian waters and Bay of Biscay (Garrido et al. 2015; Bachiller et al. 2015). In the literature, cannibalism has been proposed as a self-regulatory mechanism that depending on the density of the clupeids, allows for self-regulation of population abundance (Alheit 1987; Szeinfeld 1991; Pájaro et al. 2007; Bachiller and Irigoien. 2015). On the other hand, intraguild predation was reported as compensation mechanisms that can regulate the biomass of competing species (Bachiller et al. 2015) and can eventually explain the fluctuation between the stock of clupeoids (Szeinfeld 1991). Given the increase in abundance (Martins et al. 2013) and the northward expansion of several PF such as chub mackerel and anchovy related with a warming trend that is being observed in the northeast Atlantic (Relvas et al. 2009), these mechanisms should be considered as potential contributors to the recent decline in sardine abundance in Iberian coastal waters (Garrido et al. 2015).

4.5. Conclusions

This study presents the first representation of a food web model fitted to time series in the Portuguese continental shelf ecosystem. In summary, our results suggest that the main factors that drive the PCSE variability between 1986 and 2017 were trophic interactions, fishing and environmental forcing. On the other hand, when considering the recent decline of Iberian sardine, the most important were environmental drivers, introduced through SST forcing, followed by fishing. Moreover, key sardine trophic interactions that helped to explain sardine dynamics were predators of sardine eggs (chub mackerel, horse mackerel and bogue). Furthermore, a flow control hypothesis test showed that model parametrization allows explaining sardine behaviour through a typical wasp-waist control mechanism, characteristic of upwelling systems. This study enables us to further the knowledge and improve our understanding of PCSE dynamics and provide some insights helpful to identify key factors responsible for the decline of sardine stock. Future work can include the development of projection scenarios that will assess the potential effects of key pressures might have on future sardine stock and ecosystem.

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Chapter 5

Detecting regime shifts in the Portuguese Continental Shelf Ecosystem within the last three decades

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Chapter 5 – Detecting regime shifts in the Portuguese Continental Shelf Ecosystem within the last three decades

Abstract

Marine ecosystems are affected by diverse pressures and consequently may undergo significant changes that can be interpreted as regime shifts. In this study, we used integrated trend analysis that combines multivariate statistics and methodologies to identify abrupt changes in time-series, in order to test a hypothesis about the occurrence of regime shifts in the Portuguese Continental Shelf Ecosystem (PCSE). We used two types of data describing ecosystem drivers (fishing mortality and environmental/climatic indices) and ecosystem state (observed and modelled biomass and ecosystem indices). Modelled biomass and ecosystem indices were outputs of Ecopath with Ecosim temporal model parametrised for PSCE between 1986 and 2017. The analyses indicated that the regime shifts in the PCSE have occurred during three periods in the last three decades: “early regime” until the mid-1990s, followed by “transition regime” in-between and “late regime” since the mid-2010s. The detected regime shifts are characterised by changes in the pelagic community that became more dominant when compared to the demersal community and shifted from sardine, the main fishing resource, abundant in the “early regime”, to other less valuable pelagic fishes such as chub mackerel that dominated the “late regime”. The “early regime” was characterised by high catch, a larger proportion of demersal species, and higher diversity while, the “late regime” was represented by lower catch, an increase in higher trophic level predatory fish and lower diversity. Moreover, the “late regime” showed lower resilience and reduced maturity when compared to the “early regime”. Changes described in the ecosystem were probably related to: (1) the shift in the north Atlantic environmental conditions that affected small pelagic fish and lower trophic levels groups; (2) reduction in fishing pressure; and (3) internal triggers, related to the indirect trophic interactions that might have benefited higher trophic level fish and impacted the pelagic community. In the context of PCSE management, this study highlighted a need to consider the possibility of regime shifts in the management process. For example, regime specific harvest rates and environmental reference points should be considered when an indication of abrupt change in the ecosystem exists.

Keywords: Portuguese continental shelf ecosystem, regime shift, ecosystem modelling, integrated trend analysis, sardine decline, environmental forcing

5.1. Introduction

Marine ecosystems worldwide are affected by increasing natural and anthropogenic pressures and consequently undergo significant changes at unprecedented rates. Affected by these changes, ecosystems can reorganise and still maintain the same function, structure, and identity (Walker et al. 2004). However, under some circumstances, the ecosystem may undergo changes that modify the system's structure and function and this process can be described as a shift to a new regime (Holling 1973; May 1977; Scheffer et al. 2001). Usually, a regime shift is triggered by large-scale climate-induced variations (Parsons and Lear 2001), intense fishing exploitation (Daskalov 2002) or both (Llope et al. 2011). Criteria used to define regime shifts vary and the changes that have to occur in order to consider that a system has undergone a regime shift are not well-defined (Lees et al. 2006). Normally, regime shifts are defined as high amplitude, low-frequency and often abrupt changes in species abundance and community composition that are observed at multiple trophic levels (McKinnell et al. 2001). These changes are expected to occur on a large spatial scale and take place concurrently with physical changes in the climate system (McKinnell et al. 2001; Scheffer et al. 2001; Cury and Shannon 2004; deYoung et al. 2004; Wooster and Zhang 2004; Collie et al. 2004; Lees et al. 2006). Regime shifts have been described in several marine ecosystems including Northern Benguela (Heymans and Tomczak 2016), the North Sea (Weijerman et al. 2005) and the Baltic Sea (Tomczak et al. 2013). In large upwelling ecosystems, it is common to observe decadal fluctuations in species abundance and their replacements (Curry et al. 2000). These fluctuations might be irreversible and might be an indicator of the new regime, as was the case in the Northern Benguela ecosystem (Heymans and Tomczak 2016). However, changes in the upwelling systems might be interpreted as fluctuations within the limits of natural variability for an ecosystem, and not as an indicator of the regime shift (Cury and Shannon 2004).

The Portuguese Continental Shelf Ecosystem (PCSE) constitutes the northernmost part of the Canary Current Upwelling System and is characterised by seasonal upwelling that occurs during the spring and summer as a result of steady northerly winds (Wooster et al. 1976; Fiúza et al. 1982). It has recently changed in the abundance of coastal pelagic species such as sardine, chub mackerel, horse mackerel, blue jack mackerel and anchovy (ICES 2008, 2017a; Martins et al. 2013; Garrido et al. 2015). Moreover, in the last decades, an increase in higher trophic level species has been documented (Leitão 2015a). The causes underlying changes in the pelagic community are not clear but it has been suggested that they result from a complex

interplay between environmental variability, species interactions and fishing pressure (Leitão et al. 2014a; Leitão 2015b; chapter 3; Veiga-Malta et al. 2019). There is evidence, that changes in the intensity of the Iberian coastal upwelling (resulting from the strengthening or weakening northern winds) had occurred in the last decades. However, the character of these changes is contradictory where some authors observed intensification of upwelling-favourable winds (Miranda et al. 2012; Pires et al. 2013) while others documented their weakening (Sydeman et al. 2014; Barton et al. 2013). In the latest review of upwelling rate and intensity along the Portuguese coast, Leitão et al. (2019) documented a successive weakening of the upwelling since 1950, that lasted till mid/late 1970s in the north-west and south-west and till 1994 in the south coast. In recent years (1985–2009) an increase in upwelling index in all studied regions was documented while additionally upwelling intensification was observed in the south (Leitão et al. 2019). Moreover, a continuous increase in water temperature, ranging from 0.1°C to 0.2°C decade⁻¹ has also been documented (Baptista et al. 2017).

Understanding the changes that occurred in ecosystems, including their causes, timeline and impacts, is very important from the standpoint of ecosystem management as the potential of regime shifts raises several challenges for management (Crépin et al. 2012; Sguotti and Cormon 2018). Therefore, identifying regime shifts and accounting for these changes are important in the context of Ecosystem-based management (Levin and Mölmann 2015). This relates also to fisheries management because a regime shift might cause significant changes to the structure of the ecosystem and consequently impact the harvesting of fish stocks (Folke et al. 2004), as has been reflected in Portuguese fishery landings profiles in the last half-century (Leitão 2015a).

Mölmann et al. (2009) used the Integrated Trend Analysis (ITA) approach that combines multivariate statistics (Principal Components Analysis, PCA) and methodologies to identify step changes in time-series such as Sequential t-test Analysis of Regime Shifts (STARS, Rodionov 2004) and Chronological Clustering (CC, Legendre *et al.* 1985) to demonstrate the reorganization of the Baltic Sea ecosystem. By integrating hydroclimatic, nutrient, plankton and fisheries data into the ITA approach they identified two stable states between 1974 and 2005, separated by a transition regime in 1988–1993. Heymans and Tomczak (2016) and Tomczak et al. (2013) combined ITA with outputs of Ecopath with Ecosim modelling approach (www.ecopath.org) and used Ecological Network Analysis (ENA) indicators as described by Ulanowicz (1986), to test for the changes in food web organisation and to describe changes that occurred in the Northern Benguela and the Baltic Sea.

The main objective of this study is to investigate the hypothesis that a regime shift occurred in the PCSE during the study period. Two types of data describing ecosystem drivers (fishing mortality and environment/climatic indices) and ecosystem state (biomass and ecosystem indicators), and ITA methodology (PCA, STARS and CC) were used to: (1) assess the changes in the PCSE over the last three decades; (2) extract the common ecosystem trends (PCA); (3) detect significant shifts in datasets (STARS, CC); (4) compare times when the shifts occurred in different datasets; (5) explore the relationship between extracted trends and (6) discuss the role of ecosystem drivers in the shifts describing ecosystem state.

5.2. Material and methods

5.2.1. Study site

The PCSE is situated in the northeast Atlantic between 36.5° and 42°N and between 10.5° and 7.5°W (Figure 5.1) and covers an area of around 25,000 km². Sea surface temperature (SST) in the Portuguese shelf waters varied from 13°C and 17°C in the north and 15°C and 21°C in the south in the winter and summer, respectively. The western Portuguese coast is affected by seasonal upwelling that occurs during spring and summer due to steady northerly winds (Wooster et al. 1976; Fiúza et al. 1982). Also, the Iberian Peninsula is influenced by mid-term atmospheric phenomena such as Atlantic Multidecadal Oscillation (AMO) and North Atlantic Oscillation (NAO) (Trigo et al. 2004; Santos et al. 2011).

In the Portuguese continental shelf, the most important fishing fleet in terms of volume of catch is the purse seine while the fleets that target more valuable species and are important due to the value of catch as opposed to volume, are bottom-trawl and multi-gear fleet. Purse-seine fisheries target mainly pelagic fish, where the most landed species are sardine (*Sardina pilchardus*), chub mackerel (*Scomber colias*) and horse mackerel (*Trachurus trachurus*) (INE 2018). According to National Portuguese Statistical Institute (INE) statistics, bottom-trawlers that operate on the continental shelf target finfish while the multi-gear fleet targets sardine (but its catch is negligible), cephalopods, bivalves and crustaceans.

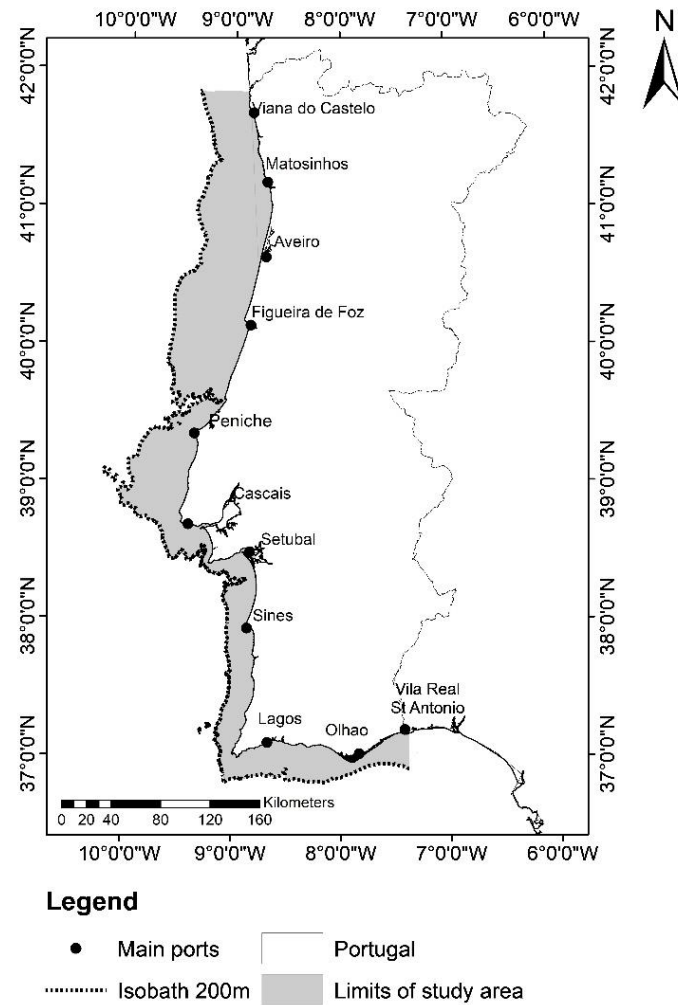


Figure 5.1 Map showing limits of the study area (200 m isobath).

5.2.2. Data and model

To test the hypothesis of the occurrence of regime shifts in the PCSE during the last 30 years, we used data describing ecosystem drivers that include (1) fishing mortality, (2) environmental variables and climatic indices, and data describing ecosystem state that includes (1) observed biomass, (2) modelled biomass and (3) ecosystem indicators (Table 5.1, Figure 5.2).

Table 5.1 Groups of data used in Integrated Trend Analysis (ITA) and their sources. For functional groups that consist of one species, a Latin name was provided in the brackets. For other functional groups, the list of species that are aggregated into the group is provided in Table A5.1 in annex 5).

Data groups	Source
Ecosystem drivers	
Fishing mortality	
Demersal piscivorous fish, Rays, Benthopelagic piscivorous fish (BFP), Sparids, Bogue (<i>Boops boops</i>), Horse mackerel (<i>Trachurus trachurus</i>), Benthopelagic invertivorous fish (BFI), Mackerel (<i>Scomber scombrus</i>), Blue jack mackerel (<i>Trachurus picturatus</i>), Anchovy (<i>Engraulis encrasicolus</i>), Sardine (<i>Sardina pilchardus</i>), Hake (<i>Merluccius merluccius</i>)	Stock reduction analysis (SRA) output ICES Stock assessment output (ICES, 2018ab) An estimate of fishing mortality (F)
Environmental/climatic variables	
<u>Environmental variables</u>	
Sea surface temperature (SST)	Met Office (https://www.metoffice.gov.uk/hadobs/sst3data)
Upwelling Index (UI)	Spanish Institute of Oceanography (IEO) (http://www.ieo.es/interactivo.html)
<u>Climatic indices</u>	
Atlantic Multidecadal Oscillation (AMO)	NOAA Earth System Research Laboratory (http://www.esrl.noaa.gov/psd/data/timeseries/AMO)
North Atlantic Oscillation (NAO)	NOAA Climate Prediction Centre-National Weather Service (http://www.cpc.ncep.noaa.gov/data/teledoc/ea.shtml)
Eastern Atlantic pattern (EA)	NOAA Climate Prediction Centre-National Weather Service (http://www.cpc.ncep.noaa.gov/data/teledoc/ea.shtml)
Ecosystem state	
Observed biomass	
<u>Demersal community</u>	
Hake (<i>Merluccius merluccius</i>),	Stock assessment output, (ICES 2018a) An estimate of ICES spawning stock biomass (SSB)
Benthic cephalopods, Sharks, Demersal invertivorous fish, Flatfish	BT survey
Rays, Demersal piscivorous fish (DFP), Sparids	Stock reduction analysis output
<u>Pelagic community</u>	
Adult and juvenile sardine (<i>Sardina pilchardus</i>), Horse mackerel (<i>Trachurus trachurus</i>),	Stock assessment output (ICES 2018b) For adult sardine and horse mackerel: an estimate of ICES spawning stock biomass (SSB) For juvenile sardine estimate of ICES recruitment
Squids,	BT survey
Chub mackerel (<i>Scomber colias</i>),	Acoustic survey
Bogue (<i>Boops boops</i>), Mackerel (<i>Scomber scombrus</i>), Blue jack mackerel (<i>Trachurus picturatus</i>), Anchovy (<i>Engraulis encrasicolus</i>)	Stock reduction analysis output
<u>Benthopelagic community</u>	
Benthopelagic piscivorous fish (BFP), Benthopelagic invertivorous fish (BFI)	Stock reduction analysis output

Modelled biomass

Mammals and birds

Bottlenose dolphin, Harbour porpoise, Stripped dolphin, EwE model output
Seabirds, Common dolphin, Minke whale

Demersal community

Hake (*Merluccius merluccius*), Rays, Sharks, Demersal EwE model output
invertivorous fish (DFI), Demersal piscivorous fish (DFP),
Benthic Cephalopods, Sparids, Flatfish

Pelagic community

Tunas, Squids, Bogue (*Boops boops*), Chub mackerel EwE model output
(*Scomber colias*), Horse mackerel (*Trachurus trachurus*),
Mackerel (*Scomber scombrus*), Blue jack mackerel
(*Trachurus picturatus*), Anchovy (*Engraulis encrasicolus*),
Juvenile sardine, Adult sardine (*Sardina pilchardus*)

Benthopelagic community

Benthopelagic piscivorous fish (BFP), Benthopelagic EwE model output
invertivorous fish (BFI)

Invertebrates and Plankton

Henslow's crab (*Polydora henslowii*), Shrimps, EwE model output
Macrozoobenthos, Suprabenthic invertebrates,
Macrozooplankton, Meso/Microzooplankton,
Phytoplankton

Ecosystem indicators

Biomass-based

Demersal per pelagic biomass (Dem/Pel B), Predatory EwE model output
biomass (Pred B), Kempton's index (Kempton Q), Shannon
diversity index (Shannon)

Catch-based

Total catch (Tot C), Demersal per pelagic catch (Dem/Pel EwE model output
C), Predatory catch (Pred C), Pelagic catch (Pel C),
Demersal catch (Dem C)

Trophic-based

Mean trophic level of the catch (mTLc), Mean trophic level EwE model output
of the community (mTLco)

Ecological network analysis (ENA)

Relative ascendancy (A/C), Finn's cycling Index (FCI), EwE model output
Turnover rate (TotP/TotB), Entropy (H), Redundancy (R)

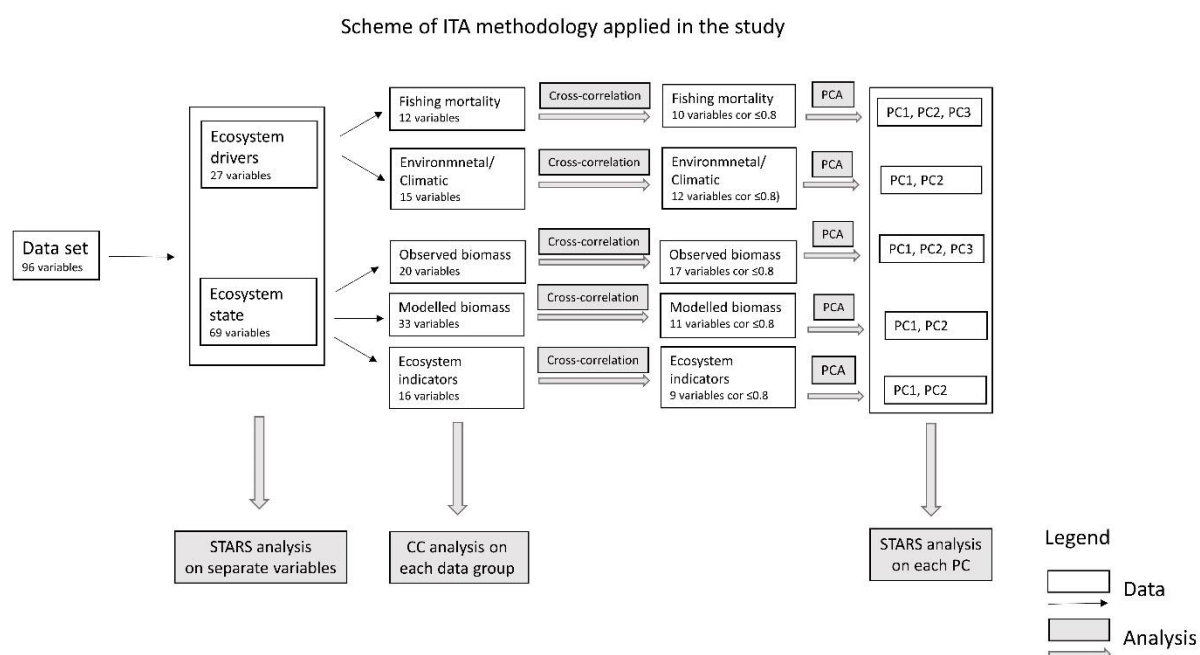


Figure 5.2 Scheme of Integrated Trend Analysis (ITA) methodology applied in this study.

Fishing mortality and observed biomass data used in this study were also used as inputs of the EwE model, describing the PCSE between 1986 and 2017. The static version of this model was developed by Veiga-Malta et al. (2019) (chapter 3) and further updated and fitted to 32 years of time-series data by Szalaj et al. (2021) (chapter 4). Moreover, modelled biomass and ecosystem indicators data used in the study come as an output of this EwE model.

The model was developed using the EwE modelling software that uses a set of differential equations to describe the ecosystem's food web structure, its functioning, and dynamics. It has been described in detail by Christensen and Pauly (1992); Pauly et al. (2000); Christensen and Walters (2004) (www.ecopath.org). Using EwE data to assess the PCSE, allows for the integration of time-series data into the analysis that are not available from other sources, such as biomass of lower trophic level species and marine mammals. The EwE model estimated these groups and using them in the ITA provides a more complete picture of the studied ecosystem. In addition, the EwE model provided an extensive suite of indicators describing the ecosystem's properties, its structure and functioning. The use of these data allows for the assessment of the changes that occurred in the PCSE at the whole ecosystem level. Model description and details regarding model parametrization are available in the study by Szalaj et al. (2021) (chapter 4). In summary, the model covers the area of the Portuguese Continental Shelf (0–200 m; ICES subdivisions 9a), consists of 33 functional groups (Figure

5.3) and includes three fishing fleets: bottom trawl, pelagic and multi-gear. Functional groups aggregate the species that live in a similar environment and have a similar diet. A detailed description of species that comprise each functional group is available in Table A5.1 in annex 5.

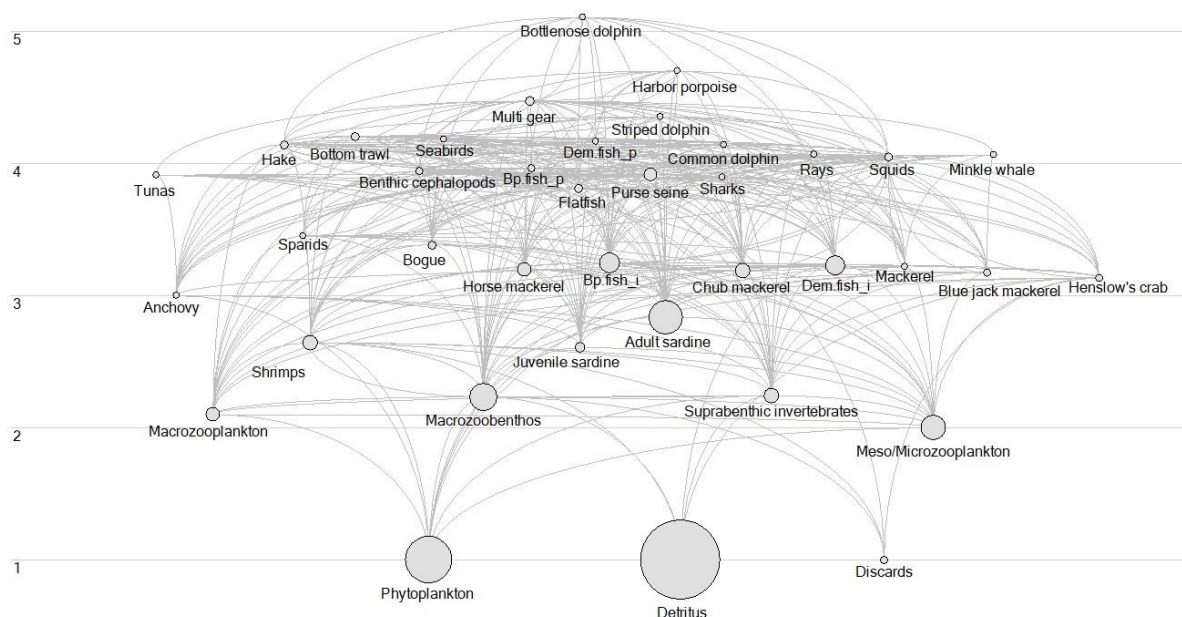


Figure 5.3 Flow diagram of the Portuguese Continental Shelf Ecosystem (PCSE) in 1986. The list of species and functional groups are described in Veiga-Malta et al. (2019) (chapter 3). Bp.fish_p: Benthopelagic piscivorous fish; Bp.fish_i: Benthopelagic invertivorous fish; Dem.fish_i: Demersal invertivorous fish; Dem.fish_p: Demersal piscivorous fish and Suprabenthic inv: Suprabenthic invertebrates-

5.2.2.1. Ecosystem drivers data

Data describing ecosystem drivers consisted of two data groups: (1) fishing mortality and (2) environmental variables and climatic indices (Table 5.1).

Fishing mortality (F) data for the majority of functional groups was calculated using Stock reduction analysis (SRA, Kimura et al. 1984) and implemented as a stochastic SRA (Walters et al. 2006) while F for sardine and hake was obtained from stock assessment outputs (ICES 2018ab). A detailed description of the SRA methodology and obtained results are provided in annex 4.

Environmental variables consisted of annual, summer and winter means of Sea surface temperatures (SST) and Upwelling Index (UI) while climatic indices included annual, summer

and winter means of Atlantic Multidecadal Oscillation (AMO), North Atlantic Oscillation (NAO) and Eastern Atlantic pattern (EA).

5.2.2.2. Ecosystem state data

Data describing ecosystem state consisted of three data groups: (1) observed biomass; (2) modelled biomass and (3) ecosystem indicators.

5.2.2.3. Observed biomass data

Observed biomass data consisted of the biomass data aggregated into 20 functional groups (Table 5.1). These data were used to calibrate the PCSE EwE model between 1986-2017 (Szalaj et al. 2021; chapter 4). When possible, we used the outputs of stock assessment models as biomass estimates (i.e., sardine, hake and horse mackerel). For other species, when enough data were available, we estimated plausible biomass (B_{SRA}) trends using SRA. For the majority species (demersal piscivorous fish, rays, sparids, bogue, benthopelagic invertivorous and piscivorous fish, mackerel, blue jack mackerel) we used bottom trawl (BT) survey data as abundance estimates for SRA input, with the exception of anchovy for which we used abundance estimates obtained from acoustic surveys. For species that lacked sufficient data to perform an SRA, the abundance index trends were taken directly from BT surveys (sharks, squids, benthic cephalopods, flatfish, demersal invertivorous fish), with exception of the biomass for chub mackerel which was taken from an acoustic survey. Portuguese bottom trawl surveys are carried out in autumn (September-October) at predefined stations in the Portuguese Exclusive Economic Zone at depths varying from 20 m to 500 m depth (ICES 2017b). In this study, only data that referred to the continental shelf (depth <200 m) was considered. BT survey biomass estimates were calculated using the swept area method. Portuguese acoustic surveys (PELAGO survey series) are performed annually in spring (April-May) in an area that covers the Portuguese continental shelf. Acoustic fish data were obtained following the methodology described in ICES (2016) by performing echo-integration along 1 nm Elemental sampling distance unit (ESDU, distance measure used in acoustic surveys) and supported by fish sample collection. Both acoustic and BT surveys were performed by the Portuguese Institute of Sea and Atmosphere (IPMA).

5.2.2.4. Modelled biomass data

Modelled biomass data for 33 functional groups that range from plankton to marine mammals (Figure 5.3, Table 5.1) were obtained from the EwE model fitted to the time series for the PCSE between 1986–2017 (chapter 4; Szalaj et al. 2021). A full list of functional groups used in this study is presented in Table A5.1 in annex 5.

5.2.2.5. Ecosystem indicators data

Various indicators that describe ecosystem properties were extracted from the EwE model fitted to the time series for the PCSE between 1986–2017. Among the available indices, 16 indicators that represent distinctive processes, were used in the analysis. They are: (1) Demersal per pelagic biomass (Dem/Pel B); (2) Predatory biomass (Pred B); (3) Kempton's index (Kempton Q); (4) Shannon diversity index (Shannon); (5) Total catch (Tot C); (6) Demersal per pelagic catch (Dem/Pel C); (7) Predatory catch (Pred C); (8) Pelagic catch (Pel C), (9) Demersal catch (Dem C); (10) Mean trophic level of the catch (mTLc); (11) Mean trophic level of the community (mTLco); (12) Relative ascendancy (A/C); (13) Finn's cycling index (FCI); (14) Turnover rate (TotP/TotB); (15) Entropy (H) and (16) Redundancy (R). Their definitions are presented in Table 5.2.

Table 5.2 Ecosystem indicators calculated from Ecopath with Ecosim (EwE), that describe the Portuguese Continental Shelf ecosystem (PCSE) between 1986 and 2017.

Ecosystem indicators		Definition	Description
Biomass-based indicators			
1	Demersal per pelagic biomass (Dem/Pel B)	Sum of the biomass of demersal species/sum of the biomass of pelagic species	Explores processes benefiting the demersal or pelagic compartments of the ecosystem. In general, this ratio is expected to increase with fishing (Cury et al. 2005).
2	Predatory biomass (t km ⁻² year ⁻¹) (Pred B)	Sum of the biomass of all species with a trophic level ≥ 4	Includes biomass of all the groups with TL≥4 and tends to decrease with increasing fishing pressure in marine ecosystems (Rochet and Trenkel 2003).
3	Kempton's index (Kempton Q)	$Kempton\ Q = Q90 = \frac{0.8S}{\log(\frac{R_2}{R_1})}$	Where: S is the total number of functional groups in the model; R1 and R2 are the representative biomass values of the 10th and 90th percentiles in the cumulative abundance distribution. It defines the inverse slope of the species-abundance curve. Describes diversity by considering functional groups with TL≥3. This indicator tends to decrease with

			ecosystem degradation (Kempton and Taylor 1976).
4	Shannon diversity index (Shannon)	$Shannon = - \sum_{i=1}^N p_i \ln p_i$	Where N is the total number of species in the community ecosystem, p_i is the proportion of total abundance represented by species i . The Shannon index increases as both the richness and the evenness of the community increase.
Catch-based indicators			
5	Total catch (t km ⁻² year ⁻¹) (Tot C)	$Tot C = \sum_i Y_i$	Where Y_i is the yield of compartment/species i . Includes total landings and discards of the different fleets and provides an idea of the overall fishing impact on the ecosystem (Pauly et al. 1998).
6	Demersal per pelagic catch (Dem/Pel C)	Sum of the catch of all demersal species/sum of the catch of all pelagic species	Explores fishing strategy and assess its focus on the demersal vs pelagic compartment.
7	Predatory catch (t km ⁻² year ⁻¹) (Pred C)	Sum of the catch of all species with a trophic level ≥ 4	Expresses the catch of the groups with TL ≥ 4 . It tends to increase with increasing fishing impact in the marine ecosystem.
8	Pelagic catch (t km ⁻² year ⁻¹) (Pel C)	Sum of the catch of all pelagic species	Includes total landings and discards of the fleets directed towards pelagic species. It provides an idea of the fishing impact on the pelagic ecosystem.
9	Demersal catch (t km ⁻² year ⁻¹) (Dem C)	Sum of the catch of all demersal species	Includes total landings and discards of the fleets directed towards demersal species. It provides an idea of the fishing impact on the demersal ecosystem.
Trophic-based indicators			
10	Mean trophic level of the catch (mTLc)	$mTLc = \frac{\sum_i TL_i \cdot Y_i}{\sum_i Y_i}$ $TL_j = 1 + \sum_j DC_{ij} \cdot TL_i$	Where Y_i is the yield of compartment i ; TL_i is the trophic level of that compartment; TL_j is the trophic level of predator j ; TL_i is a trophic level of prey i and DC_{ij} is the proportion of prey i in the diet of predator j . Expresses the Trophic Level (TL) of the catch, reflects the fishing strategy of the fleet and is used to quantify the impact of fishing (Pauly et al. 1998). It is expected to decrease with the increase of fishing (Shannon et al. 2009).
11	Mean trophic level of the community (mTLco)	$mTLco = \sum_i TL_i \frac{B_i}{B}$	Where TL_i is the trophic level of species B_i is the species biomass and B is the total biomass. Describes the TL and reflects the structure of the ecosystem. It is used to quantify the impact of fishing (Rochet and Trenkel 2003).
Ecological network analysis (ENA) indicators			
12	Relative ascendancy (%) (A/C)	$A = \sum_{i,j} (T_{ij}) \cdot \log \left(\frac{T_{ij} \cdot TST}{T_j \cdot T_i} \right)$ $C = \sum_{ij} T_{ij} \log \left(\frac{T_{ij}}{TST} \right)$	Where A is ascendancy where T_{ij} is the flow between two compartments i and j and it includes all outflows from each compartment, T_i is the sum of all material leaving the i th compartment, and T_j is the sum of all flows entering the j th compartment. C is the development capacity where TST is the sum of all flows T_{ij} in the system. Relative ascendancy is an index of the organisation of the food web (Ulanowicz

			1986). It is negatively related to maturity (Christensen 1995) which is related to the system's growth and development (Ulanowicz 1986).
13	Finn's cycling index (%) (FCI)	$FCI = \frac{TST_c}{TST_{tot}}$	Finn's cycling index is the proportion of the total system throughput (TST_{tot}) that is recycled in the system (TST_c). Quantifies the relative amount of recycling in the system and is an indicator of stress and structural differences (Finn, 1976). It is considered an indicator of ecosystem's ability to maintain its structure and integrity (Monaco and Ulanowicz 1997) and an indicator of stress (Ulanowicz 1986). An increase in FCI would suggest that the system has a capability to recover faster from a perturbation, due to an increased system's recycling and consequently higher capacity to conserve nutrients. It is important to keep in mind that a system would be expected to take longer to recover (lower FCI) when it is in a more degraded state (Vasconcellos et al. 1997).
14	Turnover rate (TotP/TotB)	The total Production / Total Biomass ratio	System turnover rate is an indicator of the average size of organisms in an ecosystem (Shannon et al. 2009). It is hypothesized that fishing reduces the mean size of organisms in ecosystems therefore the turnover rate is expected to increase with fishing (Shannon et al. 2009).
15	Entropy (H)	$H = - \sum_{ij} \frac{T_{ij}}{TST} * \log \left(\frac{T_{ij}}{TST} \right)$	Where T_{ij} is the flow between two compartments and TST is the sum of all flows in the system Entropy represents the total number and diversity of flows in the system (Mageau et al. 1998). The diversity of flows is similar to diversity assessed by the Shannon diversity index (Shannon-Wiener) but considered flows instead of abundance (Ulanowicz and Norden 1990).
16	Redundancy (R)	$R = - \sum_{i=1}^n \sum_{j=1}^n (T_{ij}) \cdot \log \left(\frac{T_{ij}^2}{\sum_{j=1}^n T_{ij} \cdot \sum_{i=1}^n T_{ij}} \right)$	Where: T_{ij} is the flow between two compartments. This index is considered as an index of the system's resilience (Heymans et al. 2007) and it has been linked with ecosystem stability (Christensen 1995). It describes the distribution of energy flow pathways in the system. If the R is high, it indicates that they are many alternative pathways for energy flows to get from one compartment/functional group to another that allows compensation for the environmental stress, while lower R indicate that flows are constrained and energy is channelled through more specific pathways.

5.2.3. Integrated analysis

Data described in subsection 2.2. was subjected to an Integrated Trend Analysis (ITA) that was performed using the method described by Diekmann and Möllmann (2010) (Figure 5.2). It integrates the following statistical methods: (1) Principal Component Analysis (PCA); (2) Sequential t-test Analysis of Regime Shifts (STARS; Rodionov 2004) and (3) Chronological Clustering (CC; Legendre et al. 1985). The PCA and CC analyses were performed using R (R Core Team, 2020), packages *vegan* (Oksanen et al. 2019) and *rioja* (Juggins 2020). The script was obtained from Diekmann et al. (2012). The STARS analysis was performed using STARS software written in Visual Basic for Application (VBA) Excel 2002, available at: sites.google.com/climateologic/download.

The PCA, based on the correlation matrix, was performed separately on fishing mortality data (PCA_FM), environmental/climatic variables (PCA_ENV_CLIM), observed biomass (PCA_B_obs), modelled biomass (PCA_B_model) and ecosystem indicators (PCA_indices). Before analysis, each dataset was checked for cross-correlation (Pearson) and variables that are highly correlated (>0.8 , Table A5.2–A5.6 in annex 5) were excluded from the PCA. The list of the variables included in the PCA analysis is shown in Table 5.3.

Table 5.3 Variables used in Principal Components Analysis (PCA) after selection process (criteria for selection: cross-correlation ≤ 0.8).

Name of PCA analysis	PCA_FM	PCA_ENV_CLIM	PCA_B_obs	PCA_B_model	PCA_indices
Type of data used in PCA analysis	Ecosystem drivers		Ecosystem state		
	Fishing mortality	Environmental/ climatic variables	Observed biomass	Modelled biomass	Ecosystem indicators
Variables used in PCA analysis (Cor≤ 0.8)	Sardine	SSTm	Adult sardine	Adult sardine	Dem/Pel B
	Anchovy	SSTw	Juvenile sardine	Juvenile sardine	Shannon
	Horse mackerel	AMOm	Anchovy	Anchovy	Tot C
	Mackerel	NAOm	Chub mackerel	Horse mackerel	Pred C
	Blue jack mackerel	NAOw	Mackerel	Hake	TL catch
	Hake	NAOs	Blue jack mackerel	Rays	R
	Rays	EAm	Tunas	Benthopelagic invertivorous fish	FCI
	Benthopelagic piscivorous fish	EAw	Hake	Benthic Cephalopods	H
	Benthopelagic invertivorous fish	EAs	Rays	Squids	TotP/TotB
	Demersal piscivorous fish	UIm	Benthopelagic piscivorous fish	Stripped dolphin	
		UIw	Benthopelagic invertivorous fish	Suprabenthic invertebrates	
		UIs	Demersal invertivorous fish		
			Sparids		
			Flatfish		
			Sharks		
			Benthic cephalopods		
			Squids		
Number of variables used	10	12	17	11	9

The number of meaningful principal components (PC) that were considered further in the analysis was assessed by the *scree plot* that shows how much variation each PC captures from the data and the *broken stick plot* that demonstrates how many PCs should be retained. Also, variable loadings for each meaningful PC were checked and the variables whose loadings values were < 0.3 were excluded from further analysis. Year scores for the meaningful principal

components (mainly PC1 and PC2) were plotted against time to display temporal relationships (PC trends). Then PC trends were subjected to STARS analysis to detect the occurrence of regime shifts in the ecosystem. Moreover, the relationship between PC trends extracted from the data describing ecosystem state and ecosystem drivers were explored with cross-correlation (Spearman correlation).

To identify significant shifts in mean values of a given time series, STARS was performed separately on each time series of the whole dataset and on the time series of PC scores (PC trends). The STARS method is based on a sequential analysis of change points in the time series using the Student t-test. At each observation, the procedure calculates a Regime Shift Index (RSI) to determine whether the following observation values are significantly different from the mean of the previous regime. The method and its use in the detection of shifts in marine systems were discussed in Strinimann et al. (2019). In order to account for serial correlations (red noise component), the prewhitening procedure that adjusts the significance level of the shifts by calculating effective degrees of freedom, described in Rodionov (2006), was used. In this study, the red noise component was modelled by the first-order autoregressive model (AR1) and estimated based on the ordinary least squares (OLS) as suggested by Marriot and Pope (1954) and Kendall (1954). Parameters that control the scale and magnitude of potential regime shifts (significance level and cut-off length) and weights assigned to outliers (Huber's weight parameter) were set a priori to 0.05, 10 and 3 respectively according to Tomczak et al. (2013) and Heymans and Tomczak (2016). The magnitude of the detected regime shifts was assessed using RSI when the positive value indicates an increase and the negative value indicates a decrease.

The CC discontinuity analysis is a clustering technique that groups only sequential samples and has been used to identify the abrupt changes in time-series. It is used for multivariate datasets and clustering is based on the calculation of a similarity matrix of the time-series based on Euclidian distances. The CC analysis was performed separately on the same data groups as the PCA (fishing mortality, environmental/climatic variables, observed biomass, modelled biomass and ecosystem indicators). According to Diekmann and Möllmann (2010), the significance level α (considered as a clustering-intensity parameter) and connectedness level were set to 0.01 and 50% respectively. To make results interpretable in relation to PCA, data were standardised prior to the calculation of the similarity matrix.

5.3. Results

5.3.1. Ecosystem changes, key functional groups, and key drivers (PCA)

In PCA_FM that included fishing mortality variables, three PCs that in total explained 72.8% of variance were retained (Table 5.4).

Table 5.4 Contribution of each variable to meaningful principal components for each PCA performed. Loadings values in bold showed the highest contribution.

Variable abbreviation	Variable name	Meaningful PCs loadings			
PCA_FM	PCA on fishing mortality	PC1	PC2	PC3	Total
Variance Explained (%)		33.8	22.7	16.2	72.8
F_DFP	Demersal piscivorous fish	1.2	-0.4	0.1	
F_Rays	Rays	1.3	0.2	0.0	
F_BFP	Benthopelagic piscivorous fish	1.0	-0.8	-0.2	
F_HOM	Horse mackerel	0.8	0.4	0.8	
F_BFI	Benthopelagic invertivorous fish	0.2	0.8	-0.6	
F_MAC	mackerel	0.8	0.9	0.3	
F_JAA	Blue jack mackerel	-0.6	-0.6	0.7	
F_ANE	Anchovy	0.2	-0.8	0.7	
F_PIL	Sardine	0.3	0.0	-0.5	
F_HKE	Hake	0.4	-0.8	-0.8	
PCA_ENV_CLIM	PCA on environmental/climatic variables	PC1	PC2		
Variance Explained (%)		31.2	23.4		54.6
AMOm	Annual average of Atlantic multidecadal oscillation	1.0	-0.2		
NAOm	Annual average of North Atlantic oscillation	-0.7	0.9		
NAOw	Winter average of North Atlantic oscillation	-0.3	1.1		
NAOs	Summer average of North Atlantic oscillation	-0.5	-0.1		
EAm	Annual average of Eastern Atlantic pattern	1.0	0.3		
EAw	Winter average of Eastern Atlantic pattern	0.5	0.2		
EAs		1.0	0.3		
SSTm	Annual average Sea surface temperature	0.9	0.7		
SSTw	Winter average Sea surface temperature	0.6	0.8		
UI_m	Annual average Upwelling index	-0.2	0.7		
UI_w	Winter average Upwelling index	-0.6	0.9		
UI_s	Summer average Upwelling index	0.7	-0.2		
PCA_B_obs	PCA on observed biomass	PC1	PC2	PC3	
Variance explained (%)		34.1	23.1	16.1	80.7
B_ANE_o	Anchovy	-0.8	0.6	-0.1	
B_PIL_o	Adult sardine	1.0	-0.1	-0.1	

B_PIL_Juv_o	Juvenile sardine	1.0	0.0	0.0
B_MAC_o	Mackerel	-1.1	-0.2	0.0
B_MASo	Chub mackerel	-0.5	-0.5	-0.3
B_Sparids_o	Sparids	-1.1	-0.2	0.0
B_Flatfish_o	Flatfish	0.1	0.2	0.9
B_Hake_o	Hake	0.1	1.1	-0.2
B_JAA_o	Blue jack mackerel	-0.5	0.7	-0.3
B_DFI_o	Demersal invertivorous fish	-0.2	0.4	1.0
B_BFI_o	Benhopelagic invertivorous fish	0.8	0.3	0.3
B_BFP_o	Benthopelagic piscivorous fish	-0.2	1.0	-0.1
B_Ben_Ceph_o	Benthic cephalopods	0.0	-0.2	0.9
B_Squids_o	Squids	0.4	0.9	0.1
B_Rays_o	Rays	-1.0	0.5	0.1
B_Sharks_o	Sharks	-0.2	0.1	0.9
B_Tunas_o	Tunas	0.8	0.7	-0.2
PCA_B_model	PCA on modelled biomass	PC1	PC2	
Variance explained (%)		47.0	32.4	79.4
B_Supra_inv_m	Suprabenthic invertebrates	-0.3	-0.9	
B_PIL_m	Adult sardine	0.9	-0.7	
B_PIL_Juv_m	Juvenile sardine	0.9	-0.7	
B_ANE_m	Anchovy	-1.0	-0.4	
B_BFI_m	Benthopelagic invertivorous fish	0.1	-1.1	
B_HOM_m	Horse mackerel	-1.3	0.0	
B_Ben_Ceph_m	Benthic cephalopods	-1.1	0.1	
B_Squids_m	Squids	-1.2	0.1	
B_Rays_m	Rays	-1.1	-0.6	
B_Hake_m	Hake	0.1	-1.2	
B_Stripped_dolphin_m	Stripped dolphin	-0.5	-0.9	
PCA_indices	PCA on ecosystem indicators	PC1	PC2	
Variance explained (%)		51.0	33.7	84.7
Dem_Pel B	Demersal per Pelagic biomass	-1.3	0.2	
Shannon	Shannon diversity index	-1.0	0.1	
Tot C	Total catch	-1.0	0.8	
Pred C	Predatory catch	-0.6	1.1	
mTLc	The trophic level of the catch	1.1	0.0	
R	Redundancy	-0.7	-1.2	
FCI	Fins cycling index	-1.2	-0.5	
H	Entropy	-0.2	1.3	
TotP_TotB	Turnover rate	-1.1	-0.6	

The time trajectory of PC1_FM presented a relatively stable trend until around 1998, followed by a decrease till the end of the study period (Figure 5.4a). Variables that contributed

the most and positively related to this PC trend were fishing mortality of demersal piscivorous fish and rays (Table 5.4).

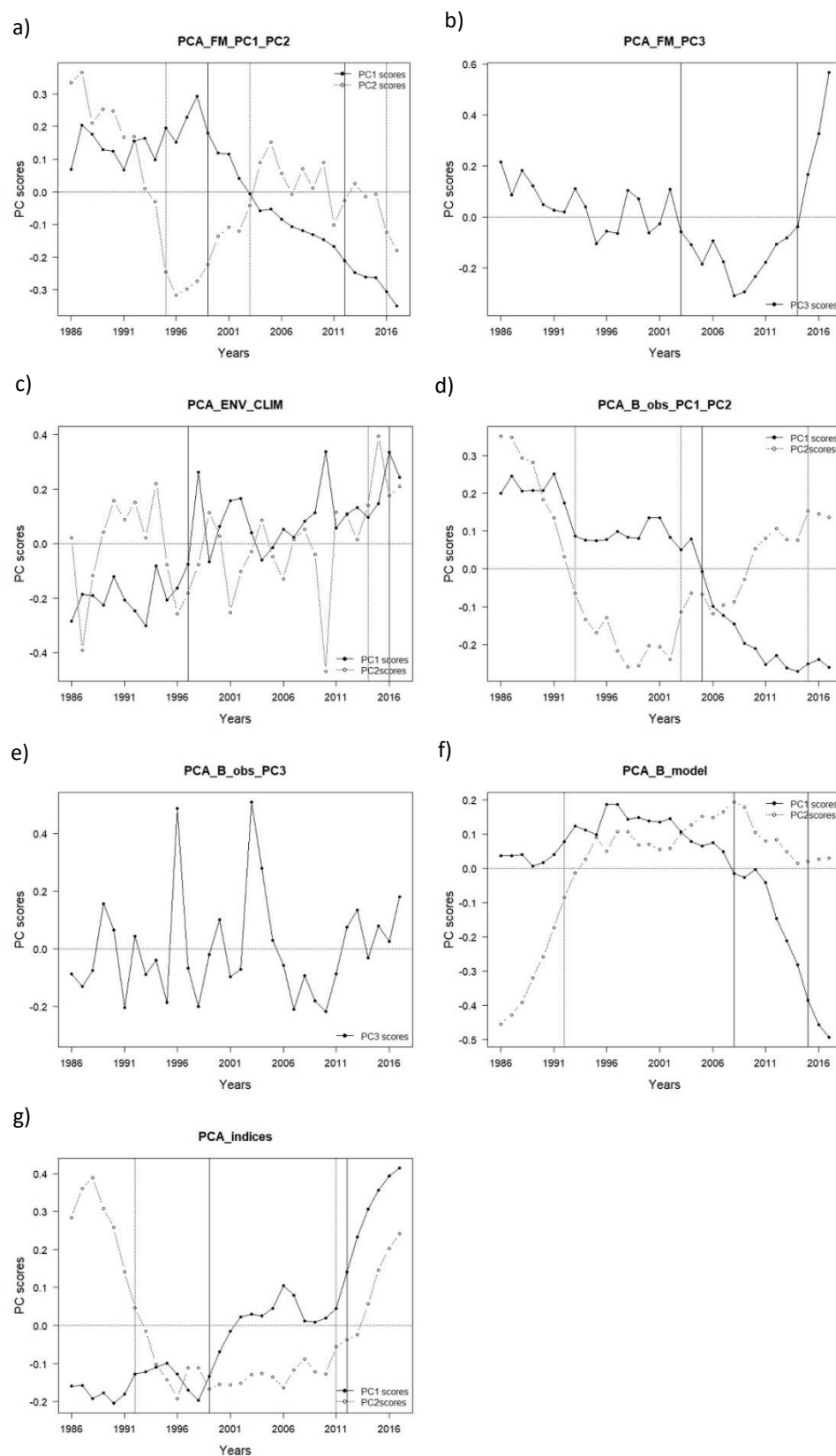


Figure 5.4 Results of Principal Component Analysis (PCA); Time-trajectory of PC scores of PCA performed on a) fishing mortality PC1 and PC2 (PCA_FM_PC1_PC2); b) fishing mortality PC3 (PCA_FM_PC3); c) environmental/climatic variables PC1 and PC2 (PCA_ENV_CLIM) ; d) observed biomass PC1 and PC2 (PCA_B_obs_PC1_PC2); e) observed biomass PC3 (PCA_B_obs_PC3); f) modelled biomass PC1 and PC2 (PCA_B_model); g) ecosystem indicators PC1 and PC2 (PCA_indices) (black dots – PC1, PC3 white dots - PC2).

The trend of PC2_FM showed an initial decrease until 1996, followed by an increase till 2006 and a further slight decrease until the end of the study period (Figure 5.4 a). The variables that positively contributed to this trend were fishing mortality of benthopelagic invertivorous fish and mackerel, while fishing mortality of benthopelagic piscivorous fish, anchovy and hake contributed negatively (Table 5.4).

The trend of PC3_FM showed an initial gradual decrease with time till about 2008, followed by a sharp increase till the end of the study period (Figure 5.4 b). The variables that contributed positively to this PC trend were fishing mortality of blue jack mackerel, horse mackerel (both positively) and sardine (negatively) (Table 5.4).

In the PCA_ENV_CLIM that included environmental/climatic variables, two retained PCs explained in total 54.6% of the variance (Table 5.4). The trend of PC1_ENV_CLIM showed a gradual increase with time and variables SST, AMO and EA showed the largest positive contribution to this trend (Table 5.4, Figure 5.4 c). The time trajectory of PC2_ENV_CLIM fluctuated till 2010 without any clear trend, then increased substantially (Figure 5.4 c). This trend was mainly explained by NAO and Upwelling index (both annual and winter averages) (Table 5.4).

In the PCA_B_obs that included EwE input biomass data, three retained PCs explained 73.5% of the variance (Table 5.4). The time trajectory of PC1_B_obs which explained 33.8% of the variance, showed a decreasing trend that represented the biomass trend of sardine and benthopelagic invertivorous fish (Table 5.4, Figure 5.4 d). The variables that showed an opposite trend to PC1_B_obs were pelagic fish (anchovy and mackerels), sparids and rays (Table 5.4). Time trajectory of PC2_B_obs that explained 23.7% of the variance and showed an initial sharp decrease until 1998 followed by an increase (Figure 5.4 d) represented the biomass trend for blue jack mackerel, hake, benthopelagic piscivorous fish and squids (Table 5.4). The trend of PC3_B_obs that explained 15.9% of the variance, did not show any clear tendency and reflected the biomass of demersal invertivorous fish and benthic cephalopods (Table 5.4, Figure 5.4 e).

In the PCA_B_model that included EwE output biomass data, two retained PCs explained 79.4% of the variance. The time trajectory of PC1_B_model fluctuated without any clear trend till around 2006, when it substantially decreased (Figure 5.4 f). It represented the modelled biomass trend for sardine (Table 5.4). The opposite trend was observed for other pelagics (horse mackerel and anchovy), cephalopods and rays. The trend of PC2_B_model

increased till 1996, then stabilised and fluctuated till the end of the study period (Figure 5.4 f). It reflected the opposite trend to modelled biomass of hake, benthopelagic invertivorous fish, suprabenthic invertebrates and striped dolphin (Table 5.4).

Both PC1_indices and PC2_indices explained 51.0% and 33.7% of the total variance respectively (Table 5.4). The time trajectory of PC1_indices showed an increasing trend (Figure 5.4 g) that reflected the trend of mTLc (Table 5.4). The opposite trend to PC1_indices was observed for Tot C, Dem/Pel B, diversity (Shannon), and ecological network analysis indices (FCI, and TotP/TotB) (Table 5.4). The trend of PC2_indices sharply decreased until 1996, stabilised and since 2010 increased again (Figure 5.4 g). The variables that reflected this trend were Pred C and H while R showed the opposite trend (Table 5.4).

5.3.2. Relationship between ecosystem drivers and ecosystem state

The PC trends extracted from the observed biomass data group showed significant correlations with PC trends extracted from fishing mortality and environmental/climatic data groups (Table 5.5). The statistical correlation was observed between PC1_B_obs and PC1_FM ($R=0.82$, $p<0.01$), PC1_ENV_CLIM ($R=-0.66$, $p<0.01$) and PC3_FM ($R=0.35$, $p=0.05$). The largest correlations for PC2_B_obs and PC3_B_obs were found for PC2_FM ($R=0.68$, $p<0.01$) and PC2_ENV_CLIM ($R=0.38$, $p=0.03$) respectively. A statistical correlation was also found between PC trends extracted from modelled biomass and ecosystem drivers' data (Table 5.5). Here, the PC1_B_model had the largest statistically significant correlation with PC1_FM ($R=0.76$, $p<0.01$) followed by PC2_ENV_CLIM ($R=-0.46$; $p<0.01$) and PC2_FM ($R=-0.38$, $p=0.03$). On the other hand, PC2_B_model shown the largest correlation with PC3_FM ($R=-0.78$, $p<0.01$), followed by PC1_ENV_CLIM ($R=0.43$, $p=0.01$) and PC2_FM ($R=-0.37$, $p=0.04$).

Table 5.5 Spearman cross-correlation between PCs extracted from different groups of data. Values in bold indicate significant correlations ($p \leq 0.05$).

	PC1_B_obs	PC2_B_obs	PC3_B_obs	PC1_B_model	PC2_B_model	PC1_FM	PC2_FM	PC3_FM	PC1_ENV_CLIM	PC2_ENV_CLIM	PC1_indices	PC2_indices
PC1_B_obs	1											
PC2_B_obs	0.02	1										
PC3_B_obs	-0.14	0.10	1									
PC1_B_model	0.55	-0.77	-0.06	1								
PC2_B_model	-0.44	-0.61	-0.20	0.19	1							
PC1_FM	0.82	-0.33	-0.20	0.76	-0.2	1						
PC2_FM	0.32	0.68	-0.09	-0.38	-0.37	-0.04	1					
PC3_FM	0.35	0.33	0.22	-0.02	-0.78	0.21	0.01	1				
PC1_ENV_CLIM	-0.66	-0.2	-0.03	-0.32	0.43	-0.62	-0.40	-0.16	1			
PC2_ENV_CLIM	-0.29	0.31	0.38	-0.46	-0.27	-0.41	0.02	0.27	0.02	1		
PC1_indices	-0.88	0.04	0.26	-0.52	0.34	-0.86	-0.22	-0.25	0.62	0.27	1	
PC2_indices	0.14	0.86	0.03	-0.62	-0.70	-0.11	0.55	0.54	-0.23	0.41	-0.14	1

Also, statistical correlations were found between the PC trends extracted from the ecosystem indicators data group and both types of ecosystem drivers (Table 5.5). PC1_indices had the largest correlation with PC1_FM ($R = -0.86$, $p < 0.01$) followed by PC1_ENV_CLIM ($R = 0.62$, $p < 0.01$) while PC2_indices showed the largest correlation with PC2_FM ($R = 0.55$, $p < 0.01$), PC3_FM ($R = 0.54$, $p < 0.01$) followed by PC2_ENV_CLIM ($R = 0.41$, $p = 0.02$).

5.3.3. Regime shift detection (STARS and CC)

Significant shifts detected by STARS were observed for many variables representing ecosystem drivers and ecosystem state (Figure 5.5; 5.6; 5.7; 5.8; Table A5.7 in annex 5).

Among fishing mortality variables, significant shifts in the mid-90s were observed for fishing mortality of sparids, bogue, mackerel, benthopelagic piscivorous fish and anchovy (Figure 5.5). The second shift in the mid-2000s was observed for fishing mortality of piscivorous fish, rays, sparids, and among small pelagic fish (SPF) for horse mackerel and anchovy (Figure 5.5). The last shift in the mid-2010s was observed for fishing mortality of all species (excluding fishing mortality of piscivorous fish and bogue).

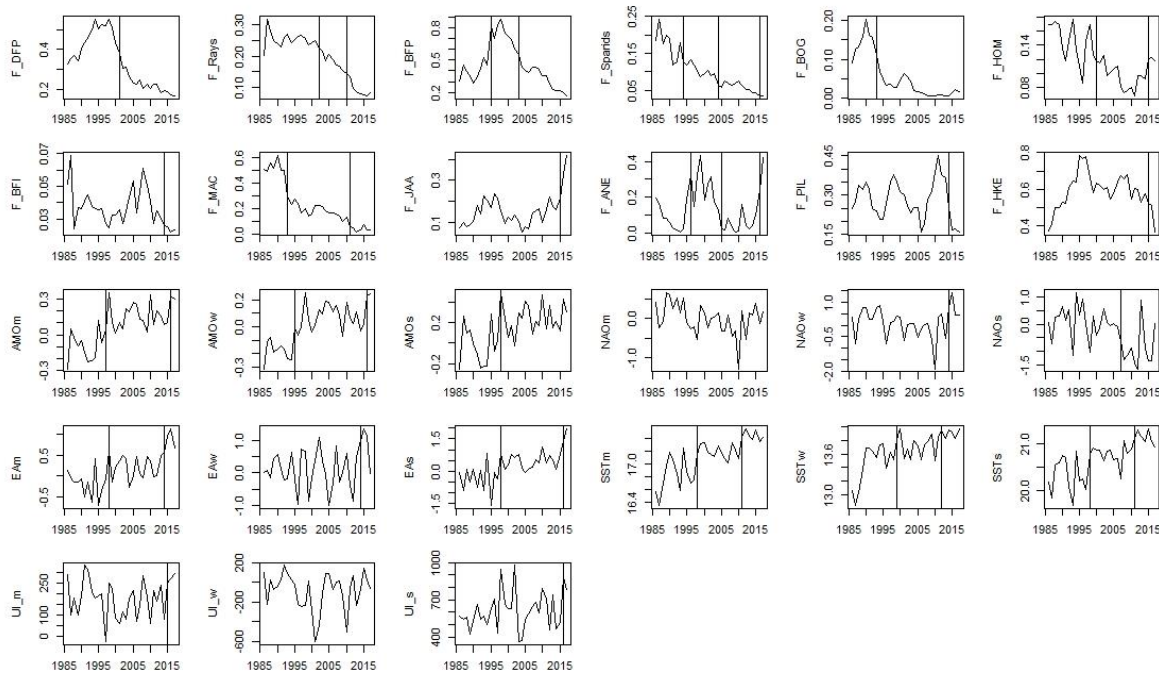


Figure 5.5 Time-series of ecosystem drivers data that includes fishing mortality and environmental/climatic variables. Significant shifts detected by STARS analysis are displayed on the plots as solid and dashed vertical line for shifts significant at $p \leq 0.05$ and $p \leq 0.1$, respectively. Abbreviations, used in the figure, are explained in Table A5.7 in annex 5.

Considering environmental/climatic variables, STARS detected significant shifts in the SST, AMO, EA in the mid-90s, followed by mid-2010s (2011–2016) (Figure 5.5). For NAO and UI, STARS detected only one shift in the mid-2010s (2014–2016) (Figure 5.5).

Among observed biomass variables, STARS detected significant shifts in the mid-90s for sardine, anchovy, mackerel, sparids, piscivorous fish, squids and hake. The second shift in the mid-2000s was observed for benthopelagic invertivorous fish, bogue, sparids and rays. The last shift in the mid-2010s was observed for benthopelagic invertivorous fish and SPF (horse mackerel and bogue) (Figure 5.6).

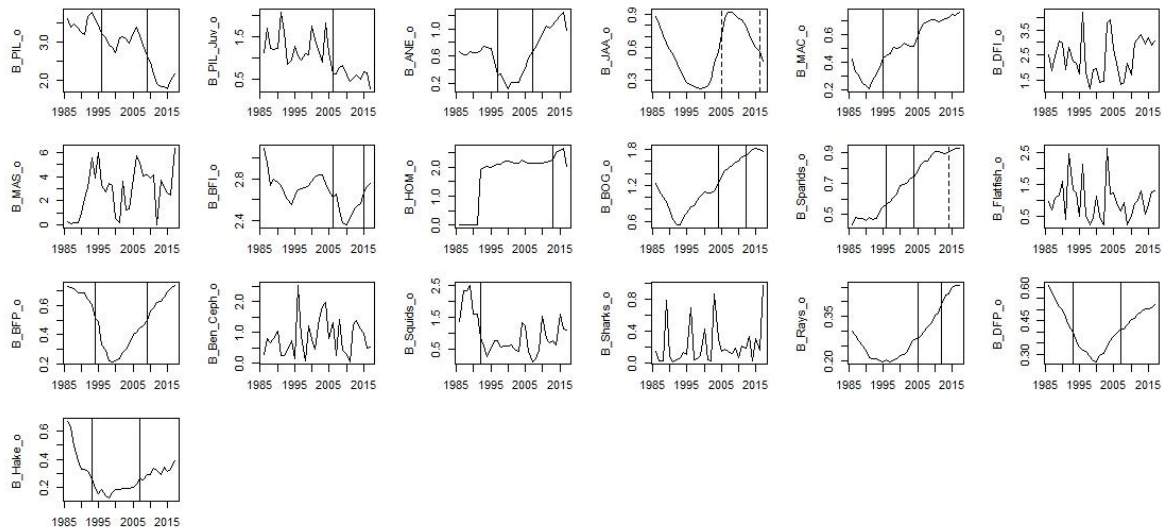


Figure 5.6 Time-series observed biomass data. Significant shifts detected by STARS analysis are displayed on the plots as solid and dashed vertical line for shifts significant at $p \leq 0.05$ and $p \leq 0.1$, respectively. Abbreviations, used in the figure, are explained in Table A5.7 in annex 5.

For modelled biomass variables, STARS detected significant shifts mainly in the mid-2000s and mid-2010s. In the mid-90s a shift in biomass was detected only for sardine, anchovy, blue jack mackerel, bogue, and benthopelagic piscivorous fish. In the mid-2000s the shifts were detected in the biomass of cephalopods, lower trophic level (TL) groups and invertebrates, chub mackerel and fish feeding on invertebrates. Further shifts in the mid-2010s, were detected for sardine and other SPF (horse mackerel, chub mackerel and bogue), cephalopods and lower TL functional groups (Figure 5.7).

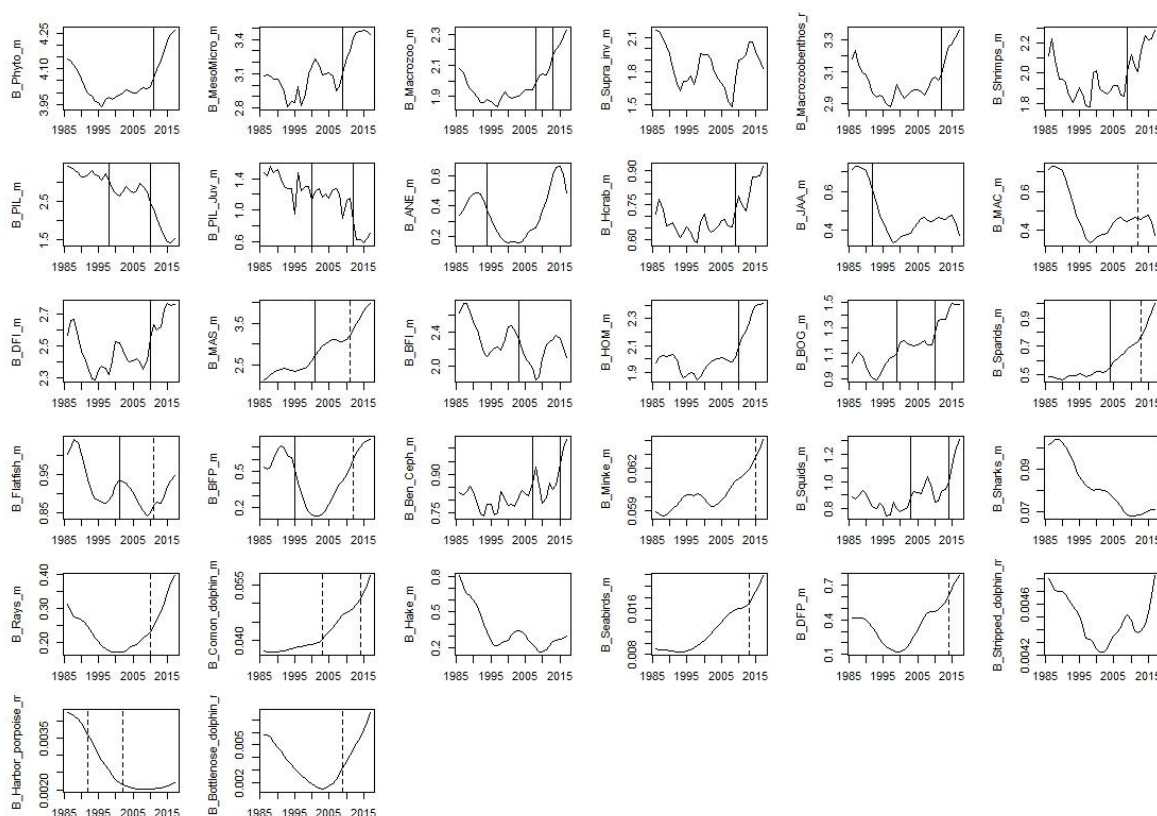


Figure 5.7 Time-series of modelled biomass data. Significant shifts detected by STARS analysis are displayed on the plots as solid and dashed vertical line for shifts significant at $p \leq 0.05$ and $p \leq 0.1$, respectively. Abbreviations, used in the figure, are explained in Table A5.7 in annex 5.

For ecosystem indices, significant shifts were mainly detected in the mid-90s and mid-2010s. The shift in the mid-2000s was only detected for Dem/Pel C and Kempton Q (Figure 5.8).

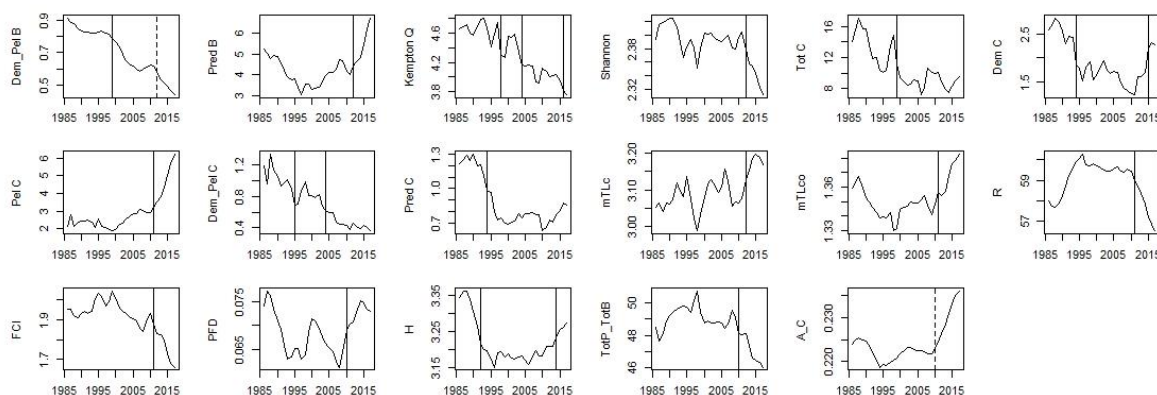


Figure 5.8 Time-series of ecosystem indicators data. Significant shifts detected by STARS analysis are displayed on the plots as solid and dashed vertical line for shifts significant at $p \leq 0.05$ and $p \leq 0.1$, respectively. Abbreviations, used in the figure, are explained in Table A5.7 in annex 5.

Shifts in the mid-90s were detected for catch related indices (Tot C, Dem C, Pred C, Dem/Pel C), Dem/Pel B, Kempton Q and H (Figure 5.8). Shifts after 2010 were detected for Pred B, diversity indices (Kempton Q, Shannon), catch related indices (Dem C, Pel C, mTLc) and ENA indices (FCI, R, H and Tot P/Tot B) (Figure 5.8).

Shifts at similar times were also detected by STARS performed on PCA results (PC trends) and CC analysis performed on separate data groups (Table 5.6). When performed on PC trends extracted from the fishing mortality data, STARS indicated that significant shifts occurred mainly in 1995 and 1999 (for PC2_FM and PC1_FM respectively), 2003 (for PC2_FM) and 2012–2016 (for PC1_FM and PC2_FM), while CC detected discontinuity in the fishing mortality data in 1992 and 2003 (Table 5.6).

Table 5.6 Results of the Sequential t-test Analysis of Regime Shift (STARS) on Principal Component Analysis (PCA) output and Chronological Clustering (CC) analysis. STARS regime shift years were identified in time series of PC1, PC2 and PC3 scores using $p \leq 0.05$ significance level. Regime Shift Index (RSI) values for PC1/PC2/PC3 are presented. Symbols $\uparrow$ and $\downarrow$ indicate increasing and decreasing trend, respectively.

Data group	Analysis				
	STARS on PCs				CC
	PC1	PC2	PC3	RSI	
Fishing mortality (FM)	1999 $\downarrow$ 2012 $\downarrow$	1995 $\downarrow$ 2003 $\uparrow$ 2016 $\downarrow$	2003 $\downarrow$ 2014 $\uparrow$	-0.9/-0.6 -0.4/-0.6 -0.7/-0.4/2.2	1992 2003 -
Environmental/climatic (ENV_CLIM)	1997 $\uparrow$ 2016 $\uparrow$	2014 $\uparrow$		1.0/ 0.7/0.7	1995 2002 2009
Observed biomass (B_obs)	2005 $\downarrow$ 2013 $\downarrow$	1993 $\downarrow$ 2003 $\uparrow$ 2015 $\uparrow$	- - -	-1.3 -2.9/0.8 -0.1/0.4	1990 - -
Modelled biomass (B_model)	2008 $\downarrow$ 2015 $\downarrow$	1992 $\uparrow$		1.0 -2.1 -1.6	1998 - 2015
Ecosystem indicators (Indices)	1999 $\uparrow$ 2012 $\uparrow$	1992 $\downarrow$ 2011 $\uparrow$		0.6/-0.4 1.8/1.4	1990 1999 2012

For STARS performed on PC trends of environmental/climatic variables significant shifts were detected in 1997 for PC1_ENV_CLIM and 2014–2016 for PC2_ENV_CLIM and PC1_ENV_CLIM respectively while CC detected discontinuity in 1995, 2002 and 2009 (Table 5.6).

Considering PC trends of observed biomass, STARS detected significant shifts in 1993 for PC2_B_obs, 2003–2005 for PC2_B_obs and PC1_B_obs respectively and 2013–2015 for PC1_B_obs and PC2_B_obs (Table 5.6). The CC detected significant discontinuity only in 1990 (Table 5.6).

When performed on PC trends extracted from modelled biomass data group, STARS detected significant shifts in 1992 (for PC2_B_model), 2008 (for PC1_B_model), and 2015 (for PC1_B_model) while CC showed discontinuity in the modelled biomass data in 1998 and 2015 (Table 5.6).

For STARS performed on PC trends of ecosystem indicators, significant shifts in the ecosystem were detected in 1992 for PC2_indices, 1999 for PC1_indices and 2011 and 2012 for PC2_indices and PC1_indices, respectively (Table 5.6). The CC showed discontinuity in the ecosystem indicators data in 1990, 1999 and 2012 (Table 5.6).

5.4. Discussion

This study provides a comprehensive overview of the changes observed in the PCSE in the last three decades (Figure 5.9). Ecosystem changes were assessed by using a large dataset that included information on ecosystem drivers and ecosystem state. Observed changes were confirmed by the detection of significant shifts in all used datasets.

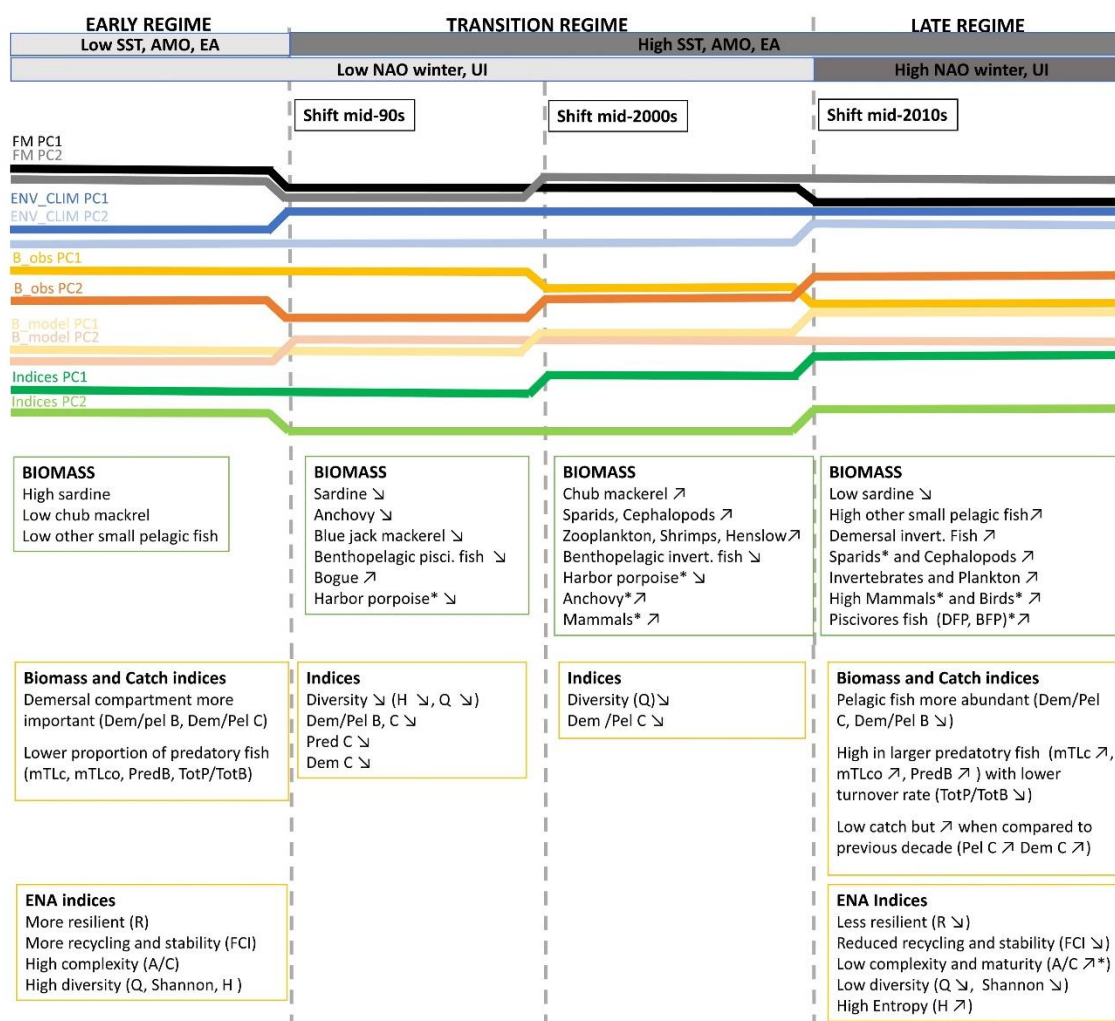


Figure 5.9 A conceptual diagram displaying the changes in the Portuguese Continental Shelf Ecosystem (PCSE) between 1986 and 2017. Variable names marked by * : for these variables shift was detected at $p \leq 0.1$ significance level. For the remaining variables, shifts were detected at $p \leq 0.05$. Detailed information about detected shifts that were summarised in the conceptual diagram is presented in Figure 5.5 and Table A5.7 in annex 5. Abbreviations, used in the figure, are explained in Table A5.7 in annex 5.

5.4.1. Description of PCSE changes

5.4.1.1. Changes in ecosystem drivers

The major changes in the ecosystem drivers occurred in the mid-1990s. Firstly, we observed a decrease in the fishing mortality of most functional groups. This can be related to the substantial reduction of the Portuguese fleet that decreased by 30% between 1989 and 1996 (INE 1987–1997). Secondly, in the mid-90s, an increase in SST, AMO and EA, has been reported. Around 1995, AMO entered a warm phase and since then the yearly SST means in North Atlantic including, the Iberian upwelling region has been $\geq 0.5^\circ\text{C}$ higher than in the

previous 65 years (Alheit et al. 2014). Later in the mid-2010s, we detected the change in winter NAO (that enters its high phase) and in the intensity of the upwelling. Changes observed in both these variables are in line with the findings by Borges et al. (2003) that demonstrated that in the Iberian shelf, a high NAO phase is associated with more favourable upwelling winter wind conditions.

5.4.1.2. Changes in ecosystem state (biomass)

During the studied period, we have seen considerable changes in the biomass of many functional groups. In the mid-90s the biomass of sardine, the main commercial pelagic fish started to decline while an abundance of other small pelagic fishes such as bogue and chub mackerel increased. Later, in the mid-2000s further changes in the biomass of functional groups in the ecosystem have been reported. During this time, we observed not only a further decrease of sardine and increase of other pelagics but also an increase of lower TL groups (zooplankton, invertebrates), sparids and cephalopods started to be apparent. After 2010, we still observed a decrease in sardine with a concurrent increase of other SPF and lower TL groups. Additionally, during this time an increase in predatory, high TL and demersal fish has been detected.

5.4.1.3. Changes in ecosystem state (indicators)

Changes in the ecosystem were also reflected in the ecosystem indicators. The major changes in ecosystem indicators data were observed in the mid-90s and later in the mid-2010s. In the mid-90s a major change was described by a decrease in Dem/Pel B, and catch related indices (Tot C, Dem C, Dem/Pel C and Pred C). A decrease in Dem/Pel B can be explained by an increase in biomass of pelagic species, discussed above. On the other hand, a decrease in catch related indices is probably related to the reduction of fishing effort observed in the PCSE during the last three decades (Bueno-Pardo et al. 2020). Later in the mid-2010s, a further reduction in Dem/Pel B was observed. At this time, an increase in TL indices indicating a rise of higher TL fish has also been documented (mTLc, mTLco, Pred B, TotP/TotB). Moreover, around this time, the indices that describe ecosystem stability and resilience shifted (FCI, R).

5.4.2. Causes of ecosystem changes

The correlation analysis indicates that the changes in ecosystem trends (biomass and indicators) are statistically correlated with the changes in fishing and environmental/climatic variables.

5.4.2.1. Fishing

Fishing has been documented as a major driver of the marine ecosystems worldwide (e.g. Pauly et al. 1998; Coll et al. 2008; Llope et al. 2011). Moreover, it has been highlighted as an important driver of the PCSE (chapter 4; Szalaj et al. 2021).

The important role of fishing detected in this study can be explained by the considerable changes observed in the Portuguese fishing sector in the last 50 years. Since the late 1980s, reported landings dropped approximately 52%, from 197,000 to 94,700 t in 2014 (Bueno-Pardo et al. 2018). Moreover, after the implementation of the European Common Fisheries Policy (EU CFP) (since 1983), a steady decrease of fishing effort started to be notable with a decrease of 75% and 50% in the number of boats and fishers respectively (Leitão et al. 2014b). A decrease in fishing effort, observed after enforcement of EU CFP measures, could affect an increase in biomass of some species observed in the study. For example, an increase in predatory higher TL fish, that manifested after 2010 can be linked with the reduction in fishing pressure. Observed in this analysis, a decrease in fishing mortality of most functional groups since the mid-90s, (demersal and benthopelagic piscivorous fish, rays, sparids, bogue, horse mackerel and mackerel), might have positively impacted the high TL predatory fish and demersal fish whose abundance increased and shifted after 2015 (with a time lag). A link between fishing and high TL predatory fish established in this study is based not only on the biomass data (observed increase in the biomass of demersal and benthopelagic piscivorous fish) but also based on ecosystem indicators. An increase in indices, mTL_c and mTL_{co} , that are linked with the decreasing fishing pressure (Pauly et al. 1998; Rochet and Trenkel 2003), were observed in this study. This is in line with the study by Leitão (2015a) that assessed the profiles of Portuguese fisheries landings since 1950. In this study, Leitão (2015a) documented an increase in the mean trophic level of the catch, by approximately 0.2 units per decade. However, in this study, we used fishing mortality data for only 10 functional groups, and this considerably limits the assessment of the impact of fishing on this system. Fishing mortality data for eight commercial groups, that were included in the biomass data (chub mackerel,

sparids, flatfish, demersal and benthopelagic invertivorous fish, cephalopods and sharks) were not considered as fishing drivers.

5.4.2.2. Environmental/climatic drivers

The PC trends extracted from environmental/climatic drivers data showed significant correlations with all PC trends extracted from ecosystem data.

The importance of environmental variability to drive marine ecosystems has been reported worldwide (e.g. Parsons and Lear 2001; Lehodey et al. 2020). This has been particularly prominent in the large upwelling systems (e.g., Shannon et al. 2004). The PCSE is located at the northern limit of the Canary Current upwelling system and during spring and summer it is affected by the seasonal upwelling (Wooster et al. 1976; Fiúza et al. 1982). Moreover, changes in the PCSE have been linked to environmental variability (e.g., chapter 4; Szalaj et al. 2021).

A decrease in sardine biomass and an increase in other pelagic fish and rays were both represented by PC1 in both data sets (observed and modelled biomass data groups). Additionally, in the observed biomass dataset, PC1 was represented by sparids, benthopelagic invertivorous fish and tunas (for which data was not introduced in PCA_B_model) while for modelled biomass data set, PC1 was also represented by cephalopods. PC1_B_obs and PC1_B_model showed a statistically significant correlation with PC1_ENV_CLIM and PC2_ENV_CLIM respectively. PC1_ENV_CLIM represented SST, AMO and EA variables, while PC2_ENV_CLIM represented NAO and UI trends. Therefore, based on this analysis it seemed that all these environmental/climatic variables might have played a role in the overall biomass changes observed in the study.

It is possible that the changes in environmental drivers that were apparent in the mid-90s, (SST, AMO, EA) affected the ecosystem and manifested with different time lag depends on the functional groups. In the PCSE, the productivity of species representing the functional groups for which significant shifts were observed in the mid-2000s, has been already documented as being influenced by environmental variability. Firstly, we have a large number of studies that link sardine recruitment and productivity with SST, chlorophyll concentration (Chla) (Santos et al. 2012; Leitão et al. 2014a; Garrido et al. 2017), NAO, wind conditions (Santos et al. 2012; Leitão et al. 2014a) and coastal upwelling (Santos et al. 2001; Malta et al. 2016; Santos et al. 2012).

Moreover, other pelagic species such as Atlantic horse mackerel (*Trachurus trachurus*) and anchovy (*Engraulis encrasicolus*) catch rates were linked with upwelling, the magnitude of northern wind and SST (Santos et al. 2001; Leitão 2015b; Ullah et al. 2012). Also, among cephalopods, cuttlefish (*Sepia officinalis*) catch rates were associated with the SST, winter NAO and autumn wind magnitude (Ullah et al. 2012). Furthermore, by using a statistical multi-model approach, Baptista et al. (2015) found that environmental factors such as winter SST and NAO affected short term variation of catch rates of common two-banded seabream (*Diplodus vulgaris*) in the south and southwest of Portugal. Also, they found that these species catch rates were associated with autumn and a yearly wind magnitude component, that can be treated as a proxy for the upwelling condition. All these studies were performed using statistical models. It is, therefore, encouraging that results from the study using different methods such as the outputs of ecosystem model and discontinuity analyses, established similar associations.

After 2010, we still observed a decrease in sardine and a concurrent increase in other SPF and lower TL groups. Additionally, during this time an increase in predatory, higher TL and demersal fish was also detected. When analysing shifts in data describing drivers, we observe that around this time the shift in winter NAO (that enters its high phase) and in the intensity of upwelling was detected. In the Iberian shelf, a high NAO phase is associated with more favourable upwelling winter wind conditions (Borges et al. 2003) that may favour lower trophic groups (phytoplankton, zooplankton, benthos). This can quickly promote the abundance of lower TL groups that rely directly on plankton as a food source (Barth et al. 2007). An increase in lower TL groups was initiated earlier in the mid-2000s but the shift in NAO in the mid-2010s might have further enhanced the change that initiated earlier.

5.4.2.3. Internal drivers (trophic interactions)

The effect of environmental variability on some species (functional groups) might have been intensified by the internal, trophic interactions that exist between these species. The importance of trophic interactions in the dynamics of the marine ecosystems has been well documented worldwide (e.g., Coll et al. 2008; Alexander et al. 2015). Also, it has been demonstrated as the main factor driving PCSE dynamics between 1986 and 2017 (chapter 4; Szalaj et al. 2021).

In the context of this study, an increase in lower TL groups due to the environmental conditions, could pronounce through the food web and promote the abundance of fish of prey

that consequently might have benefited the groups at higher TL including cephalopods, demersal fish and higher TL predatory fish. Also, the effect of environmental variability on some species (functional groups) might be exaggerated by the existence of the predator-prey loop between these species. This can be a case for sardine and chub mackerel. The increase in the biomass of chub mackerel observed after 2001 (that possibly benefited from increased temperature) may have caused increased pressure on sardine recruitment as it has been established that sardine eggs are chub mackerel's preferred prey (Garrido et al. 2015). At the same time, increased biomass of other species such as bogue, horse mackerel and mackerel might have added pressure on sardine due to the predation on its eggs and juveniles (Garrido et al. 2015).

5.4.3. Implications to ecosystem structure and function (ENA indices)

Other than the changes evident from the direct observations and modelled biomass, the ENA indices provide information about the changes that occurred at the whole ecosystem level. Analysis of ENA indices showed that not only has the abundance of functional groups altered but also the cycles and pathways that are implied by the ecosystem food web showed considerable alterations within the last thirty years.

ENA indices (R, FCI and A/C), indicate that after 2010, the ecosystem became less stable and less resilient with reduced maturity and complexity. Lower stability and resilience, reflected by the R, is implied by the reduction in the number of pathways through which energy flow is transferred. Moreover, reduction in R and increase in A/C implies lower maturity of the system which become more constrained and less complex. Lower FCI indicates that the system's recycling and its ability to conserve nutrients are reduced and therefore, its capacity to endure in the face of resource scarcity has diminished. These characteristics indicate structural differences (Finn 1976) and decreased stability (DeAngelis et al. 1989; Loreau 1994). Reduced resilience and stability concur with the observed decrease in diversity indices as it has been demonstrated that a system with greater biological diversity is usually more resilient than the one with less diversity (Oliver et al. 2015). It is not clear, what has caused the changes in the ecosystem structure and its flows. However, the most prominent change (the change of the highest magnitude) observed in the last decades was the decline of sardine. Indeed, the effects of the changes in dominant small pelagic fish on the ecosystem food web in the upwelling systems, have been broadly discussed (Cury et al. 2000). Moreover, based on the Ecopath model and description of the Iberian shelf food web structure, it has been demonstrated that

sardine played an important role in the Iberian ecosystem, being an important key linkage between primary producers and top predators (chapter 3; Veiga-Malta et al. 2019). Moreover, the Ecosim simulations demonstrated that sardine has an important role in a wasp-waist scenario (chapter 4; Szalaj et al. 2021). This confirmed its key role in the Iberian upwelling system as a biomass-dominant species at mid-trophic levels that channel most of the energy flow in the ecosystem. Therefore, it seems probable that sardine decline disturbed important trophic links and pathways through which the flow of energy passes. At the same time, the other small pelagic fish were not well linked to the rest of the food web with few animals predating on them and being not very important for the fishery. For example, bogue was only caught as a bycatch of the purse seine fishery and catches of chub mackerel only become important after 2000 when a decline of sardine occurred and fisheries managed to find alternatives for economic compensation (INE 2001–2019). Therefore, when pelagic energy flow was redirected to the other SPF (that were not as important prey for top predators and fisheries as sardine was before 1995), disruption in the energy flow pathways occurred. Consequently, ecosystem stability was reduced, and the ecosystem became less resilient. Similar changes were described in the Northern Benguela upwelling system, where a shift in dominant pelagic species coincided with the simplification of the food web and reduced resilience (Heymans and Tomczak 2016).

5.4.4. Assessment of the methodology

Methods that comprised of ITA methodology has been used to detect ecological and climatic regime shifts and they have been widely discussed and considered adequate (e.g., Rodionov and Overland 2005; Möllmann et al. 2009; Diekmann and Möllmann 2010; Tomczak et al. 2013). However, the use of EwE outputs in this type of analysis is rare and to our knowledge, there are only two studies that applied this approach to detect and describe regime shifts. One in the Baltic Sea and the other in the Northern Benguela (Tomczak et al. 2013; Heymans and Tomczak 2016). The main advantage of this approach is the possibility to use more data inputs, that EwE provides, for example, the data of functional groups for which observations do not exist and ecosystem indicators. Among the latter, ENA indicators can be especially valuable in the studies of ecosystem regime shifts as discussed by Tomczak et al. (2013). For example, the redundancy that was linked with ecosystem resilience (Heymans et al. 2007) is directly related to regime shift definition. Therefore, we argue that using this

approach is very beneficial in the studies that aim to detect and describe ecosystem regime shifts.

However, we are aware of the limitations of our analyses, such as high cross and autocorrelations. Planque and Arneberg (2018) criticised the use of PCA as a method for ecosystem assessment of marine ecosystems because the ITAs inputs usually share a similar trend and have autocorrelation properties. The authors demonstrated that most of the patterns revealed by the PCA can emerge from random time-series and that the fraction of the variance that cannot be accounted by random processes is minimal. In the context of our study, these findings are worrying and this limitation should be taken into consideration when interpreting the results. We tried to minimize this effect by excluding highly correlated variables prior to PCA. Also, the ITA methodology used in this study combines different methods and not all of them rely on PCA. For example, STARS performed on separate time series accounts for autocorrelation (prewhitening method described in the Material and methods section) and detected shifts in similar years (time ranges) that STARS performed on PCA output. Moreover, the CC method confirmed dissimilarity in the datasets in similar years as STARS on PCA results. However, to confirm and consolidate the conclusions of this study, as a future recommendation we would suggest to replicate the analysis using other methods that are not so sensitive to cross and autocorrelation and compare its outputs with the results obtained in this study.

Moreover, our analysis is fed with data that constitute the output of a modelling approach therefore our results are affected by the assumptions of the model. EwE is a commonly used approach (Colléter et al. 2015) and its best practices, pros and cons have been widely discussed (Heymans et al. 2016; Walters et al. 1997). When building and calibrating the EwE model for the PCSE, we considered the best practice guide (Heymans et al. 2016), reported uncertainties and thoroughly discussed limitations (chapter 4; Szalaj et al. 2021). Moreover, the model was well fitted to most groups with observation data, and we have confidence in the model and data it provided (chapter 3; chapter 4; Veiga-Malta et al. 2019; Szalaj et al. 2021). This was also reflected in this study because the results obtained from the analyses performed on observed biomass are in line with the results obtained from modelled biomass.

5.4.5. Regime shifts in the PCSE and North Atlantic

The performed analyses allowed to detect three shifts in data, in the mid-90s, mid-2000s and mid-2010s. However, based on the analysis of the results and the review of the literature, only two of them, in the mid-90s and mid-2010s, could be considered as shifts to a new regime. The shifts in the mid-90s and mid-2010s were detected by STARS on all PC trends regardless of the data group used, while the shift in the mid-2000s was mainly detected in the biomass data (when considering main PCs). Moreover, the timing of the shifts detected in the mid-90s and mid-2010s in this study coincided with the time of ecosystem regime shifts documented in the other regions of the North Atlantic. The mid-90s shift is well documented in the northern hemisphere and a large set of previous studies described it and linked it with large scale atmospheric variations (e.g., Cabrero et al. 2018; Alheit et al. 2014; Beaugrand et al. 2015). For example, Alheit et al. (2014), linked the complex ocean-atmosphere changes in the mid-90s with a regime shift in the ecosystems of the Northeastern and Central Atlantic. He discussed that when in the mid-1990s, three events including: (1) decrease of the NAO index; (2) the weakening of the Atlantic Meridional Overturning Circulation (AMOC) and (3) the contraction of the subpolar gyre (SPG) occurred, a substantial redistribution of water masses in the Northeast Atlantic happened. This affected most ecosystems in the region causing a change in the abundance of the small pelagic clupeoid fish and their northward migration. Moreover, Cabrero et al. (2018) demonstrated that in the Iberian shelf, sardine entered a new regime in the late 1990s triggered by large-scale ocean climate processes. He concluded that the combination of climate and oceanographic conditions, including NAO, EA, SST, AMO and UI intensity, contributed to this regime shift.

Also, a reference to the mid-2010s shift in the Northern Atlantic appeared in the recent literature. For example, Tanner et al. (2020) found that the abrupt changes in the growth of two deep-sea scorpaenid fishes off the central islands of the Azores and the island of Madeira occurred not only in the late 90s but also around 2014. This coincides with a significant shift in the mid-2010s detected in this study. Tanner et al. (2020) associated the shift in 2014 with a large-scale abrupt biological shift that was predicted by Beaugrand et al. (2019) to occur after 2014 in response to a strong El Nino event that affected the Northern Hemisphere climate. In the study by Beaugrand et al. (2019), a model based on the numerically generated thermal niche of pseudo-communities was used and the shifts predicted by the model were validated with observed community shifts in 14 oceanic regions. This study is of special interest to us, as the shift in the mid-2010s, that was detected in our analysis, is not well documented in the scientific

literature. A few substantial climate events occurred around this time: exceptionally cold North Atlantic Ocean temperatures, 2015 severe European heatwave (Duchez et al. 2016) and the change in AMO phase (Frajka-Williams et al. 2017). However, these events are quite recent, and their ecological consequences are not yet well studied and understood.

The mid-2000 regime shift that was detected in this study did not relate to any relevant environmental pressure observed in the North Atlantic in our dataset or the literature. Generally, the time between 2005 and 2014 is considered a relatively quiet period when referring to the climatic drivers in the Northern hemisphere (Beaugrand et al. 2015). Moreover, this shift was not reflected in the changes observed in the ecosystem indicators analysed in the study. Therefore, we considered the period between the first shift in the mid-90s and the shift in the mid-2010s as the “transition regime” during which the changes triggered by a previous shift in the mid-90s manifested in the ecosystem with the time lag whose length depends on the functional group.

From this analysis, it is not clear whether the shift was caused solely by the environmental/climatic causes because both analysed ecosystem drivers’ trends (fishing and environmental/climatic) correlated with ecosystem state trends. However, based on the literature and a well-documented climatic shift in the North Atlantic we can infer that climatic variability played a major role. However, the effect of fishing pressure should not be completely disregarded as fishing is a well-documented driver of marine ecosystems worldwide (e.g., Coll et al. 2008; Alexander et al. 2015) and substantial changes in the fishing sector has been documented during the last three decades in the PCSE (Leitão et al. 2014b; Bueno-Pardo et al. 2020). Moreover, regime shifts are commonly triggered by a combination of fishing and environmental/climatic factors acting together (e.g., Daskalov et al. 2007; Möllmann et al. 2009). In the case of the PCSE, although we have documented a decrease in fishing effort (Bueno-Pardo et al. 2020), many Portuguese fish stocks are considered overfished (Leitão 2015a). As we discussed in section 4.2.1 (chapter 4), the impact of fishing on the ecosystem has not been fully captured in this study. Therefore, the hypothesis of the fishing cause of the PCSE regime shift should be explored in future studies.

At this stage, it is impossible to say if the current regime is stable or reversible as the PCSE as an upwelling system might have a wide range of natural variability (Black et al. 2014). If the observed ecosystem food web changes are linked with sardine decline as discussed above (in the previous subsection) then it is unknown what effect sardine recovery may have on the

ecosystem. The latest ICES sardine stock assessment indicated that the 2019 sardine recruitment estimate constitutes the highest value since 2004 and is above the long-term geometric mean (ICES 2020). That might suggest that the sardine productivity trend is shifting. However, at that stage it is unknown whether the increase in sardine recruitment will continue and sardine stock will recover to the level prior to the mid-1990s and what impact would that potential increase have on the food web.

5.4.6. Implications for management

The potential occurrence of regime shifts might have considerable implications for the productivity of the commercial stocks and consequently to the fisheries. Therefore, the awareness of regime shift in the management of the ecosystems is of utmost importance and should be included in the management plan of marine systems (deYoung et al. 2008). This management should include not only timely detection and adaptation to a new regime but also prevention (deYoung et al. 2008; Crépin et al. 2012). The latter is crucial and should focus on building and maintaining the resilience of desired ecosystem states (Levin and Lubchenco 2008). Nevertheless, sometimes, regime shifts cannot be prevented, and in these circumstances, timely detection is important in order to act quickly to alleviate the adverse effects and adapt to a new reality (Crépin et al. 2012).

After the detection of regime shifts, the adaptation in the form of adaptive management should take place. For example, a regime-specific harvest rate strategy could be implemented when an indication towards a shift to an alternate ecosystem state exists (Polovina 2005, MacCall 2002). This study demonstrated that one of the possible mechanisms behind the described regime shift is environmentally related therefore in the context of PCSE management, efforts should be focused on establishing reference points at which the change in environmental pressure might result in an abrupt change in the ecosystem (Large et al. 2015).

5.5. Conclusion

The ITA presented in this study pointed to the occurrence of two regime shifts in the PCSE in the mid-90s and around the mid-2010s. Interpretation of results allowed for the identification of three periods: “early regime” till the mid-90s, “transition regime” till mid-2010s, and “late regime” since the mid-2010s in the last three decades. Differences between

“early regime” and “late regime” are evident in all components of the ecosystem and at multiple trophic levels. They include changes in species abundance as well as community composition. Moreover, ecological network analysis indices indicate that the internal food web structure and organisation of the ecosystem have changed. Specifically, detected regime shifts are characterised by changes in the pelagic community: (1) it became more dominant when compared to the demersal community; (2) a shift from the main commercial stock of sardine to less commercially viable small pelagics had occurred. Moreover, an increase in higher TL predatory fish and demersal fish was observed.

Changes described in the ecosystem were probably caused by two types of external drivers. First, environmental forcing (related to an increase in SST, AMO, EA, NAO, and intensification of the upwelling conditions) possibly affected lower TL groups and SPF, and second, reduction in fishing pressure probably benefited high TL predatory and demersal fish. Moreover, the internal triggers, related to indirect trophic interactions also might play a role in the observed ecosystem change. An increased abundance of lower trophic level functional groups and fish of prey might benefit higher TL groups such as cephalopods, demersal and predatory fish. Furthermore, the competition and intraguild predation between sardine and other pelagic fish might have contributed to the changes in the pelagic community.

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Chapter 6

Predictions of sardine and the Portuguese continental shelf ecosystem dynamics under future fishing, trophic and SST scenarios

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Chapter 6 – Predictions of sardine and the Portuguese continental shelf ecosystem dynamics under future fishing, trophic and SST scenarios

Abstract

We used the Ecopath with Ecosim ecosystem model to assess the future effects of multiple stressors on sardine and the Portuguese continental shelf ecosystem. We assessed individual and combined impacts of changes in sardine fishing pressure, trophic interactions and sea surface temperature (SST). This study demonstrated that the greatest impact on sardine stock is caused by projected SST rise whose effect is dominant and detrimental to sardine stock regardless of other conditions, including fishing at maximum sustainable yield (MSY). The largest impact on ecosystem stability, maturity and diversity of flows was observed under the trophic scenarios that simulate changes in biomass of sardine predators and competitors. Moreover, these stressors alongside fishing at MSY are projected to play an important role in the future evolution of the sardine stock. Results presented in this study can assist long-term and strategic management of the Iberian sardine stock.

Keywords: Future predictions, Multiple stressors, Ecosystem modeling, Ecopath with Ecosim, *Sardina pilchardus*, Portuguese shelf

6.1. Introduction

Human and environmental pressures on marine ecosystems are increasing globally (Halpern et al. 2015) causing habitat and biodiversity loss (Worm et al. 2006; McCauley et al. 2015), changes in species distribution (Chen et al. 2011; Froese et al. 2012; Poloczanska et al. 2013), food web dynamics (Branch 2015; Ullah et al. 2018), ecosystem structure and its function (e.g., Tam et al. 2017). This affects marine ecosystem services including the productivity of commercial fish stocks which in turn, impairs the ability of marine ecosystems to feed a growing human population (Worm et al. 2006). While the effects of the increasing fishing pressure and sea surface temperature (SST) on single species are well studied and documented (Poloczanska et al. 2013), the knowledge about future consequences of anthropogenic and combined pressures at the whole marine ecosystem level, even though considered a pressing issue, is still limited (Harley et al. 2006; Halpern et al. 2007). The interest in the ecosystem models, as tools that can provide future assessments and support decision-makers to manage future ecosystems, is increasing. Even though the forecasts produced by these models, are characterised by some important limitations (Maris et al. 2017) and include high uncertainty (Link et al. 2012), their potential for ecosystem management in the context of an ecosystem-based management (EBM) approach is well established (Fulton et al. 2011; Townsend et al. 2019; Heymans et al. 2020).

The Ecopath with Ecosim (EwE) modelling framework (Christensen and Walters 2004) is a versatile tool that can be used to hindcast and forecast the ecosystem impacts of anthropogenic stressors. It has been used to answer a variety of research questions related to the ecosystem impacts of fishing (Coll et al. 2008), climate change (Serpetti et al. 2017; Bentley et al. 2017) and invasive species (Corrales et al. 2018). Also, it has been used to investigate the reasons behind fish stock declines in the West Coast of Scotland (Alexander et al. 2015), and the Baltic Sea (Costalago et al. 2018).

The Portuguese continental shelf ecosystem (PCSE) is situated in a biogeographic transition zone, between temperate and subtropical waters. Consequently, it is abundant in both temperate and subtropical fish species that have their southern or northern distribution limits along the coast (Briggs 1974), making these species particularly vulnerable to climate change. Changes in the occurrence of species in these areas have been reported and linked with a recent climate change. For example, Cabral et al. (2001) and Vinagre et al. (2011) reported an increase

in species with tropical affinities and a decrease in temperate species along the Portuguese coast.

One of the most pronounced changes in species abundance along the Portuguese coast was observed for sardine (*Sardina pilchardus*) whose stock declined considerably in recent years (ICES 2017). Understanding declines in fishing stocks is challenging because often it is difficult to distinguish between the impacts related to trophic interactions, environmental factors and fishing. In the case of the Portuguese sardine stock, it has been suggested that its decline might be related to complex inter-trophic dynamics between several pelagic species (Martins et al. 2013, chapter 4; Szalaj et al. 2021a). Some authors have observed an increase in other coastal pelagic species that compete and prey upon sardine eggs and larva. For example, an increase in biomass was recently observed for chub mackerel (*Scomber colias*), horse mackerel (*Trachurus trachurus*), blue jack mackerel (*Trachurus picturatus*) and anchovy (*Engraulius encrasicolous*) (ICES 2017; Martins et al. 2013; Garrido et al. 2015). Another plausible cause for sardine decline may be related to a change in environmental conditions, especially an increase in SST. It has been documented that the spawning of sardine in Portuguese coastal waters is limited to the narrow range of SST that varied between 12°C and 17°C (Stratoudakis et al. 2007). Moreover, a decline in sardine recruitment has been linked with an increase in SST (Malta et al. 2016; Garrido et al. 2017). In addition, species that prey on sardine eggs and compete for resources with sardine such as chub mackerel might be favoured by the increasing SST as their upper limit of optimal temperature for reproduction is reported to be higher than in the case of sardine (Vasconcelos et al. 2012). Lastly, an alternative explanation for sardine decline may be related to fishing pressure, suggesting that sardine stock may be unable to sustain fishing pressure in recent decades. Even though in the last 30 years sardine fishing effort has considerably decreased (from about 190,000 tonnes in 1986 to about 22,000 tonnes in 2017), until 2017 sardine fishing mortality was maintained at a relatively high level, between 0.2 to 0.4 with a peak of approximately 0.57 in 2011 (ICES 2017).

In this paper, we used the time-dynamic Ecosim model of the PCSE fitted to a time-series between 1986–2017 (chapter 4; Szalaj et al. 2021a) to explore sardine dynamics and ecosystem effects under the potential future fishing, trophic interactions and SST scenarios. This study mainly focuses on the sardine and pelagic community but also aims to assess the overall ecosystem effects. The following key research questions were identified: (1) how changes in fishing pressure and biomass of key sardine predators and competitors might impact sardine stock and the ecosystem? (2) what effects will future IPCC (Intergovernmental Panel

on Climate Change) SST scenarios have on sardine stock and the ecosystem? (3) how combined stressors may affect sardine and the ecosystem? (4) which stressors have the largest impacts on sardine and the ecosystem and (5) under what conditions sardine stock would be able to recover.

6.2. Material and methods

6.2.1. Study area

The Portuguese continental shelf ecosystem (PCSE, Figure 6.1) is situated in the northeast Atlantic and it covers an area of around 25,000 km². Mean sea surface temperature in the studied area ranges from 13°C and 17°C, in the north, and 15°C and 21°C, in the south in the winter and summer, respectively.

Portuguese fishing fleets operate three main types of gear: purse-seine, bottom trawl and multi-gear. In 2017, the Portuguese fleet consisted of 4,019 fishing vessels of which 84% were small vessels with a gross tonnage less than 5 (INE 2018).

Portuguese continental waters are dominated by small and medium pelagic species such as sardine *Sardina pilchardus*, chub mackerel (*Scomber colias*) and horse mackerel (*Trachurus trachurus*) (Arístegui et al. 2009; García-Seoane et al. 2019). Other abundant, ecologically and commercially important species are hake (*Merluccius merluccius*), blue whiting (*Micromesistius poutassou*) (Silva et al. 1997; Sousa et al. 2005) and cephalopods *Loligo* spp. and *Octopus* spp. (Moreno et al. 2009).

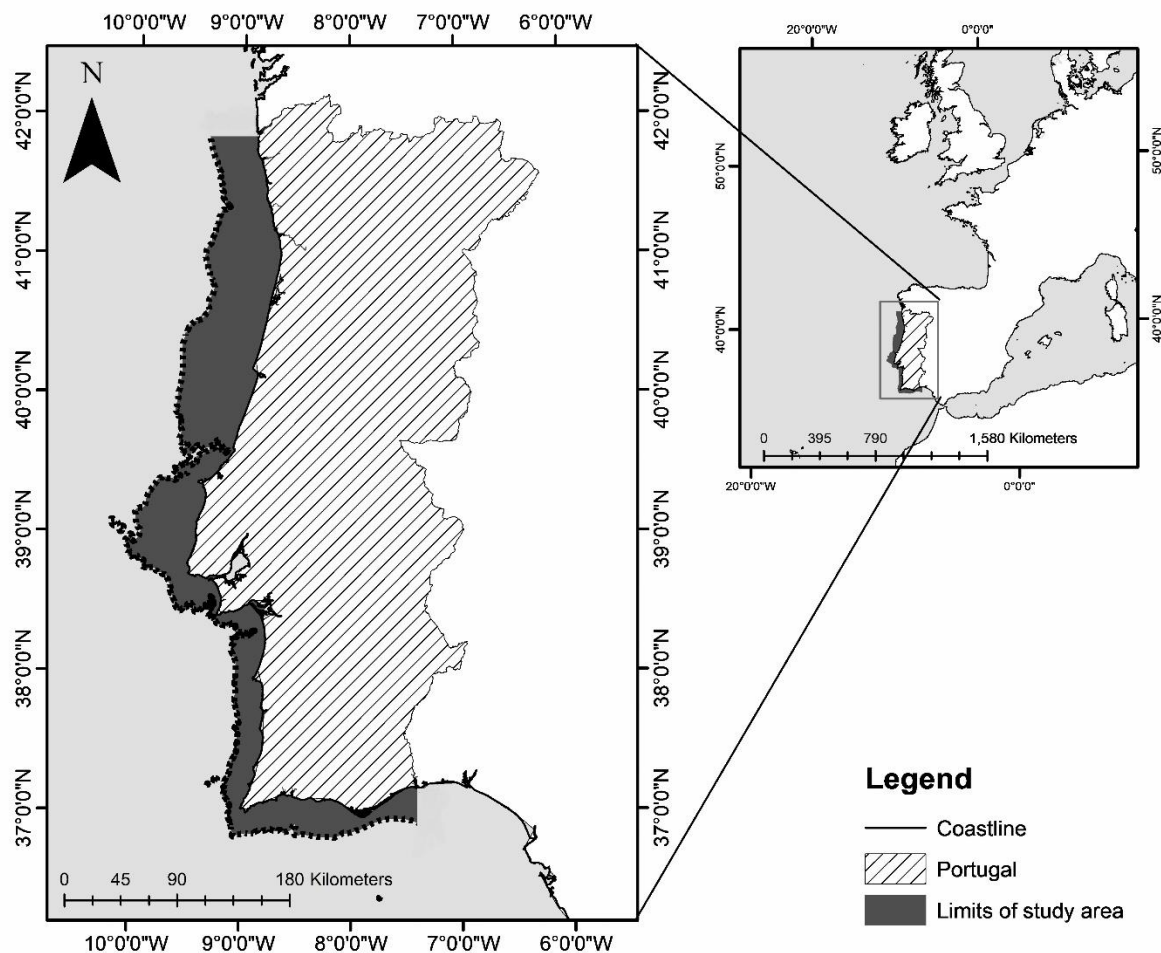


Figure 6.1 The limits of the Portuguese continental shelf ecosystem.

6.2.2. Modelling approach

Ecopath with Ecosim (EwE) software (Christensen and Walters, 2004) was used to model future PCSE. The EwE modelling approach combines three main modules: static trophic mass balanced analysis Ecopath (Christensen and Pauly 1992), dynamic temporal routine Ecosim (Walters et al. 1997) and the spatial-temporal dynamic module Ecospace (Walters et al. 1999).

The Ecopath mass-balance model was developed using EwE (www.ecopath.org) in order to describe the structure and functioning of the PCSE and to assess the role of sardine in the ecosystem (chapter 3; Veiga-Malta et al. 2019). The model covered the Portuguese continental shelf up to 200 m in depth. It described the ecosystem between 2006 and 2009, consisted of 31 functional groups distributed into 5 trophic levels (Figure A6.1 in annex 6;

Table 4.1 in chapter 4) and considered three fishing fleets: purse-seine, bottom trawl and multi-gear.

The Ecopath model, describing PCSE, developed by Veiga-Malta et al. (2019) (chapter 3) was adapted to the year 1986 and the time dynamic model Ecosim was constructed and fitted to time series data from 1986 to 2017 (chapter 4; Szalaj et al. 2021a). Updated model parameters are provided in Table 4.1 in chapter 4. The model was used to assess the historical impact of fishing activities, trophic interactions, and Sea surface temperature (SST), on changes in the ecosystem and sardine stock biomass. This model was used in the present study, in order to run future projections scenarios. Description of time series used to drive and calibrate the model, with their sources are provided in Table 4.2 in chapter 4.

Ecosim uses a set of differential equations to describe biomass dynamics, expressed as:

$$\frac{dB_i}{dt} = g_i \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - (M_i + F_i + e_i) B_i \quad \text{Equation 6.1}$$

where dB_i/dt is the biomass growth rate of the group (i) during time t, g_i is the net growth efficiency of the group (i); M_i is the natural mortality rate; F_i is the fishing mortality rate; e_i and I_i is the emigration and the immigration rate respectively and B_i is the biomass. Consumption rates (Q_{ij}) are calculated based on the “foraging arena” theory (Ahrens et al. 2012), which divides the biomass of prey into two fractions: vulnerable and non-vulnerable. The trophic flow between the vulnerable and non-vulnerable fraction is determined by a transfer rate (vulnerability - v_{ij}) between the two states. For each predator-prey interaction, consumption rates are calculated as:

$$Q_{ij} = \frac{v_{ij} a_{ij} B_i B_j T_i T_j S_{ij} M_{ij} / D_j}{v_{ij} + v'_{ij} T_i M_{ij} + a_{ij} M_{ij} B_j S_{ij} T_j / D_j} \cdot f(Env_{function}, t) \quad \text{Equation 6.2}$$

Where a_{ij} is the rate of effective search for prey (i) by a predator (j), v_{ij} is the vulnerability parameter, T_i represents prey relative feeding time, T_j is the predator relative feeding time, B_i is prey biomass, B_j is predator abundance, M_{ij} is the mediation forcing effects, and D_j represents effects of handling time as a limit to consumption rate. Environmental response function ($f(Env_{function}, t)$) links functional group dynamics with the environmental drivers that change with time. The intercept between the environmental driver and environmental response function is used to determine a multiplier factor, that modifies the consumption rate of the

functional group when the environmental driver deviates from the optimum values (Corrales et al. 2017).

The effect of SST increase on sardine spawning was incorporated through the Environmental response function ($f(\text{Env}_{\text{function}}, t)$) and time series of annual average SST from 1986 to 2017 were used to drive the temporal dynamics of sardine. The environmental response function for sardine, which used the trapezoid function to define sardine spawning optimal and tolerance ranges, was adapted from Szalaj et al. (2021a) (chapter 4). The mean, optimal and tolerance SST rates for sardine spawning were adapted from Coombs et al. (2006) and Stratoudakis et al. (2007). A time series of future SST IPCC scenarios were obtained from the Royal Netherlands Meteorological Institute Climate Explorer (<https://climexp.knmi.nl>). When running scenarios into the future, few species (i.e., sardine, anchovy, blue jack mackerel and horse mackerel) were unstable or collapse within 10 years, therefore we changed the vulnerability configurations for these species (updated vulnerability configurations are presented in Table A6.1 in annex 6)

6.2.3. Simulations of future scenarios

We used calibrated time dynamic PCSE Ecosim model (chapter 4; Szalaj et al. 2021a) to evaluate the effect of the multiple sardine stressors on the evolution of sardine stock and ecosystem.

Future scenarios, that assessed the effects of different sardine stressors were run for 30 years and included: baseline scenario (Sc1); fishing scenarios that simulate various sardine fishing mortality levels (Sc2-Sc5); trophic interaction scenarios that simulate the expected future changes in biomass of functional groups that directly interact with sardine (Sc6-Sc9); SST scenarios that simulate future IPCC SST projections (Sc10-Sc11); and combined scenarios that consider effects of multiple stressors (Sc12-Sc15) (Table 6.1).

Table 6.1 List of scenarios and respective stressors conditions.

Scenario	Name	Sardine fishing	Sardine trophic interactions	SST
Sc1	Baseline	Maintained at 2017 level - $F_{2017}=0.172$	As model predicts	Maintained at 2017 level
Fishing scenarios				
Sc2	FEwE	$F=0.12$	As model predicts	Maintained at 2017 level
Sc3	FMSYa	$F=0.064$	As model predicts	Maintained at 2017 level
Sc4	FMSY	$F=0.032$	As model predicts	Maintained at 2017 level
Sc5	Fhigh	$F=0.24$	As model predicts	Maintained at 2017 level
Trophic interactions scenarios				
Sc6	MAS_increase	Maintained at 2017 level - F_{2017}	Chub mackerel biomass forced to increase	Maintained at 2017 level
Sc7	BOG_increase	Maintained at 2017 level - F_{2017}	Bogue biomass forced to increase	Maintained at 2017 level
Sc8	ANE_increase	Maintained at 2017 level - F_{2017}	Anchovy biomass forced to increase	Maintained at 2017 level
Sc9	Ceph_decrease	Maintained at 2017 level - F_{2017}	Squids and benthic cephalopods biomass forced to decrease	Maintained at 2017 level
SST scenarios				
Sc10	RCP45	Maintained at 2017 level - F_{2017}	As model predicts	Model increase of SST corresponding to the moderate future greenhouse gases concentrations RCP45 based on the CMIP5 multi-model ensemble projections (Sillmann et al. 2013). Radiative forcing in RCP4.5 peaks at about 4.5 W/m^2 (~540 ppm CO_2) in the year 2100 (Thomson et al. 2011).
Sc11	RCP85	Maintained at 2017 level - F_{2017}	As model predicts	Model very high future greenhouse gases concentrations RCP85, based on the CMIP5 multi-model ensemble projections (Sillmann et al. 2013). Radiative forcing in RCP8.5 assumes a high rate of radiative forcing increase, peaking at 8.5 W/m^2 (~940 ppm CO_2) in the year 2100 (Riahi et al. 2011).

Combined scenarios				
Sc12	RCP45_FMSY	Actual reference FMSY recommended by ICES (2020)	As model predicts	Model increase of SST corresponding to the moderate future greenhouse gases concentrations RCP45 based on the CMIP5 multi-model ensemble projections (Sillmann et al. 2013). Radiative forcing in RCP4.5 peaks at about 4.5 W/m ² (~540 ppm CO ₂) in the year 2100 (Thomson et al. 2011).
Sc13	MAS_FMSY	Actual reference FMSY recommended by ICES (2020)	Chub mackerel biomass forced to increase	Maintained at 2017 level
Sc14	RCP45_MAS	Maintained at 2017 level - F_{2017}	Chub mackerel biomass forced to increase	Intermediate (model moderate future greenhouse gases concentrations)
Sc15	Ceph_FMSY	Actual reference FMSY recommended by ICES (2020)	Cephalopods biomass forced to decrease	Maintained at 2017 level
Sc 16	MAS_Ceph	Maintained at 2017 level - F_{2017}	Chub mackerel biomass forced to increase, and cephalopods biomass forced to decrease	Maintained at 2017 level

Among fishing scenarios, we assessed the future effects of FEwE that is FMSY obtained from the EwE considering the full compensation approach (Sc2). EwE can estimate FMSY using two approaches, the full compensation and the stationary approach. The former considers the changes in biomass of species as a result of the trophic interactions with the assessed species. The stationary approach does not account for these ecosystem effects and in that sense is similar to the conventional single species assessment methods. Therefore, in this study, to account for species interactions we used the FMSY estimated using the full compensation approach. Moreover, the full compensation FMSY equals target fishing mortality (F_{tgt}) from ICES Harvest Control Rule 1 (HCR1) and HCR2 that is preferred by stakeholders (ICES 2019); FMSY_a, an alternative fishing at maximum yield assessed by ICES that equals F_{tgt} from HCR12 (ICES 2019) (Sc3); FMSY, the actual 2020 reference fishing at maximum yield assessed by ICES (2020) (Sc4); and F_{high} , the fishing mortality rate that will allow catching 50,000 tonnes of sardine, the number desired by the fishing community (Sc5). In these scenarios, juvenile sardine fishing mortality was scaled accordingly to the levels

adopted for adult sardine F. These scenarios considered the constant 2017 level of SST and evolution of functional groups that interact with sardine as the model predicted.

In trophic interaction scenarios, we included simulations that assessed the future effects of the hypothetical changes in the biomass of the species that directly interact with sardine or have high niche overlap. We considered the following scenarios: increase in biomass of chub mackerel (Sc6), bogue (Sc7) and anchovy (Sc8) and decrease in the biomass of cephalopods (Sc9). These scenarios were chosen based on the premises in the literature and expert knowledge about the future evolution of these species in PCSE. Chub mackerel, bogue and anchovy are species whose increase in the PCSE has been noted in the last decades (Martins et al. 2013; Garrido et al. 2015; García-Seoane et al. 2019; Leitão et al. 2018). These species have tropical affinities (high-temperature preferences in AquaMaps; Kaschner et al. 2019) and have been previously classified as warm-water species based on their mean preference temperatures (e.g. Leitão et al. 2018). Therefore, their increase in PCSE has been linked with an increase in SST (Martins et al. 2013; Leitão et al. 2018; García-Seoane et al. 2019; chapter 5; Szalaj et al. 2021b) and they are expected to thrive in the future warming Portuguese continental shelf waters. On the contrary future distribution of cephalopods is expected to decrease due to a decrease in future suitability conditions in the Iberian coast and the Bay of Biscay (Schickele et al. 2021a). To standardise the effect of changes in species biomass on sardine and the ecosystem, we simulated the gradual increase or decrease of the species at a similar level of $30 \pm 2.6\%$ by the last year of simulation (2047) in reference to a baseline scenario. These scenarios considered constant sardine fishing mortality and SST at the level of 2017.

In SST scenarios we assessed the impact of sea warming on sardine using future SST based on CMIP5 multi-model ensemble projections (Sillmann et al. 2013), extracted for the study area from the Royal Netherlands Meteorological Institute Climate Explorer (<https://climexp.knmi.nl>). SST projections anomalies did not match the historic SST anomalies used to drive the model, therefore we scaled SST projections to match historic SST anomalies (Figure A6.2). We explored four IPCC SST projection scenarios RCP 2.6, RCP 4.5, RCP 6.0 and RCP 8.5 that simulate various radiative forcing corresponding to low, moderate, high and very high future greenhouse gases emissions, respectively. The results from all scenarios were very similar therefore only two of them were further explored and analysed: RCP 4.5 (Sc10) and RCP 8.5 (Sc11). Radiative forcing in RCP4.5 peaks at about 4.5 W m^{-2} ($\sim 540 \text{ ppm CO}_2$) in year 2100 (Thomson et al. 2011) while RCP8.5 assumes a high rate of radiative forcing increase, peaking at 8.5 W m^{-2} ($\sim 940 \text{ ppm CO}_2$) in the year 2100 (Riahi et al. 2011). In these

scenarios, sardine fishing mortality was kept constant at the level of 2017 and the biomass of sardine predators and competitors evolved as the model predicted. In addition, we evaluated the combined impact of the multiple stressors on sardine through five scenarios that consider the joint impact of fishing exploration, trophic interactions and SST (Sc 12–16).

Among combined scenarios, we assessed a scenario that considered SST increase and fishing at MSY (Sc12). This scenario was chosen to assess if the effect of SST increase on sardine, can be alleviated by FMSY. Also, we included two scenarios that consider forced biomass of the most significant predator of sardine eggs (chub mackerel). In scenario 13, an increase in biomass of chub mackerel was combined with actual FMSY (Sc13). This scenario was chosen to assess if the effect of an increase of a sardine egg predator, can be alleviated by FMSY. In Scenario 14, an increase in the biomass of chub mackerel was combined with the effect of RCP45 SST rise (Sc14). This scenario was designed to assess the impact of two possible sardine stressors that are expected to occur in future simultaneously. Moreover, we assessed the combined effect of the decrease in cephalopod biomass (that are important adult sardine predators with FMSY (Sc15) and joint effects of increase and decrease in chub mackerel and cephalopods respectively (Sc16).

6.2.4. Assessment of the ecosystem effects

Future changes in the biomass of selected functional groups were analysed. The focus of the study was to investigate the evolution of depleted sardine stock and potential changes of the pelagic component of the ecosystem. Therefore, analysed groups were chosen considering their importance with relation to sardine and the pelagic domain of the ecosystem. Moreover, a selection of ecosystem indicators was used to assess the impact of simulation scenarios on the structure and function of the ecosystem over time. Chosen indicators were commonly used to assess changes in ecosystem properties and food-web dynamics (e.g., Tomczak et al. 2013; Heymans et al. 2014; Corrales et al. 2018; chapter 5; Szalaj et al. 2021b). They are: (1) Total biomass (Total B); (2) Invertebrate biomass (Invertebrates B); (3) Demersal per pelagic biomass (Dem/Pel B); (4) Demersal per pelagic catch (Dem/Pel C); (5) Mean trophic level of the catch (mTLc); (6) Mean trophic level of the community (mTLco) and Ecological network analysis (ENA) indicators as described by Ulanowicz (1986), including (7) Redundancy (R), (8) Relative ascendancy (A/C), (9) Finn's Cycling Index (FCI), (10) Turnover rate

(TotP/TotB), (11) Average mutual information (AMI) and (12) Entropy (H). Their description is presented in Table 6.2:

Table 6.2 Description of ecosystem indicators analysed in the study.

Indices	Definition	Description
Biomass based indices		
1	Total biomass (t km ⁻² year ⁻¹) (Total B)	Sum of the biomass of all species in the ecosystem (excluding detritus)
2	Invertebrate biomass (t km ⁻² year ⁻¹) (Invertebrates B)	Sum of the biomass of all invertebrate species
3	Demersal per pelagic biomass (Dem/Pel B)	Sum of the biomass of demersal species/sum of the biomass of pelagic species
Catch based indices		
4	Demersal per pelagic catch (Dem/Pel C)	Sum of the catch of all demersal species/sum of the catch of all pelagic species
Trophic based indices		
5	Mean Trophic Level of the catch (mTLc)	$mTLc = \frac{\sum_i TL_i \cdot Y_i}{\sum_i Y_i}$ $TL_j = 1 + \sum_i DC_{ij} \cdot TL_i$ Where Y_i is the yield of compartment i; TL_i is the trophic level of that compartment; TL_j is the trophic level of predator j; TL_i is a trophic level of prey i and DC_{ij} is the proportion of prey i in the diet of predator j. Expresses the Trophic Level (TL) of the catch, reflects the fishing strategy of the fleet and is used to quantify the impact of fishing (Pauly et al.1998). It is expected to decrease with fishing (Shannon et al. 2009).
6	Mean Trophic Level of the community (mTLco)	$mTLco = \sum_i TL_i \frac{B_i}{B}$ Where TL_i is the trophic level of species B_i is the species biomass and B is the total biomass. Describes the TL of the whole ecosystem, reflects the structure of the ecosystem and is used to quantify the impact of fishing (Rochet and Trenkel 2003).
Ecological network analysis (ENA) indicators		

7	Redundancy (R)	$R = - \sum_{i=1}^n \sum_{j=1}^n (T_{ij}) \cdot \log \left(\frac{T_{ij}^2}{\sum_{j=1}^n T_{ij} \cdot \sum_{i=1}^n T_{ij}} \right)$	Where: T_{ij} is the flow between two compartments. This index is considered as an index of the system's resilience (Heymans et al. 2007) and it has been linked with ecosystem stability (Christensen 1995). It describes the distribution of energy flow pathways in the system. If the R is high, it indicates that they are many alternative pathways for energy flows to get from one compartment (functional group) to another. This allows compensation for the environmental stress, while lower R indicate that flows are constrained and energy is channelled through more specific pathways, indicating lower resilience to perturbation.
8	Relative ascendancy (A/C %)	$A = \sum_{i,j} (T_{ij}) \cdot \log \left(\frac{T_{ij} \cdot TST}{T_j \cdot T_i} \right)$ $C = \sum_{ij} T_{ij} \log \left(\frac{T_{ij}}{TST} \right)$	Where A is ascendancy where T_{ij} is the flow between two compartments i and j and it includes all outflows from each compartment, T_i is the sum of all material leaving the i th compartment, and T_j is the sum of all flows entering the j th compartment. C is the development capacity where TST is the sum of all flows T_{ij} in the system. It is an index of organisation of the food web. It is negatively related to maturity (Christensen 1995) which relates to system's growth and development (Ulanowicz 1986).
9	Finn's Cycling Index (FCI %)	$FCI = \frac{TST_c}{TST_{tot}}$	Finn's cycling index is the proportion of the total system throughput (TST_{tot}) that is recycled in the system (TST_c). It quantifies the relative amount of recycling in the system and is an indicator of stress and structural differences (Finn 1976). An increase in the FCI would suggest the system would recover faster from a perturbation, whereas a system would be expected to take longer to recover (lower FCI) when it is in a more degraded state (Vasconcellos et al. 1997).
10	System turnover rate (TotP/TotB)	The total Production / Total Biomass ratio	An indicator of the average size of organisms in an ecosystem (Shannon et al. 2009). It is hypothesized that fishing reduces the mean size of organisms in ecosystems and this indicator is expected to increase with fishing (Shannon et al. 2009).
11	Average Mutual Information (AMI)	$AMI = - \sum_{ij} \frac{T_{ij}}{TST} \cdot \log \left(\frac{T_{ij} \cdot TST}{T_j T_i} \right)$	Where, T_i is the sum of all material leaving the i th compartment of the ecosystem and T_j is the sum of all flows entering the j th compartment of the ecosystem. AMI measures the organisation of the exchanges among components. It shows how orderly and coherently the flows are connected. Is related to the resilience of the ecosystem. A rise in AMI signifies that the system is becoming more constrained and is channelling flows along more specific pathways (Ulanowicz and Abarca-Arenas 1997).

12 Entropy
(H)

$$H = - \sum_{ij} \frac{T_{ij}}{TST} \cdot \log \left(\frac{T_{ij}}{TST} \right)$$

Where T_{ij} is the flow between two compartments and TST is the sum of all flows in the system

The diversity of flows or systems entropy (H) is an indication of the total uncertainty embodied in the given configuration of flows in the system and represents the total number and diversity of flows in a system (Mageau et al. 1998). It is similar to diversity assessed by the Shannon diversity index (Shannon-Wiener) but considered flows instead of abundance (Ulanowicz and Norden 1990).

6.2.5. Assessment of the effects

The observed changes in sardine, related species and ecosystem indicators were assessed in reference to the baseline scenarios. The magnitude of the change in the assessed scenarios was measured using as a unit % and calculated in reference to the last year of simulation. In the combined scenarios, the type of interaction between the multiple stressors was assessed based on the operational definitions, according to the additive model defined by Folt et al. (1999). In this model, the type of interaction is classified in reference to the sum of effects caused by individual stressors. Under this model three types of interactions are distinguished: (1) an additive effect or null interaction that occurs when the combined effect equals the sum of the separate effects; (2) a synergistic interaction that occurs when the combined effect of multiple stressors is greater than the additive effect and (3) an antagonistic interaction that occurred when combined stressors produce a biological response that is less than the additive effect. Moreover, we considered the dominance effect that according to Côté et al. (2016) occurs when the combined effect of two stressors is equal to the effect of one of the two stressors that dominate the other.

6.2.6. Addressing uncertainty

Monte Carlo analysis built-in EwE and *Ecosampler* plug-in (Steenbeek et al. 2018) was applied to Ecosim to assess the sensitivity of outputs to the Ecopath input parameters. We run 200 simulations using the coefficient of variation obtained from the pedigree routine, which assesses the quality of the input data, in the following input variables: biomass, consumption/biomass, ecotrophic efficiency and production/biomass. Monte Carlo simulation

results were used to plot the 5th and 95th percentile confidence intervals for future scenarios of biomass and indicators trends.

6.3. Results

6.3.1. Analysis of the future changes in sardine and related groups

Intercomparison of the effects of future scenarios on sardine and other species is shown in Figure 6.2. The changes and observed effects are described in the following subsections while the explanation of the potential reasons and trophic interactions that might cause the observed effects is presented in Table 6.3.

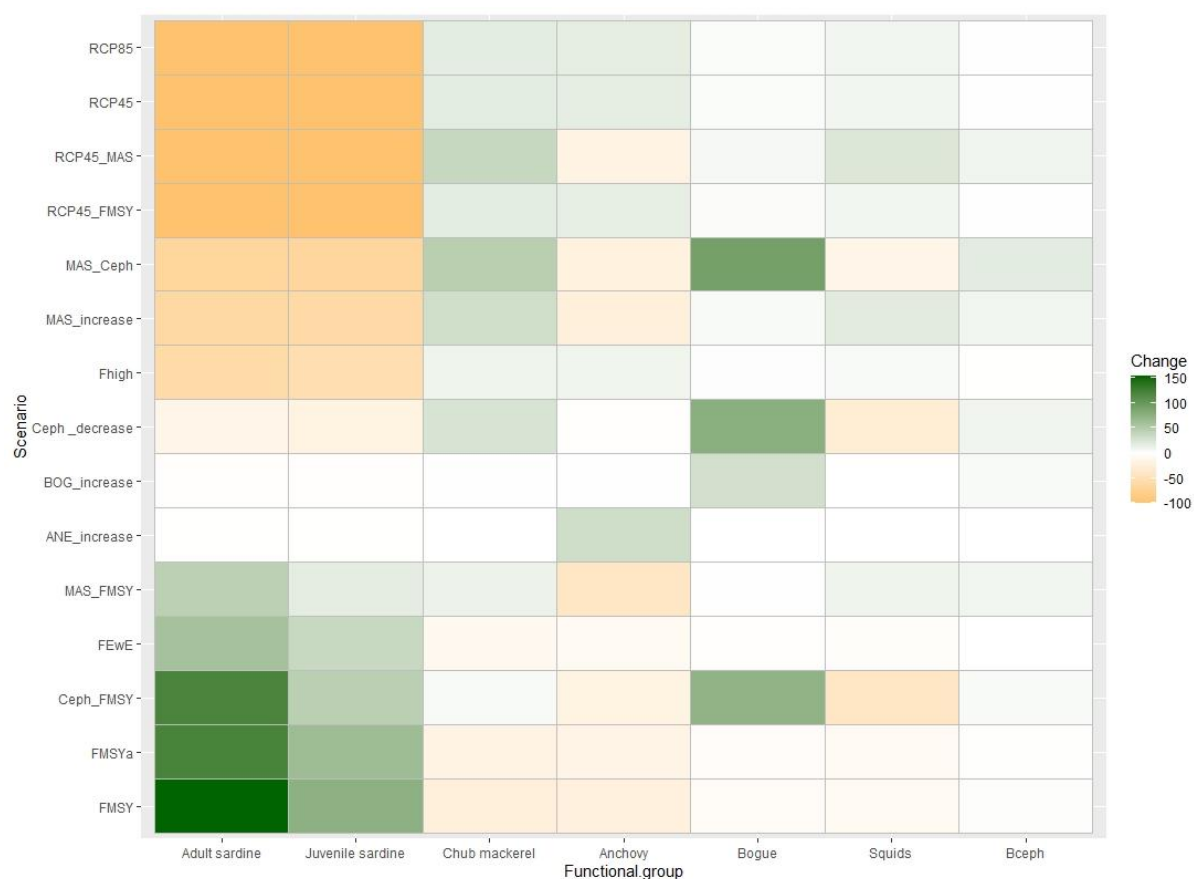


Figure 6.2 Change in biomass of selected species in relation to the baseline scenario. Change is shown in % and calculated in reference to the last year of simulation. Scenarios on the vertical axis are sorted according to the greatest effect on sardine. Abbreviations on the vertical axis that are the names of scenarios are explained in Table 6.1.

6.3.1.1. Baseline scenario

Under the baseline simulation (Sc1), the model predicted a decrease of sardine biomass by 13% in the next 30 years (Figure 6.3 a). During this time, the biomass of other small pelagic fishes that are main sardine eggs predators, such as chub mackerel and bogue, are also predicted to decrease by approximately 3% (Figure 6.3 ce). Moreover, anchovy that has a high niche overlap with sardine is projected to decrease by 30% by 2047 (Figure 6.3 d). On the other hand, the biomass of cephalopods that are important predators of adult sardine showed an increase in biomass of 6% and 10% for benthic cephalopods and squids respectively (Figure 6.3f g).

6.3.1.2. Fishing scenarios

Under scenarios that simulated a decrease in fishing effort (Sc2–4), the model showed an increase in sardine biomass and the magnitude of increase depended on the level of fishing mortality. Under the FEwE, FMSYa and FMSY sardine biomass is projected to increase by 60%, 120% and 150% respectively (Figure 6.3a).

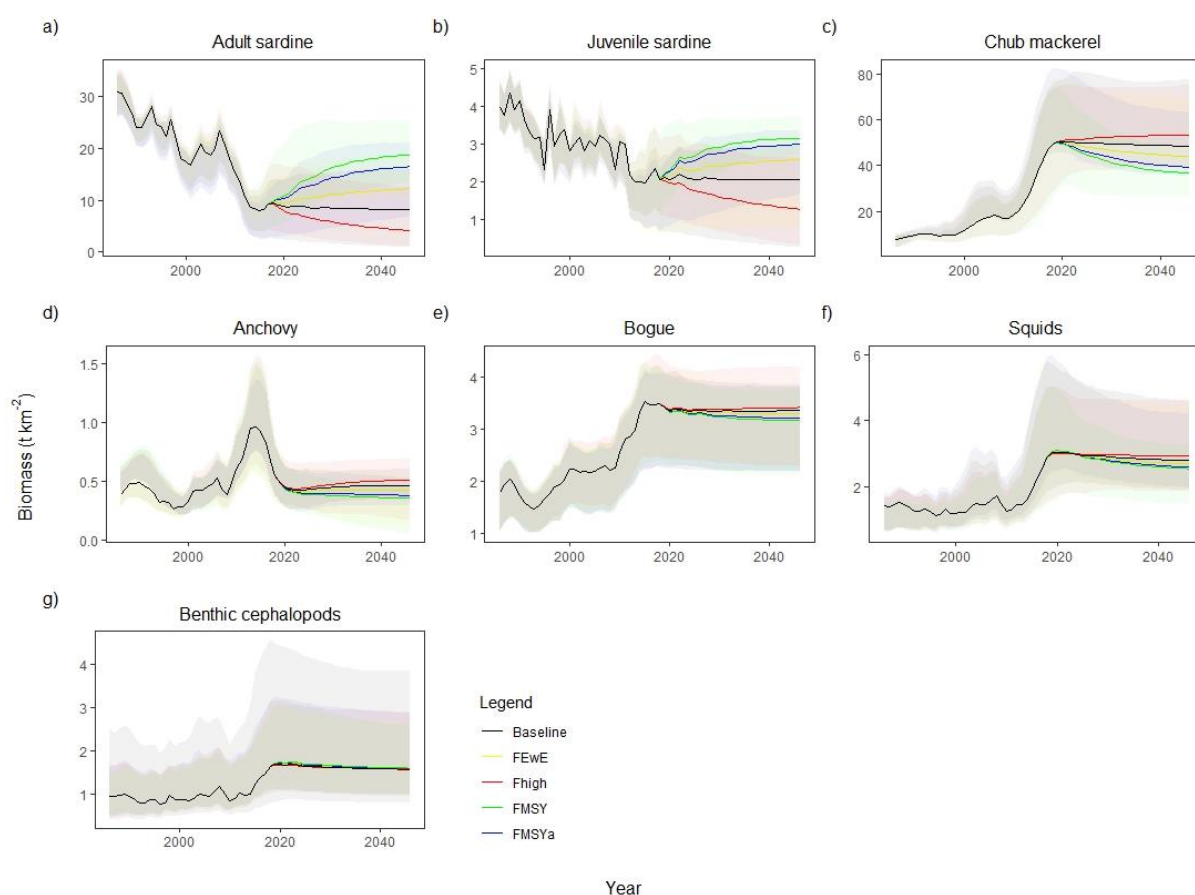


Figure 6.3 Biomass (t km⁻²) of selected species under fishing scenarios. Abbreviations of the names of the scenarios in legend are explained in Table 6.1.

On the other hand, under a scenario that considered an almost doubling of fishing effort (Sc5), a considerable decrease of sardine biomass by 60% by 2047 has been predicted when compared to the baseline scenario (Figure 6.3 a). Similar results were obtained for juvenile sardine (Figure 6.3 b). A varied fishing effort on sardine also had wide-ranging effects on its predators (Figure 6.3 c–g). In general, an increase in sardine fishing mortality had a positive impact on the biomass of sardine’s main predators (including the predators of sardine eggs) and competitors such as chub mackerel, cephalopods, bogue and anchovy (Figure 6.3 c–g). The opposite effects on sardine predators were observed under the scenarios that considered a decrease in sardine fishing mortality (Figure 6.3 c–g).

6.3.1.3. Trophic interactions scenarios

Under the scenarios that assessed sardine response to changes in its predators and competitors' biomass, the largest effect on sardine was observed for the scenarios that

considered an increase in biomass of chub mackerel and decrease in the biomass of cephalopods (Figure 6.4 a). In the case of the former, sardine biomass decreased by 64% while in the case of the latter, sardine biomass decreased by 15% by the end of the simulation, when compared to the baseline scenario (Figure 6.4 a).

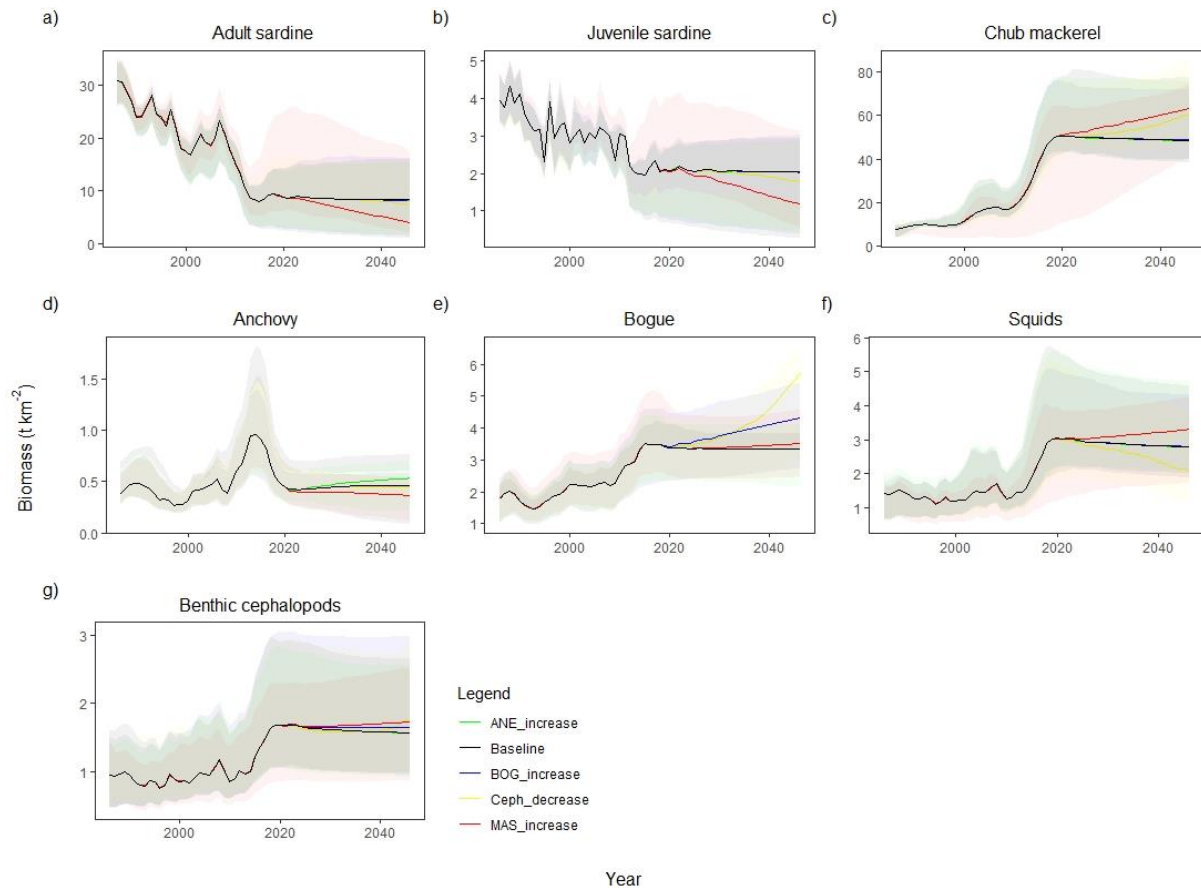


Figure 6.4 Biomass (t km⁻²) of selected species under trophic interactions scenarios. Abbreviations of the names of the scenarios in legend are explained in Table 6.1.

Also, the highest impact on other species was observed in scenarios that simulated an increase in the biomass of chub mackerel and a decrease of cephalopods.

An increase in chub mackerel biomass negatively impacted anchovy whose biomass decreased by 24% when compared to the baseline scenario (Figure 6.4 d). Moreover, this scenario positively impacted biomass of bogue, benthic cephalopods and squids that increased by 5, 9 and 19 % respectively (Figure 6.4 e–g).

A decrease in cephalopods had a positive impact on chub mackerel and bogue that increased by 26% and 77% respectively (Figure 6.4 ce). Besides their forcing to decrease, benthic

cephalopods, increased by 9% in this scenario (Figure 6.4 g). This increase was possibly related to the substantial decrease of squids that are the main competitors of benthic cephalopods.

6.3.1.4. SST scenarios

Scenarios that simulated the response of sardine to rising SST had a similar, severe effect on sardine biomass, causing its biomass to collapse between 2030 and 2040 (Figure 6.5 a). Sardine was projected to collapse approximately 10 years earlier under the scenario RCP85 which simulated high levels of greenhouse gases emissions when compared to scenario RCP45 that simulated intermediate emissions. When considering the effect on other functional groups, these scenarios had a positive impact on the biomass of sardine competitors and predators, chub mackerel, anchovy, bogue and squids (Figure 6.5 c–f).

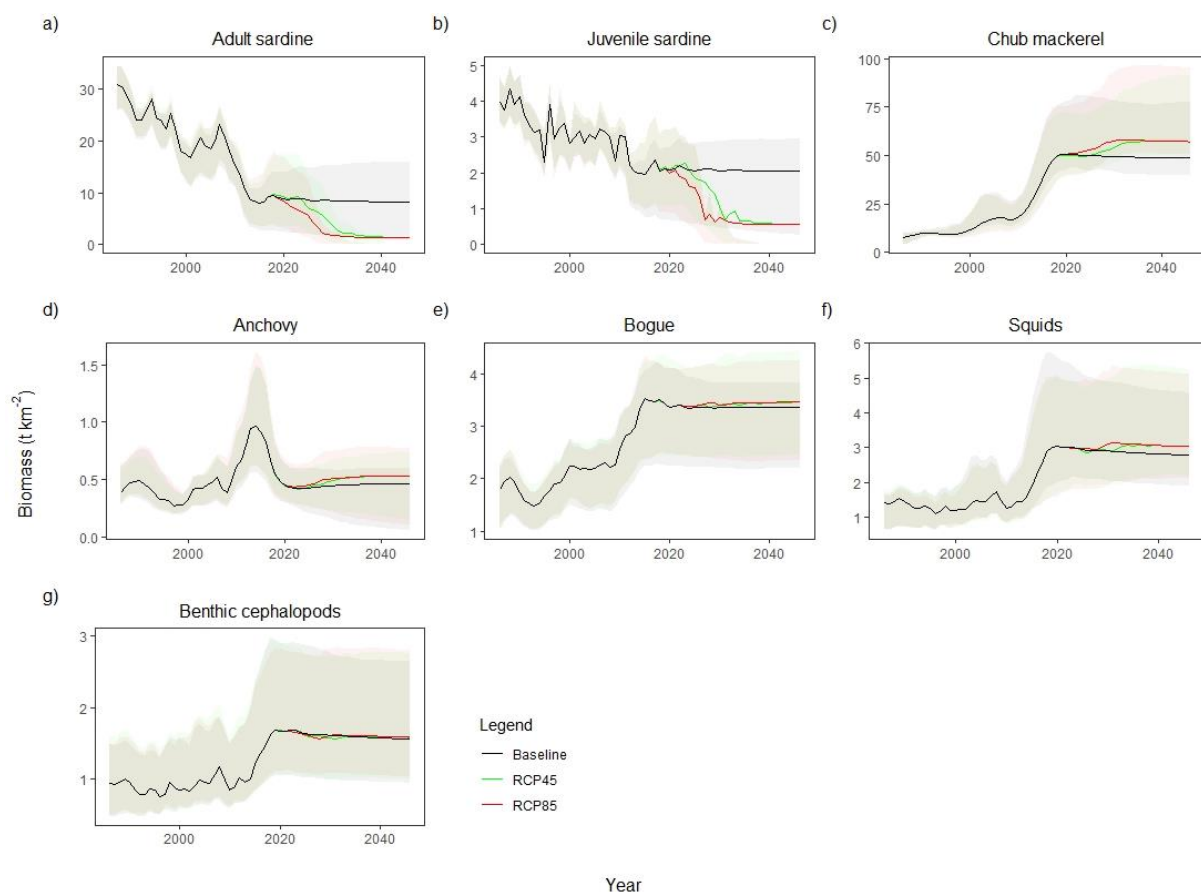


Figure 6.5 Biomass (t km⁻²) of selected species under rising SST scenarios. Abbreviations in the legend that are names of scenarios are explained in Table 6.1.

6.3.1.5. Combined scenarios

Among the combined scenarios that simulate the cumulative effect of fishing, trophic interactions and rise in SST, the largest negative impact on sardine biomass was observed under the scenarios that considered an increase in SST (Figure 6.6 a, Figure 6.2).

In the scenario that combined SST increase with FMSY (Sc12), the fishing at MSY did not considerably alleviate the negative effect on sardine biomass, delaying its collapse by only two years (Figure 6.6 a). Also, combining the effect of SST rise with increased biomass of chub mackerel (the main predator of sardine eggs) (Sc14), showed the same effect on sardine as under the scenario when the individual effect of SST rise was considered (Sc10) (Figure 6.6 a). This suggests that the effect of SST on sardine is predominant and is projected to occur before the effects of other stressors might have a chance to manifest. On the other hand, consideration of FMSY under the scenario when the main sardine predator, chub mackerel would increase (Sc13), considerably reduced the negative effect the chub mackerel had on sardine in scenario 6 that considered fishing at baseline F_{2017} (Figure 6.6 a). This suggested antagonistic effects of FMSY and an increase in chub mackerel. Similar results were observed in Sc15 that simulated a decrease in biomass of cephalopods. When combining this scenario with FMSY, sardine biomass was projected to double by 2047, while in Sc9 that consider F_{2017} , sardine biomass was expected to decrease by 15%. In the scenario that combines changes in the biomass of both main sardine predators (Sc16), the negative effect on sardine was amplified when compared to the scenarios that include these stressors individually. However, the effect was smaller than the sum of individual effects suggesting an antagonistic interaction between these stressors (Table 6.3).

Among combined scenarios, the largest impacts on the other species were observed for the scenarios that combine chub mackerel increase under FMSY (Sc13) and consider both increase and decrease of chub mackerel and cephalopods respectively (Sc16) (Figure 6.6, Figure 6.2). The former caused the largest negative impact on anchovy causing its decrease by approximately 40% (Figure 6.6 d). On the other hand, the scenario that considers changes in biomass of both sardine predators caused the largest increase in biomass of chub mackerel by 46% and bogue by 91% (Figure 6.6 ce; Figure 6.2).

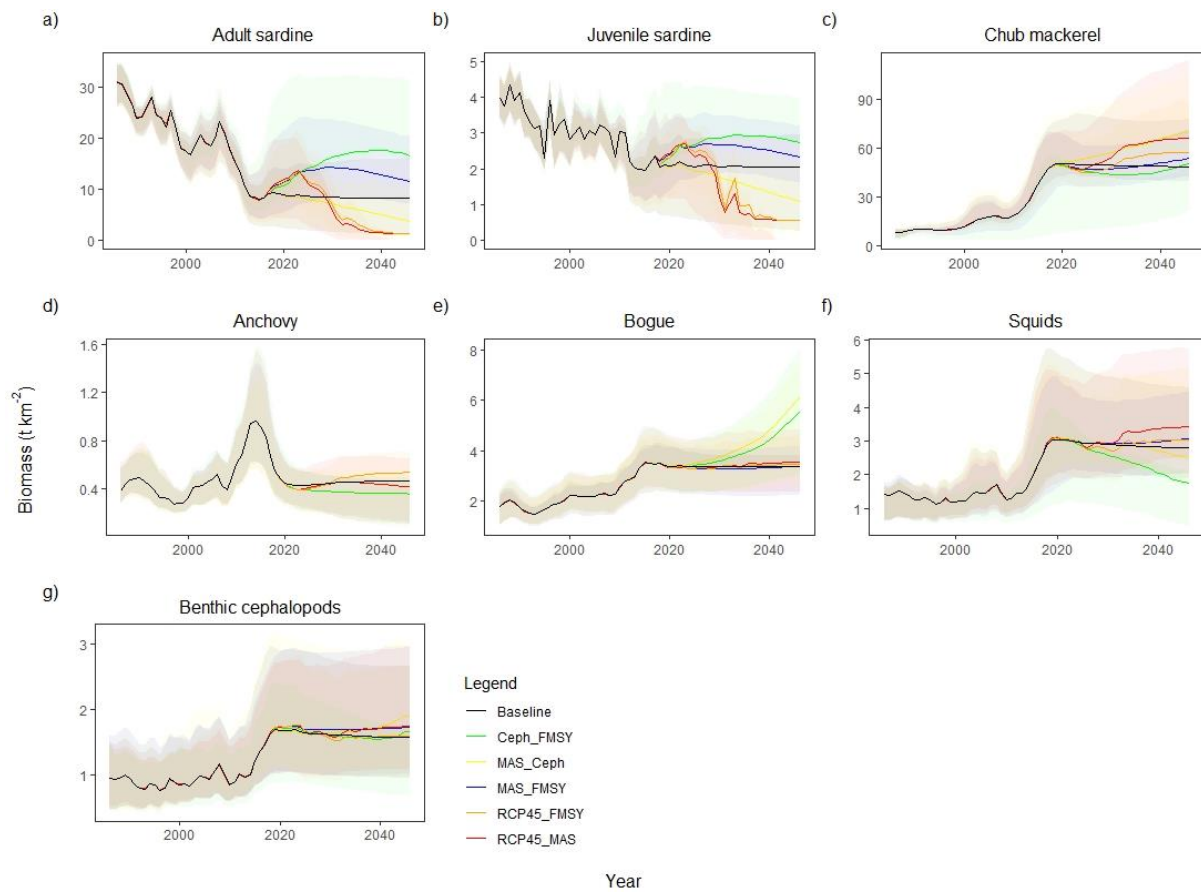


Figure 6.6 Biomass (t km⁻²) of selected species under combined scenarios. Abbreviations in the legend that are the names of scenarios are explained in Table 6.1.

6.3.2. Analysis of predicted changes in the ecosystem (ecosystem indicators)

Predicted changes in ecosystem indicators varied depending on the scenarios and indicator assessed (Figure 6.7; Figure 6.8).

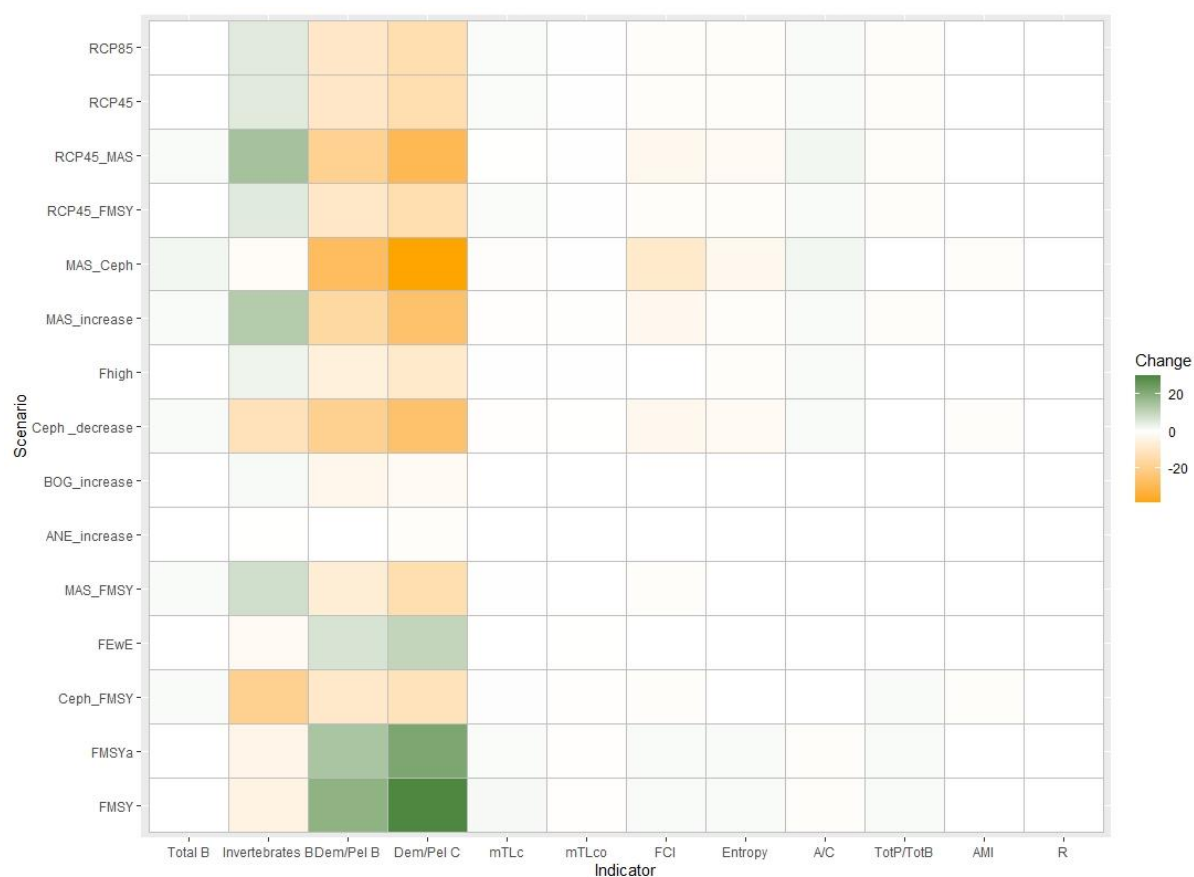


Figure 6.7 Change in ecosystem indicators in relation to the baseline scenario. Change is shown in % and calculated in the reference to the last year of simulation. Scenarios on the vertical axis are sorted according to the greatest effect on sardine. Abbreviations on the vertical (names of scenarios) and horizontal (indicators) axis are explained in Table 6.1 and Table 6.2, respectively.

In general, the indicators that varied the most among the scenarios were Dem/Pel C, Dem/Pel B and Invertebrates B, (up to 39% change when compared to the baseline scenario), followed by the FCI, Entropy and A/C (up to 9% change when compared to baseline scenario). The most stable indicators across scenarios were: Total B, mTLc, mTLco, R, AMI, TotP/TotB (up to 1 % change when compared to baseline scenario) (Figure 6.7).

In the baseline scenario, an increase in the importance of the demersal compartment between 6 and 14% (as reflected by indicators Dem/Pel C $\uparrow$ 14%; Dem/Pel B $\uparrow$ 8%) was observed (Figure 6.8 cd). Other indicators varied slightly, for example, a minor decrease in resilience and maturity ($R\downarrow$, $A/C\uparrow$, 1%) of the ecosystem was registered.

When compared to the baseline, in the scenario that simulates fishing at reduced F and FMSY, an increase in the importance of the demersal compartment of the ecosystem between 6 and 30% (as reflected by indicators Dem/Pel B $\uparrow$ 6–19%; Dem/Pel C $\uparrow$ 10–30%), with a

simultaneous decrease in invertebrate's biomass (up to 5%) was observed (Figure 6.8 b-d; Figure 6.7). Also, in these scenarios, a slight increase in mTLc was observed (mTLc $\uparrow$ 1.5%, Figure 6.8e). Ecosystem effects described by ENA indices were less pronounced and showed a slight increase in maturity (A/C $\downarrow$ up to 1%), stability (FCI $\uparrow$ up to 1.2%) and diversity of flows (Entropy $\uparrow$ up to 1%) (Figure 6.8 h-l). Opposite effects on indicators were observed for the scenario that simulates increased sardine fishing mortality.

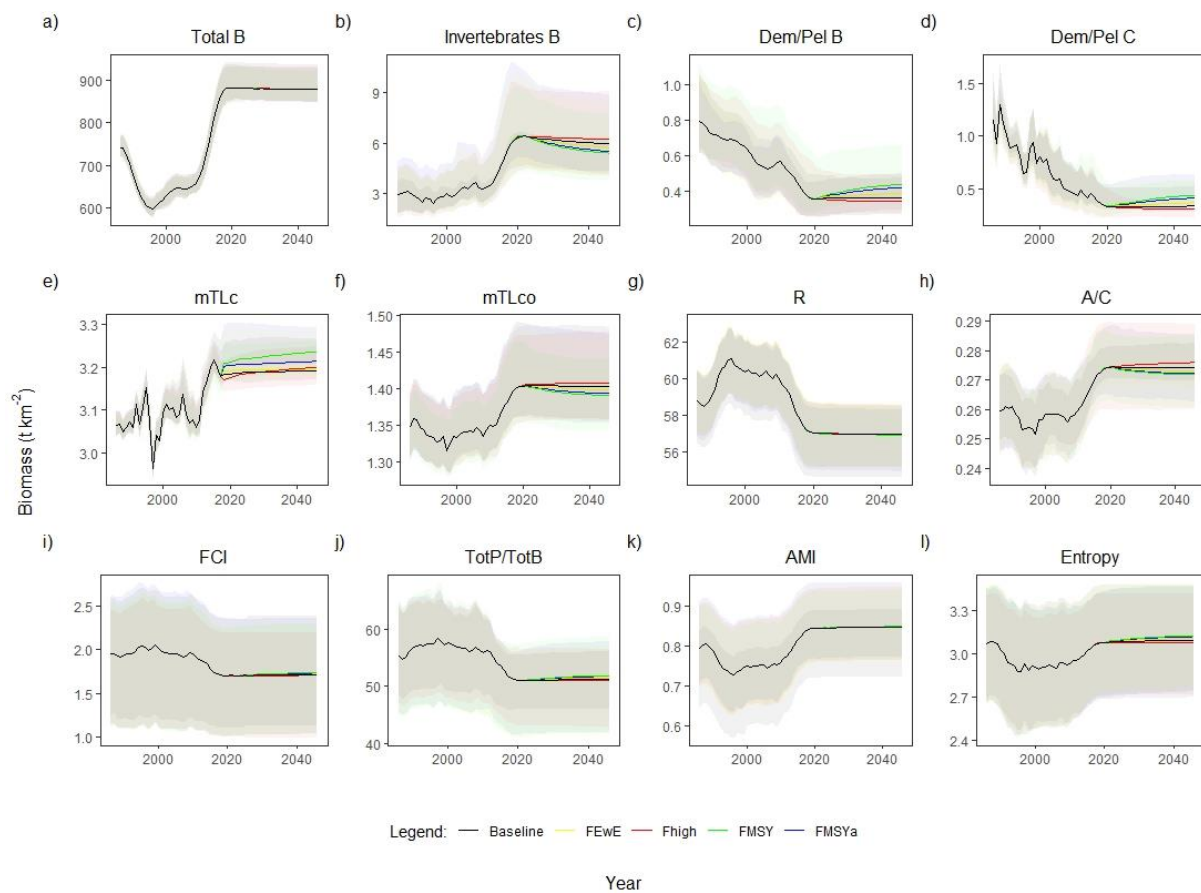


Figure 6.8 Ecosystem indicators under fishing scenarios. Abbreviations of scenarios (in legend) and indicators names (in the individual plot title) are explained in Table 6.1 and Table 6.2, respectively.

In the trophic interactions' scenarios, chub mackerel and cephalopods were sardine predators that caused the largest effects in the change of indicators (Figure 6.9). In scenarios simulating the forced biomass of chub mackerel, a decrease in the importance of the demersal compartment of the ecosystem between 16% and 26% (as reflected by indicators Dem/Pel B $\downarrow$ 16%; Dem/Pel C $\downarrow$ 26%,) with a simultaneous increase in Invertebrate's biomass was apparent (Invert B $\uparrow$ 13%) (Figure 6.9 b-d). Moreover, in this scenario, a minor decrease in the stability

(FCI $\downarrow$ 3%), maturity (A/C $\uparrow$ 1.3%) and diversity of flows (Entropy $\downarrow$ 1.4%) was observed (Figure 6.9 hil). Similar effects were observed in the scenario simulating decreased biomass of cephalopods, except for invertebrate's biomass indicator whose value decreased in this scenario by 12% (Figure 6.9 b). Changes in the ecosystem indicators in the scenarios that simulate an increase in bogue and anchovy biomass were minor (up to 4%).

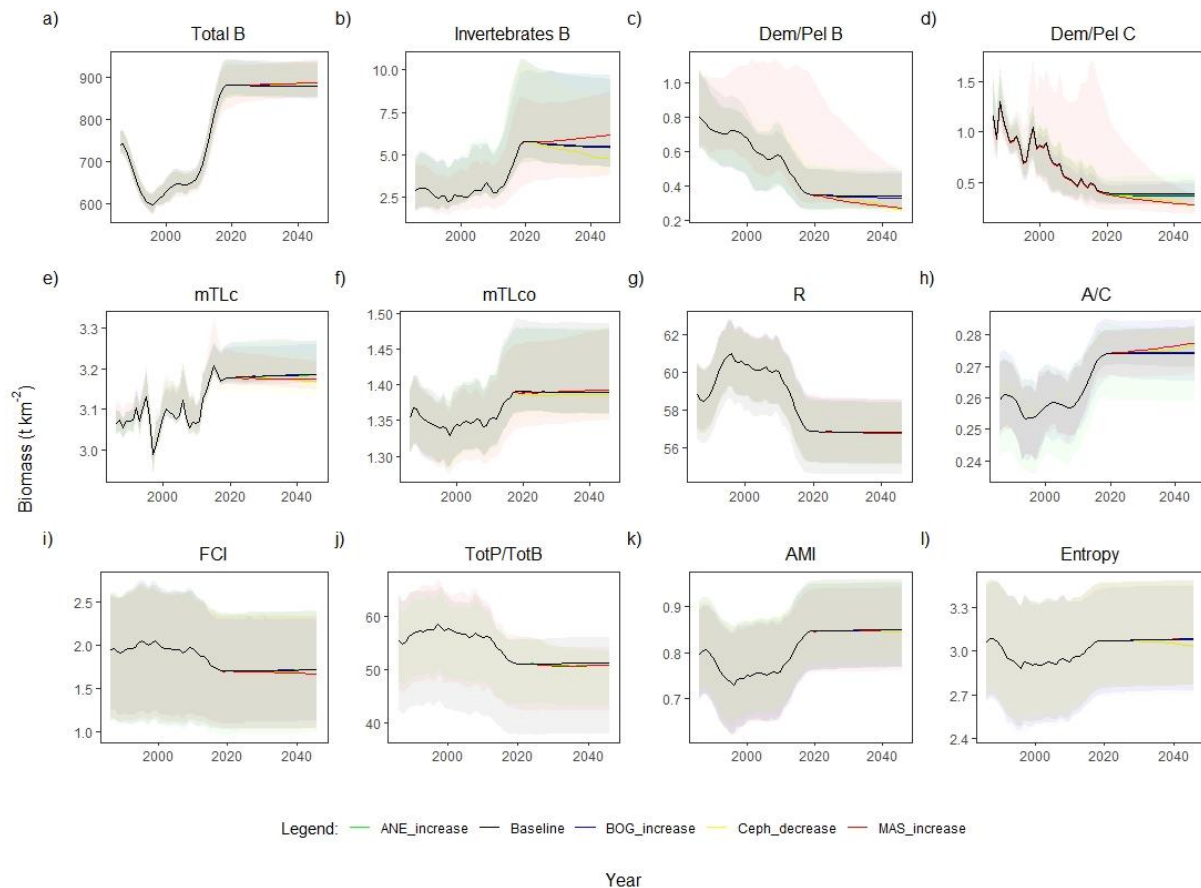


Figure 6.9 Ecosystem indicators under trophic interactions scenarios. Abbreviations of scenarios (in legend) and indicators names (in the individual plot title) are explained in Table 6.1 and Table 6.2, respectively.

Scenarios that simulate an increase in SST demonstrated a decrease in the importance of the demersal compartment of the ecosystem between 10 and 14% (as reflected by indicators Dem/Pel B $\downarrow$ 10%; Dem/Pel C $\downarrow$ 14%) and an increase in invertebrates' biomass (up to 5%) (Figure 6.10 b–d; Figure 6.7). Also, these scenarios showed a minor decrease in maturity (A/C $\uparrow$ 1.5%), stability (FCI $\downarrow$ 0.8%), and diversity of flows (Entropy $\downarrow$ 1.3%) of the ecosystem (Figures 6.7; 6.10 hil).

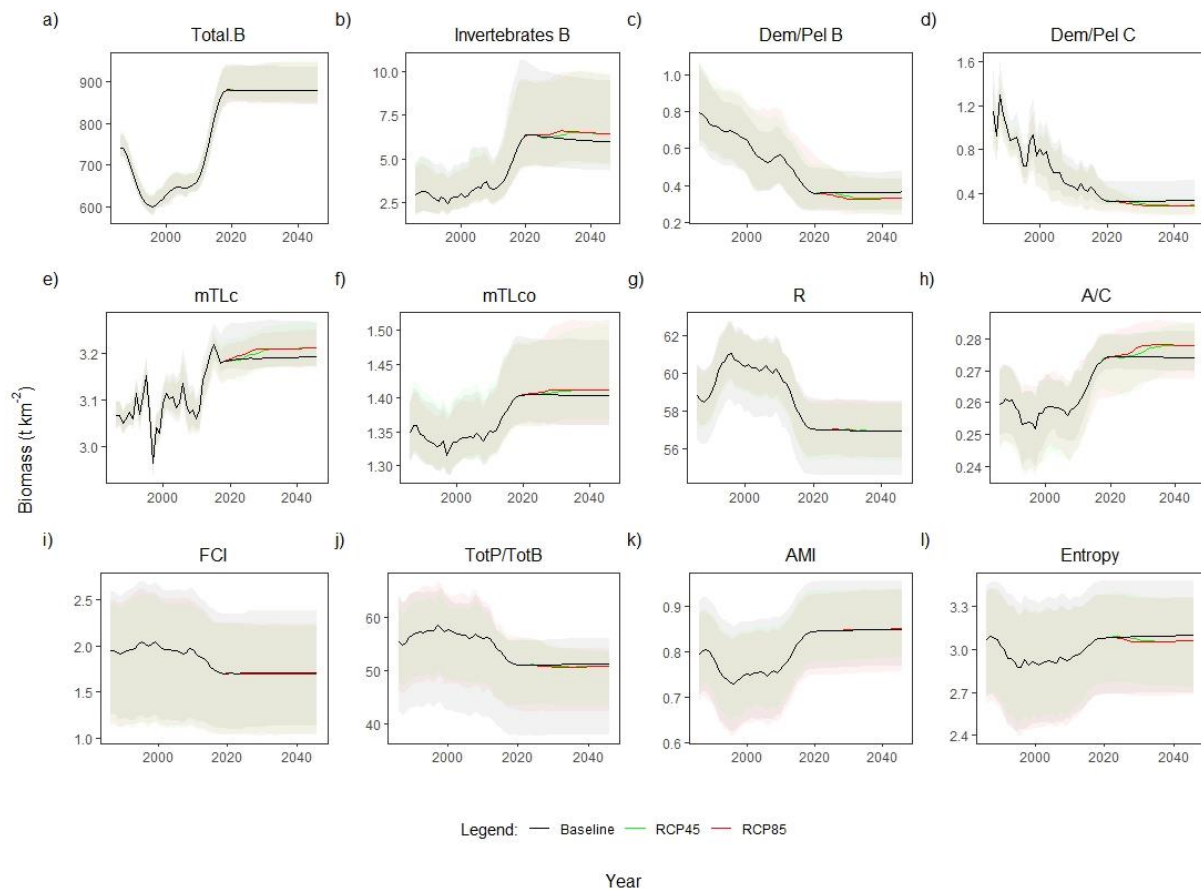


Figure 6.10 Ecosystem indicators under SST scenarios. Abbreviations of scenarios (in legend) and indicators names (in the individual plot title) are explained in Table 6.1 and Table 6.2, respectively.

The effects observed in scenarios that combine changes in predators' biomass and FMSY (Sc13 and Sc14) showed similar effects to the scenarios Sc6 and 9 that simulate the sole effect of species increase, however, their effect was less pronounced (Figure 6.11) (alleviated due to the antagonistic effects of FMSY and biomass changes). On the other hand, in Sc12 that combine rise in SST and FMSY, effects were the same that in scenarios that simulate the individual effect of a rise in SST (no alleviation effect of FMSY was observed in this case). The effects observed in the scenarios that combine multiple stressors, i.e., Sc15 (that simulate an increase and decrease in chub mackerel and cephalopods respectively) and Sc16 (that simulate an increase in chub mackerel and rise in SST) were more pronounced when compared to the effects observed in scenarios that simulate these pressures separately, suggesting the existence of additive or antagonistic effects. In general, among the combined (and all tested) scenarios, the largest changes in the ecosystem indicators were observed for Sc15 (that simulate an increase and decrease in chub mackerel and cephalopods respectively) (Figure 6.7). The changes included a decrease in the importance of the demersal compartment of the ecosystem

(as reflected by indicators Dem/Pel B↓ 28%; Dem/Pel C 30%, (Figure 6.11 c–d) and a decrease in maturity (A/C↑ 2.4%), stability (FCI↓ 9%), and diversity of flows (Entropy↓ 3.5 %) (Figure 6.11 hil).

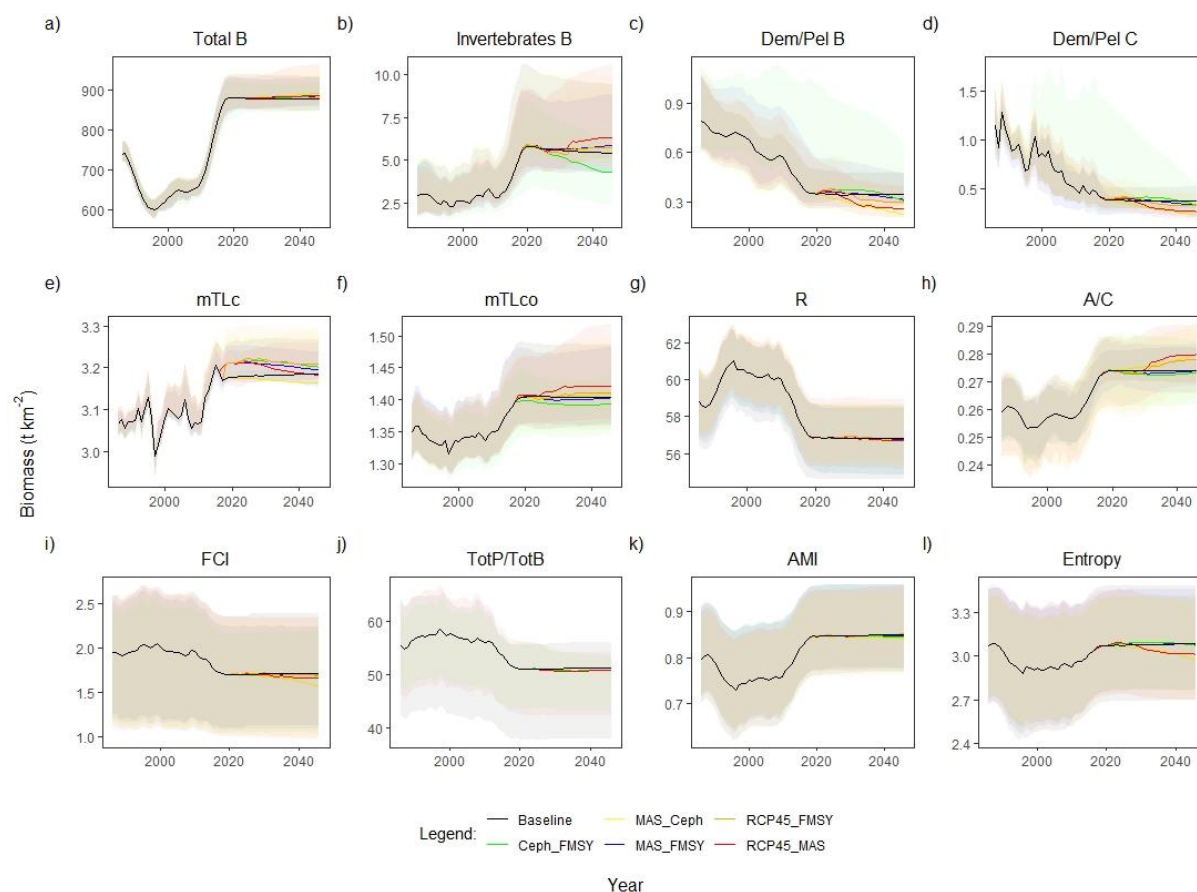


Figure 6.11 Ecosystem indicators under combined scenarios. Abbreviations of scenarios (in legend) and indicators names (in the individual plot title) are explained in Table 6.1 and Table 6.2, respectively.

Table 6.3 Trophic effects and their potential explanation across analysed scenarios. In combined scenarios, the type of interaction between combined stressors is indicated. It was calculated based on the additive model according to Folt et al. (1999). Names of scenarios and their explanation are provided in Table 6.1.

Scenario		Functional group					
		Sardine	Chub mackerel	Anchovy	Bogue	Benthic cephalopods	Squids
Fishing scenarios							
Sc2	FEwE	Increase due to reduced fishing pressure	Decrease due to reduced niche (an increase of main competitor – sardine).	Decrease due to reduced niche (an increase of main competitor – sardine)	Decrease due to increase in predation mortality caused by the increase of its main predator – benthic cephalopods	Increase due to the reduction of predation (decrease of main predator – chub mackerel) and due to the release of the niche (decrease of the main competitor – Squids)	Decrease due to reduction in the availability of the prey (decrease of its most important prey – chub mackerel) and due to the increase in competition (Benthic cephalopods are the main competitor).
Sc3	FMSY_a						
Sc4	FMSY						
Sc5	F_{high}	Decrease due to increased fishing pressure	Increase due to amplified niche (decrease of main competitor – sardine)	Increase due to amplified niche (decrease of main competitor – sardine)	Slight increase due to indirect cascading trophic interactions related with an increase in chub mackerel that acts in two ways: 1) decrease in benthopelagic invertivores fish (due to more predation from chub mackerel) --> increase in macrozooplankton (due to reduced predation from benthopelagic invertivorous fish) --> less competition for bogue (more prey availability for bogue). 2) increase in common dolphin (due to higher availability of its important prey chub mackerel) ----> decrease in horse mackerel (due to higher predation from common dolphin) ----> more prey (macrozooplankton) availability for bogue.	Slight increase due to an increase in the availability of important prey (an increase of important prey – chub mackerel), besides an increase of competition (increase in Squid). This indicates that the positive effect of the availability of important prey outnumbers the negative effect of competition with Squid.	Increase due to the increase in the availability of its most important prey – chub mackerel.
Trophic interactions scenarios							

Sc6	MAS_increase	Decrease due to increase of its important competitor and main egg predator (chub mackerel)	Increase because it was forced to increase	Decrease due to substantial increase in its main predator (squid) and important competitor (chub mackerel)	Increase due to the same reasons as in scenario Fhigh	Probably the same as above	Probably the same as above
Sc7	BOG_increase	Slight decrease due to increase in its main eggs predator (chub mackerel)	Slight increase due to decrease of its main competitor (sardine) (niche release)	Slight increase due to decrease of its main competitor (sardine) (niche release)	Increase because it was forced to increase	Increase due to increase in its important prey (bogue)	Slight increase
Sc8	ANE_increase	Slight decrease due to an increase in its important competitor (anchovy)	Slight decrease due to an increase in its important competitor (anchovy)	Increase because it was forced to increase	No change	Slight decrease, due to reduction of prey, (sardine chub mackerel)	Slight decrease, due to the reduction in prey (sardine, chub mackerel)
Sc9	Ceph_decrease	Decrease due to increase in its main competitor (chub mackerel)	Increase due to decrease of its main predator squid	Slight decrease, due to increased competition from chub mackerel, even though its main predator squid decrease	The same effects as in scenario Fhigh and MAS increase. However, in this scenario, the effect on bogue is more pronounced than in scenarios Fhigh and MAS_increase, because in this scenario simultaneous decrease in squid, one of the bogue main predator, has occurred that intensify the effect of bogue increase.	Increase through the effect of squid, less competition	Decrease because it was forced to decrease
SST scenarios							
Sc10	RCP45	Decrease due to rise in SST	Increase due to amplified niche (decrease of main competitor sardine)	Increase due to amplified niche (decrease of main competitor sardine)	The same as in scenario Fhigh, and MAS_increase	The same in Sc. Fhigh	The same as in the scenario. Fhigh and MAS_increase
Sc11	RCP85						
Combined scenarios							
Sc12	RCP45_FMSY	The same as above (in scenario RCP45. Effect of	The same as in scenario RCP45. The dominant effect of RCP45	The same as in scenario RCP45. The dominant effect of RCP45	The same as in scenario RCP45. The dominant effect of RCP45	The same as in scenario RCP45. The dominant effect of RCP45	The same as in scenario RCP45. The dominant effect of RCP45

Sc13	MAS_FMSY	climate not reduced by FMSY The dominant effect of RCP45					
		Decrease of sardine reduced by FMSY. The interactions between combined stressors were classified as antagonistic because the observed effect is less than additive.	Increase of chub mackerel reduced by FMSY. However, the effects are classified as synergistic because the effect is larger than additive.	Decrease of anchovy amplified through combined effects of MAS_increase and FMSY. However, the effect is smaller than additive therefore it is classified as antagonistic.	Increase of bogue reduced by FMSY. However, the combined effect is larger than additive therefore it is classified as synergistic.	Increase of benthic cephalopods reduced by FMSY – antagonistic effects. This happened due to a smaller increase of chub mackerel (benthic cephalopods predator) in this scenario when compared to scenario MAS_increase (due to antagonistic effect of FMSY on chub mackerel)	Additive effect of FMSY and MAS_increase on Squid.
Sc14	RCP45_MAS	The dominant effect of SST rise	Increase in chub mackerel amplified by combined effects of SST rise and chub mackerel forcing. However, the effect is smaller than the sum of individual effects therefore the interaction between stressors is classified as antagonistic.	Decrease in anchovy reduced by the effect of SST - antagonistic effects.	Increase in bogue amplified by combined effects of SST rise and chub mackerel forcing. However, the effect is smaller than the sum of individual effects therefore it is classified as antagonistic effects.	The effect is the same as in scenario MAS_increase. The dominant effect of SST rise.	Increase in squid amplified by combined effects of SST rise and chub mackerel increase. However, the effect is smaller than additive therefore it is classified as antagonistic.
Sc15	Ceph_FMSY	Decrease in sardine reduced by FMSY. antagonistic effects	Increase in chub mackerel reduced by FMSY. However, the effect is larger than the sum of individual effects therefore the interaction between stressors is classified as synergistic.	A decrease in anchovy is amplified by the combined effects of FMSY and Ceph_decrease. However, the effect is smaller than the sum of individual effects therefore the interaction between stressors is classified as antagonistic. In this scenario, a decrease in anchovy was alleviated when compared to scenario	An increase in bogue was reduced by FMSY. However, the effect was larger than the sum of the individual effects therefore the interaction between stressors was classified as synergistic.	Antagonistic effect of FMSY and Ceph on benthic cephalopods. An increase in benthic cephalopods was reduced compared to scenario Ceph_decrease due to a smaller increase of chub mackerel (benthic cephalopods predator) in this scenario when compared to scenario	Synergistic effect of cephalopods decrease and FMSY

				FMSY and not enlarged by a decrease in cephalopods, probably due to a lower increase in sardine (a main competitor of anchovy) when compared to scenario FMSY.		Ceph_increase. Even though the biomass of benthic cephalopods that is the main competitor of squid, decrease substantially, the effect of the reduced prey was more important.	
Sc16	MAS_Ceph	Decrease of sardine amplified by combined stressors but the effects are lower than additive so are classified as antagonistic.	Increase of chub mackerel amplified by combined stressors but the effects are lower than additive so are classified as antagonistic.	Antagonistic effect of cephalopods decrease and chub mackerel. The negative effect of squid on anchovy (its main predator) in this scenario was smaller than in scenario MAS_increase, Also, in this scenario occurred a larger increase in chub mackerel biomass, (one of the main anchovy competitors) than in scenario Ceph_increase.	Synergistic effect of Ceph_increase and MAS_decrease. In this scenario, the effect on Bogue is even more pronounced than in scenario Ceph_increase and Ceph_FMSY even though the decrease in squid, one of the bogue main predator, was not so large as in scenario Ceph_increase. However, the increase in biomass of chub mackerel was much larger that seemed to play a more important role.	Additive effect of combined stressors	Antagonistic effect of cephalopods decrease and chub mackerel.

6.4. Discussion

In this study we used the Ecopath with Ecosim modelling approach, to assess the future effects of multiple stressors on sardine stock in the context of the whole ecosystem. To our knowledge, this is the first study, that assesses the future impact of multiple stressors including cumulative impacts on Iberian sardine, and the Portuguese marine ecosystem. This study highlighted the potential of ecosystem modelling to increase our understanding of the effects of multiple stressors on the marine environment. Moreover, it demonstrates the complexity of the interactions between functional groups in the ecosystem and multiple stressors. This emphasises the need for their consideration in the effective management of marine ecosystems.

6.4.1. Future effects on sardine and other species

6.4.1.1. Fishing scenarios

In this study, fishing had been highlighted as the main factor whose changes have the greatest capacity to improve the sardine stock. In all scenarios that simulated decreased fishing mortality, the improvement of the stock has been documented. Moreover, in the simulation at FMSY, the recovery in sardine biomass to the level prior to 2009 was observed. These results confirm that the management measures adopted by ICES are precautionary and have the potential to be effective in rebuilding the stock. Indeed, recovery of sardine biomass has been observed recently (ICES 2020). However, since the sardine decline in 2009, FMSY recommended by ICES was rarely realised in practice (ICES 2020). Sardine is a high demand species due to its high price market and tradition of consumption. Therefore, it is difficult to maintain low catch and decision-makers are reluctant to comply ICES recommendations. Under the scenario that is the most desirable by fishers and that resemble the catch before sardine decrease prior to 2009 (~50,000 tonnes), not only is sardine recovery impaired but also, a considerable stock reduction was observed. This scenario, although preferred by fishers would affect them negatively because high catch levels cannot be sustained by the decreasing stock.

The effect of decreased sardine fishing had a negative impact on sardine competitors and predators. The negative effect on predators is counter-intuitive, and it happened due to

indirect trophic interactions between sardine predators and competitors. The main predator of adult sardine is squid whose main prey is not only sardine but also chub mackerel. Therefore, an increase in sardine biomass not only negatively affects chub mackerel but also its predator squid. This highlights the complexity of the interactions between sardine and chub mackerel and demonstrates that chub mackerel can influence sardine on multiple levels: through competition, benefiting main adult sardine predator and also being the main predator of sardine eggs (Garrido et al. 2015). These complex interactions demonstrated in these simulations classify chub mackerel as a key species to study in order to better understand sardine dynamics and its decline. The role of the dynamics between sardine and chub mackerel in explaining sardine decline has been recently widely discussed (Martins et al. 2013; Garrido et al. 2015; García-Seoane et al. 2019; chapter 4; Szalaj et al. 2021a). However, the recent studies highlighted that further research is needed to fully understand the interactions between main pelagic species in the PCSE (Garrido et al. 2015; García-Seoane et al. 2019).

6.4.1.2. Trophic interactions scenarios

Among tested scenarios, changes in trophic interactions revealed to have a similar impact on sardine as increased fishing mortality. Also, effects on other assessed species were pronounced. Moreover, results showed that the interactions between studied species are complex, multi-faceted and their understanding without in-depth analysis can be challenging.

There are several types of species interactions within the ecosystem, that (among others) can be direct, indirect intra-specific or inter-specific (Lang and Benbow 2013). Due to this complexity, and the existence of many links among species within a food web, changes to individual species can have far-reaching effects. Understanding species interactions and their impacts on the ecosystem become a crucial component of fisheries and ecosystem management (e.g., Pikitch et al. 2004). Ecosystem models played a key role in this research (Plagányi 2007), and their use demonstrated the importance of species interaction in reproducing the historical dynamics of many marine ecosystems worldwide (e.g., Colléter et al. 2015). Due to the growing intensity in pressures affecting ecosystems at all trophic levels, considerable changes in species distributions, their invasions and replacements are expected in the future changing ecosystems (Kordas et al. 2011; Fernandes

et al. 2013; Chan et al. 2018). Therefore, studying trophic interactions between changing species and assessing their impact on the other species, ecosystem and its services is becoming increasingly important to sustain ecosystem services.

6.4.1.3. SST scenarios

In this study, the rise in SST has been highlighted as the principal stressor of sardine, causing the most severe effects on the species abundance. This study demonstrated that the warming conditions of the future Portuguese coast might disfavour sardine productivity. These findings are in line with other studies that linked sardine recruitment and productivity with SST (Santos et al. 2012; Leitão et al. 2014; Garrido et al. 2017). The severe effects observed in this study highlighted the importance of climate change in the evolution of the sardine stock around PCSE, however, they did not indicate its extinction, but rather suggested their northward migration to cooler waters outside the study area. Signals of northward migration due to the rising SST has been observed in many places around the world (Perry et al. 2005; Nicolas et al. 2011) including the Iberian Coast (Leitão et al. 2018, Teixeira et al. 2014). Also, environmental suitability for sardine in the Iberian Peninsula was predicted to decrease and the expansion of the species northwards has been modelled (Schickele et al. 2021b). Furthermore, it is important to highlight that this study did not consider potential physiological adaptations to rising SST, as has been observed for terrestrial species (Logan et al. 2014). Also, in the case of sardine, some premises might suggest potential adaptation of Iberian sardine to increasing SST. By screening the variation of genes directly involved in metabolic performance, Baltazar-Soares et al. (2021), inferred the adaptive potential of sardine populations to shifts in temperature and dissolved oxygen. In their study, authors inferred that the sardine stock in the Iberian Peninsula is selected to tolerate colder sea surface temperature, as a result of adaptive mechanisms to the lower temperatures that occur in this coast due to the strong seasonal upwelling (Wooster et al. 1976; Fiúza et al. 1982). The authors discussed that the evolutionary dynamics of the sardine genetic pool purged specific haplotypes from the population due to the potentially deleterious effects.

6.4.1.4. Combined scenarios

In this study, the interactions observed between multiple stressors when assessing effects on sardine were mainly antagonistic while effects on other species were also

synergistic. These are the interactions that are the most often reported in the ecological literature (Côté et al. 2016). Moreover, the dominance effect of SST rise was observed when an increase in SST was combined with other stressors. The dominance of SST stressor indicate that it poses the highest risk for the sustainability of the sardine stock and mitigation of this stressors should be prioritised in the management process. However, the rise of SST is a global problem and cannot be directly addressed by the actions of local management. Locally managed actions such as fishing at MSY, which showed to be very effective in rebuilding sardine stock under FMSY scenarios considering the 2017 SST level, does not alleviate the negative effect of SST rise on sardine. Based on the future simulations in the west coast of Scotland, Serpetti et al. (2017) concluded that ocean warming could jeopardise the recovery of boreal stenothermal fish species such as cod, herring and haddock even when fishing at MSY. Also, Corrales et al. (2018) documented that beneficial effects of the fishing reduction in the Eastern Mediterranean Sea may be dampened by the impact of increasing SST and invasive species when acting together. These results confirmed that climate change is one of the greatest threats to marine ecosystems (Halpern et al. 2007). However, other combined scenarios demonstrated that fishing at MSY has the potential to alleviate the negative effects of the biomass changes in the species interacting with sardine. Reduced fishing pressure acted antagonistically with the pressure caused by chub mackerel increase and cephalopods decrease. These results demonstrated that the reduction of fishing effort on depleted stocks can compensate for the negative effects caused by other stressors. Moreover, this scenario is especially relevant for management as the fishing pressure is managed locally.

6.4.2. Future effects on the ecosystem

The largest effects on the ecosystem were observed for the indicators that are directly related to the changes between the pelagic and demersal compartment. The largest effects were observed under scenarios that simulate fishing at FMSY, changes in chub mackerel, cephalopods followed by SST scenarios. Scenarios that influenced the decrease in sardine biomass (due to increased F, SST and chub mackerel increase) had a negative impact on the demersal compartment while scenarios that caused an increase in sardine biomass showed an opposite effect. The negative impact on the demersal compartment observed in this study when sardine is low in biomass can be associated with the proliferation of the other SPF that compete with sardine and dominate the demersal community (by biomass). On the contrary,

when sardine is dominant, the biomass of other SPF is reduced, and consequently, the demersal compartment becomes dominant.

In this study, the largest effects on ENA indicators were observed in the scenarios that simulated combined and individual changes in the biomass of chub mackerel and cephalopods. Under these scenarios, the ecosystem stability, maturity, and diversity of flows were predicted to reduce between 1.5% and 9%. Reduction in ecosystem stability, which is an indicator of stress, and maturity might suggest that the proliferation of the other SPF with a simultaneous decrease in sardine, might be stressful for the ecosystem. Szalaj et al. (2021b, chapter 5) discussed that the decline in sardine biomass observed in PCSE in the latest decades might have disturbed important trophic links and pathways through which the flow of energy passes. The authors discussed that the reason for this disturbance might be related to the other species that competed with sardine, filled its ecological niche and might have not been so well linked to the rest of the food web. Therefore, under the scenarios, that predict the proliferation of other SPF, the disruption in the pelagic energy flow might occur. Consequently, ecosystem stability, maturity and diversity of flows might become reduced. Similar changes were described in the Northern Benguela upwelling system, where Heymans and Tomczak (2016) observed a shift in dominant pelagic species that coincided with the simplification of the food web and reduced resilience.

6.4.3. Implications to the management of sardine

Ecosystem models such as EwE can be a valuable tool in assisting single stock assessment methods in strategic and long-term management (Plagányi and Butterworth, 2004; Christensen and Walters, 2011). Ecopath with Ecosim were not developed to substitute single stock assessment methods but to complement them as they are capable to answer the questions that other methods cannot (Christensen and Walters, 2011). This potential of EwE has been recognised and new strategies to use EwE quantitative inputs in single-species stock assessment models (to provide tactical management advice) has been proposed (Bentley et al. 2021; Chagaris et al. 2020). These approaches can facilitate the inclusion of ecosystem information into management advice as they fit in the existing regulatory framework (Howell et al. 2021).

Also, this study demonstrated the potential of EwE in supporting the management of Iberian sardine. By running long term scenarios considering various sardine pressures, some

important conclusions, useful for strategical management can be inferred. For example, this study elucidates the greatest threat to sardine (rise in SST), indicates the stressors whose mitigation should be prioritised (rise in SST, fishing and predations on eggs) and finally provides more insight into complex trophic interactions between sardine and its predators, emphasising the importance of including these species in sardine management plans.

6.4.4. Limitations and future consideration

The model presented in this study used a well-recognised and studied modelling framework (Coll  ter et al. 2015). However, it does not lack limitations inherent to the model parametrisation and the design of the scenarios. Firstly, fishing scenarios simulate the effect of constant fishing mortality over a long period that in practice is unlikely to happen since the fishery is managed. Secondly, in the trophic scenarios, the change in the species was assumed arbitrarily and the magnitude of the effects of these scenarios would differ if a different percentage of biomass change would be applied. Moreover, in SST scenarios the effect of SST was assessed only for sardine. The reason we did not assess direct SST effects on other functional groups in our modelling simulations, was the lack of consistent data to define species thermal niches. We could adopt the approach applied in Serpetti et al. (2017) and Corrales et al (2018) and use the species optimum temperature ranges from the freely available AquaMaps database (Kaschner et al. 2019). However, this would not be consistent with the approach we chose to define optimum temperature ranges for sardine. Sardine is the focus of the study and we preferred to keep sardine optimum temperature ranges adopted from Strataudakis et al. (2007) and Coombs et al (2006) as these values explained the historical sardine biomass trend in the hindcast simulation very well (chapter 4; Szalaj et al. 2021a). However, due to this, our model did not account for the indirect effects of climate change on sardine through the other species whose biomass might be influenced by SST rise. Instead, we consider scenarios that simulate hypothetical changes in the species interacting with sardine for which premise exists that their distribution and abundance might change due to SST rise (cephalopods, other small pelagic fish). Another limitation of SST future scenarios can be related to the fact that in our simulations we did not consider the effect of AMO on SST. Around 1995, AMO entered a warm phase causing an accelerated increase in SST in the North Atlantic including the Iberian upwelling region (Alheit et al. 2014). In 2016 AMO entered its “low/cooling” phase, which potentially might slow the rates of temperature rise for the next 30 years. This approach was incorporated in the study by

Serpetti et al. (2017) who underlined the importance of implementing the AMO index in future temperature predictions. Finally, the results of the simulations are highly dependent on the original model configurations (vulnerabilities, calibrations etc.) and its limitations are described in Szalaj et al. (2021a) (chapter 4). The main constraints of the model are related to the data availability and quality. Therefore, while developing the EwE model, some assumptions related to the biomasses of less-studied species, their diets and F estimates were adopted.

Nevertheless, besides the above-mentioned limitations, we followed the best available literature and guidelines when developing the model and scenarios (Link 2010; Heymans et al. 2016) and we have confidence that the model provides plausible and useful results. However, we believe that the model would benefit if future developments of the model would include the following aspects: (1) SST response function for all species when consistent data will be available; (2) spatial dynamics and (3) other stressors such as changes in salinity, nutrients, primary productivity, AMO, NAO and invasive species.

6.5. Conclusions

In this study, we assessed how the potential future changes in fishing, trophic interactions and SST might impact Iberian sardine and PCSE. Based on the analysis, we found out that the greatest negative impact on sardine was caused by future SST scenarios, that predicted stock collapse by 2040. The second-largest negative impact on sardine was observed for scenarios that simulate an increased fishing pressure that corresponds to the annual sardine catch of 50,000 tonnes and a ~30% increase in biomass of chub mackerel. These results highlighted that the catch preferred by stakeholders, might not be sustainable in the long term. Moreover, the results highlighted the importance and complexity of trophic interactions between sardine, chub mackerel and squid in explaining sardine dynamics and its decline. On the other hand, simulating fishing at MSY, allowed considerable recovery of the sardine stock, to the biomass level before 2009. This indicates that current ICES recommendations are precautionary and proposed FMSY is sustainable.

Moreover, the assessment of the multiple stressors demonstrated the dominant effect of SST rise on sardine that cannot be counteracted by fishing at MSY. On the contrary, FMSY has the potential to alleviate the negative effects of changes in sardine trophic

interactions. The largest effects on the reduction of ecosystem stability, maturity and diversity of flows were observed when changes in sardine trophic interactions were simulated.

This study confirmed that EwE can be a valuable tool in assisting single stock assessment methods in strategic and long-term management. Analysis of future scenarios indicated which sardine stressors should be prioritised in the management actions. Moreover, it emphasised the complexity of trophic interactions between sardine and its predators and competitors, suggesting that consideration of these species should be included in future sardine management plans.

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Chapter 7

Final remarks and future perspectives

Chapter 7 – Final remarks and future perspectives

The present work applied an ecosystem approach (EA) to pelagic fisheries management in the Portuguese continental waters. Different methodological approaches that complement each other, were used and an overall and broad perspective of Portuguese pelagic fishery management in the context of the ecosystem approach has been provided.

The main motivation for the study was a global call to a shift to the ecosystem approach to fisheries management (EAFM) as well as the considerable decline of west Iberian sardine stock in the last decades. By late 2000, the west Iberian sardine stock had declined and since 2009 its biomass was below the limit reference point for spawning stock biomass (B_{lim}) (ICES 2020). Therefore, scientists and fisheries stakeholders focused their attention on finding the solutions to support its recovery. Special management plans were introduced in 2012 and later in 2018 (DGRM 2012; 2018). These plans relied upon effort and landing reductions and temporary closures during the spawning periods. However, recent literature and findings, indicated that the sardine decline might be related to the environmental factors and changes in the species interactions (e.g., Martins et al. 2013; Malta et al. 2016; Garrido et al. 2015). This emphasised the need to develop a more holistic approach that would include environmental and trophic aspects to the management of west Iberian sardine stock. Accounting for environmental and trophic processes in fisheries management is one of the main pillars of the EAFM (Garcia et al. 2003). At a global level, as well as in the scope of Common Fisheries Policy (CFP) in the European Union (EU), the need to shift to EAFM had been emphasised (e.g., Ramírez-Monsalve et al. 2016). However, there is still little or no consensus on how this approach should be implemented in practice (Cowan et al. 2012; Ruckelhaus et al. 2008). Therefore, EAFM and how it can be put in practice is an active and expanding field of research that gathers a growing interest among the scientific community (e.g., Ballestseros et al. 2018; Ramirez-Monsalve et al. 2021). This has been reflected in the results of the literature review on EAFM methods, performed in the initial stage of this work (chapter 1), that resulted in the selection of the 201 relevant publications from *Google scholar* and *ScienceDirect* databases (searched till January 2017). Based on this literature review among the selected approaches, the methods that were the most popular and frequently studied were modelling approaches followed by spatial methods and indicators. Therefore, in this thesis to advance an ecosystem

approach to pelagic fisheries management in Portugal, the research was based on these methodological approaches that have been explored in this thesis.

In order to explore the capability of spatial analysis to support the pelagic fishery management in Portugal within the context of EAFM, a combination of geographic information systems (GIS) and multi-criteria decision making (MCDM) was used to provide a general spatial framework supporting an ecosystem approach to west Iberian sardine stock management (chapter 2; Szalaj et al. 2018). This research synthesized existing information in a fishery system considering key aspects of EAFM and stood out as an efficient first step in an EAFM decision support framework. Moreover, in the context of Portuguese pelagic fisheries, the results of this chapter identified that the pelagic fishery in Portuguese continental waters has conflicting objectives between conservation and fisheries and their spatial assessment is crucial to better understand the economic and conservation trade-offs that management measures might imply. This is imperative in EAFM (Garcia and Cochran 2005) and has the potential to considerably facilitate the management process (Leslie and McLeod 2007).

Ecosystem modelling as a tool to support EAFM in the Portuguese continental shelf ecosystem (PCSE) was explored through the Ecopath with Ecosim (EwE) modelling approach that in turn allowed to expand knowledge and deepen understanding of PCSE dynamics. This turned out to be essential to better understand sardine stock decline and assess the evolution of the sardine stock under the possible future scenarios. Ecosystem modelling is a versatile approach that can assist in the long-term strategic management of fisheries resources within the context of the ecosystem approach (Plagányi and Butterworth 2004; Christensen and Walters, 2011).

Development of the Ecopath static model was the first step to better understand the functioning of the PCSE (chapter 3; Veiga- Malta et al. 2019). The results obtained from this research showed that biomass in PCSE was mainly concentrated in low and intermediate trophic levels as in other upwelling areas (Jarre-Teichmann and Christensen 1998). Several low- and medium-trophic-level groups were identified as dominant groups in the ecosystem, including sardine and chub mackerel. Furthermore, low trophic-level groups were responsible for the main energy flows, and overall higher impact on the ecosystem, emphasizing the importance of bottom-up control of the ecosystem structure. Moreover, the development of the

Ecopath model in chapter 3 was a foundation for further ecosystem modelling research in the context of EAFM and Portuguese pelagic fishery.

Fitting the Ecopath static model (chapter 3; Veiga-Malta et al. 2019) to available time series between 1986-2017 provided a temporal perspective and allowed for the examination of the main drivers of PCSE dynamic and sardine decline (chapter 4; Szalaj et al. 2021a). The results obtained in this chapter suggested that the main factors that drove the ecosystem dynamics were trophic interactions, fishing and sea surface temperature. The relevance of these factors in the dynamics of marine ecosystems has been emphasised in many studies worldwide (e.g., Coll et al. 2008, Alexander et al. 2015, Zimmerann et al. 2019; Brunel and Bouchel et al. 2007). The same drivers were important in explaining sardine decline among which the largest contribution was observed when incorporating sea surface temperature (SST) forcing on adult sardine, followed by fishing. The effect of SST on sardine observed in this thesis agreed with the studies that linked an increase of SST with a decrease in sardine productivity (e.g., Santos et al. 2012; Malta et al. 2016; Garrido et al. 2017). Moreover, this study elucidated the most important trophic interactions that were responsible for the sardine trend between 1986 and 2017. They were sardine eggs predators: chub mackerel, horse mackerel and bogue. This concurred with the findings obtained by Garrido et al. (2015) that emphasised the importance of intraguild predation in the pelagic Portuguese ecosystem. Martins et al. (2013) and further Garrido et al. (2015) and García-Seone (2019), discussed the potential role of sardine trophic interactions in sardine decline.

Further exploring the PCSE model by using its results to perform the integrated assessment of PCSE further deepened the understanding of the PCSE dynamic in the larger context (chapter 5; Szalaj et al. 2021b). By using statistical approaches and ecological indicators, the changes in the main trends of biomass, fishing and ecosystem indicators in the years 1986- 2017 has been analysed at the whole ecosystem level. Moreover, this study demonstrated that the changes in the PCSE and sardine that have been observed over the last three decades might be regime-shift related. To our knowledge it was the first attempt, to provide an integrated ecosystem assessment of the PCSE as well as deliver evidence of the occurrence of the regime shift at a whole ecosystem level, including all trophic groups, and ecosystem indicators. Regime shifts in the PCSE and the North Atlantic have been previously documented, but these studies were limited to the individual species (Borges et al. 2003;

Cabrero et al. 2018; Tanner et al. 2020) or ecosystem components (Alheit et al. 2014; Beaugrand et al. 2015).

The dynamic EwE model of PCSE, developed throughout this thesis, can be used to support the strategic management of the pelagic fishery in the Portuguese continental waters. In the final part of this thesis, an example of an application of EwE to support strategic management of Portuguese pelagic fishery has been presented (chapter 6). In this study, an EwE modelling approach was used to explore the possible future scenarios of main sardine stressors and assess the effects they might have on sardine and the ecosystem (chapter 6; Szalaj et al. *under review*). Research in this chapter, much like chapter 4, highlighted the importance of SST rise, fishing exploitation and trophic interaction in sardine dynamics and is in line with previous findings (Martins et al. 2013; Garrido et al. 2015; Malta et al 2016). Moreover, the scenarios that combined main sardine stressors revealed that the effect of SST on sardine is dominant and predicted that a SST increase might jeopardise the efforts of managing the stock sustainably as had been discussed in reference to other regions (Serpetti et al. 2017; Corrales et al. 2018). On the other hand, under a scenario adopting fishing mortality at maximum sustainable yield (FMSY) lately defined by the International Council for the exploration of the sea (ICES), an increase of sardine biomass, predicted in this chapter, allowed its recovery to the level prior to the decline. Also, results showed that FMSY can dampen the negative effects, the changes in trophic interactions might have on sardine.

Briefly, this research advances the application of the EA in the management of the Portuguese pelagic fishery. This was done by reviewing and applying a set of methods for the pelagic fishery in Portugal in the context of EAFM and by providing a tool (a model) capable of supporting strategic management advice for the pelagic fishery in the context of the EA. The applied methods presented in this thesis in chapters 2 to 6, are varied and complement each other, providing a wide and holistic perspective of EA of pelagic fishery management in Portugal. This research deepens understanding of the PCSE and sardine dynamics (that is the most important commercial resource of the pelagic fishery). Specifically, the findings of this thesis: (1) elucidate the main drivers responsible for the changes in the ecosystem over the last three decades; (2) allow a better understanding of the factors behind sardine decline; and (3) indicate that the changes that occurred in PCSE over the last decades might be regime-shift related. In the context of pelagic fishery management in Portugal, these findings provide important information that can benefit the strategic management of the pelagic fishery. Results

highlighted that in the context of EA, the management of this fishery should not limit its actions to fishing restrictions, such as FMSY, but also pay attention and try to consider other factors that turn out to be very important drivers of sardine change. They are rise in SST, trophic interactions, especially between sardine, chub mackerel and squid, and the possibility of regime shift occurrence. Moreover, this thesis demonstrated that the pelagic fishery has conflicting spatial objectives and spatial analysis can support their addressing through the assessment of the trade-offs between them. In this study, the ecosystem model was not-spatially explicit, but this research highlights the need for the development of a spatial ecosystem model in future.

Moreover, one of the main outputs of this thesis is the development of the time dynamic PCSE model that can serve as a valuable and effective tool able to support the strategical management advice for the pelagic fishery in Portugal. To our knowledge, this is the first time-dynamic ecosystem model developed for the Portuguese continental shelf ecosystem. There are few static ecosystem models developed for the inner systems such as Ria Formosa (Gamito and Erzini 2005) and Ria de Aveiro (Patrício and Marques 2006; Bueno-Pardo et al. 2018). But neither of them is time-dynamic and therefore able to run simulations and explore research questions related to dynamic ecosystem processes. This model was developed over a substantial time frame, incorporating the best available knowledge, benefiting from the collaboration and expertise of numerous scientists. Moreover, while developing the model at every stage the best practice guide (Link 2010; Heymans et al. 2016) were considered. Therefore, its quality is satisfactory to be used in a management context and to answer a variety of research questions that other methods are not capable of. Therefore, it is an asset that can be used to further advance the EAFM in Portugal. Even though it was built with a focus on sardine and pelagic fishery, it can be adapted to different research questions and further explored in the future. In that sense, it is a universal tool that has the potential to contribute to the operationalisation of EAFM in Portugal.

The main constraints and limitations of the present thesis were related to the data availability (quantity and quality) and uncertainty of the results. In the spatial analysis that combines GIS and MCDM, the uncertainty can be introduced at various stages (Refsgaard et al. 2007) but it was quantitatively assessed only at the initial stage of analysis that was a weights estimation. In the ecosystem modelling, the uncertainty was addressed by the Monte Carlo routine that to some extent addressed the issue of parameter uncertainty. However, it is important to keep in mind that due to the lack of data availability, some assumptions were

introduced in the Ecopath and further Ecosim. The main assumptions were the biomasses for some less-studied species, diets imported from similar species or other closely placed ecosystems and the inclusion of time series of biomass and fishing mortality (F) estimates from other models. Also due to the lack of data, only part of modelled ecosystem was driven by F and therefore the assessment of the real impact of fishing on the PCSE is limited. Through the thesis, we were using the best available knowledge and the choice of applied methods was justified by recent literature (Malczewski 2006; Colléter et al. 2015; Diekmann et al. 2012; Strinimann et al. 2019). Even though some of the used methods are burdened by alarming limitations. For example, the use of Principal Component Analysis (PCA) as a method for ecosystem assessment of marine ecosystems has been criticised due to the bias resulted from high cross- and autocorrelation of the input data (Planque and Arneberg 2017). An attempt to minimise this effect by excluding highly correlated variables prior to PCA has been taken. Even though, this limitation should be taken into consideration when interpreting the results. Moreover, the spatial analysis in chapter 2 did not account explicitly for the biological processes that resulted from the trophic interactions between species. In this study, the impact of sardine predators and competitors was assessed by accounting for the changes in their abundance and distribution. The application of the ecosystem models would benefit the assessment of trade-offs between conservation and fishing objectives. The time-dynamic ecosystem model that was developed in this study, provide a solid foundation to develop a spatial ecosystem model that will be able to answer the spatial research questions. However, this is not a small task and therefore fell outside of the scope of this PhD, but it is recommended that the future development of the PCSE model should consider a spatial-temporal framework to effectively support the ecosystem approach to pelagic fisheries management in Portugal.

This PhD has resulted in the advancement of the ecosystem approach to pelagic fisheries management by deepening our understanding of PCSE and sardine dynamics and by providing a tool (a model) capable of supporting strategic management advice for these resources in the context of EA. However, these outputs are not endpoints, but rather foundations based on which future research and policy advice can be produced. One major task, that should be undertaken in the future is related to producing ecosystem information from the ecosystem model that would provide direct advice for sardine stock assessment that would fit in the existing management framework. The research focused on producing this type of information from the EwE model has been highlighted as an important research domain in the

scope of ecosystem modelling (Howell et al. 2021) and few studies presenting examples of how this can be done in practice have been recently published (Chagaris et al. 2020; Bentley et al. 2021). In the context of sardine stock assessment, the focus on the ecosystem information that could be extracted from EwE to inform recent fishing quotas should be placed around variability in SST and the abundance of its main predators. Based on the present Ecosim model, temperature and biomass of chub mackerel (main predator of sardine eggs) were identified as important indicators of sardine biomass. Therefore, according to the approach proposed by Bentley et al. (2021), the sardine F target value could be scaled linearly within the range of ICES precautionary FMSY, according to the current value of the indicator within the historical range over the model period. For, example, if SST in the given year of the assessment, would correspond to 80% of its most disfavour (for sardine) value observed over the model period, then the F target could be adjusted to 80% of the ICES FMSY lower value. This research is still in its infancy and the example described above is just a concept and idea of how the EwE ecosystem information could be incorporated into the current management system. Future research and development of the model presented in this thesis, has the potential to refine this approach and develop a new concept of combining the ecosystem and single species modelling adjusted to sardine and Portuguese pelagic fishery. Furthermore, as mentioned above, the next big step for the PCSE model should be an advance to a spatial-temporal framework, Ecospace (Steenbeek et al. 2013). This will allow for the exploration of a wide range of other questions that can be answered only spatially. For example, which species ranges might expand or contract under future climate change (Serpetti et al. 2017) and what would be the ecosystem impacts of marine protected areas (MPA) and fishery closures (Vilas et al. 2020)? In the context of PCSE and pelagic fisheries, a spatial ecosystem model might be useful to further explore the relationship between sardine and its main predators and competitors. As the results of this thesis highlighted that chub mackerel predation on sardine eggs was an important driver of sardine decline, it would be interesting to verify these findings by assessing the interactions between chub mackerel and sardine when explicitly considering chub mackerel occurrence in sardine spawning grounds that are limited to the few areas in PCSE, especially in the north (Bernal et al. 2007; Rodríguez-Climent et al. 2017). Moreover, the spatial EwE model would help to refine the areas of temporary fishery closure that is one of the main management actions implemented in the Portuguese continental shelf since the adoption of the first sardine management plan in 2012 (DGRM 2012). Finally, the spatial model might be able to refine the impact of SST on sardine, as not all areas in Portuguese waters might warm at the same pace

and magnitude. Region-specific effects of climate change have been already highlighted by the IPCC (e.g., Collins et al. 2013). However, to verify this, it would be necessary to couple or combine the spatial EwE model with the regional climate model to assure that geographical pattern of change is considered in future SST projections.

Moreover, as mentioned above, the EwE model is a universal tool that can be modified and used to address a wide range of research questions within the PCSE. For example, among the others, it can be used to assess the impacts of landing obligation (Celić et al. 2018; Pennino et al. 2020), invasive species (Corrales et al. 2018) or to predict movement and accumulation of contaminants and tracers in food webs (Booth et al. 2016; Walters and Christensen 2018).

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ANNEXES

ANNEX 1

Supplementary material for chapter 1

Annex 1 – Supplementary material for chapter 1

Additional information

Table A1.1 Results and Description of methodological approaches that were proposed in peer review literature, as a tool for an Ecosystem approach to fisheries management. Results are based on the systematic search in Google scholar and Science direct databases using as keywords: Ecosystem fishery management and Ecosystem fisheries management in the title (Google scholar) and in the title, abstract and keyword (Science direct). The search was performed between November 2016 and January 2017.

Group	No.	Method	Brief Description	Number of records in searched databases	Years of publications
Modelling					
	1	Ecosystem models			
		<i>EwE</i>	Ecopath with Ecosim (EwE) (Polovina 1984; Christensen and Pauly 1992; Christensen and Walters 2004) is a mass-balance trophic simulator that acts as a thermodynamic accounting system. It summarizes the instantaneous flows of matter and energy in and out of ecological functional groups. It can represent human influence through removals.	55	2002–2016
		<i>Atlantis</i>	Atlantis is an ‘end-to-end’ ecosystem modelling that represents a comprehensive set of ecosystem features and processes relating to species biology, ocean physics and biogeochemistry. Primarily it is used for analysing ecological interactions between species and to assess impact of marine fisheries on the ecosystem in support of Ecosystem based management policy analysis (Fulton et al. 2004).	6	2012–2015
		<i>Osmose</i>	OSMOSE is a two-dimensional, individual-based, multi-species modelling approach which explicitly simulates the whole life cycle of the major High Trophic level (THL) functional groups of an ecosystem (Shin and Cury 2001). Its primary characteristic is that it does not specify the diet compositions of HTL groups a priori but rather assumes that predation is an opportunistic and size-based process, letting food web structure emerge from local predation and competition interactions (Shin and Cury 2001; Grüss et al. 2016).	4	2009–2016
		<i>Seapodym</i>	SEAPODYM is the spatial ecosystem and population dynamics model. It was developed in 1995, to provide a general framework allowing integration of the biological and ecological knowledge of tuna species, and potentially other oceanic top-predator species, within a comprehensive description of the pelagic ecosystem (Lehodey et al. 2005). It includes a forage (prey) sub-model describing the transfer of energy of stored biomass through functional groups of mid-trophic levels and an age-structured population sub-model of tuna predator species and their multi-fisheries.	3	2008–2015

The dynamics of forage and predators are driven by environmental forcing (temperature, currents, oxygen, and primary production) that can be predicted from coupled physical– biogeochemical models (Lehodey et al 2008).

	<i>MICE</i>	Models of Intermediate Complexity for Ecosystem assessments' (MICE) underlie the following ideas: restrict the model to focus on the main management questions under consideration and include properties that advance their use as ecosystem assessment tools (Plagányi et al. 2014). MICE are particularly useful for addressing questions such as the effects of fisheries on predator-prey relationships. The benefit to fisheries decision-making of MICE, as opposed to more complex ecosystem models, is that MICE tend to be focused on a single question of interest, rather than whole-of-ecosystem models. Furthermore, MICE are computationally simpler, allowing for exploration of a wider range of scenarios and more opportunity to incorporate uncertainty.	2	2016
	<i>MS PROD</i>	Multispecies production models (MS PROD) are developed based on surplus production fisheries models by incorporating modifications that represent species interactions. Surplus production models only require measurement of biomass and catch, making them straightforward when compared to many other fisheries modelling approaches. There are a few instances where these models have been applied in the context of multiple fish stocks (e.g., Gamble and Link 2009; Fay et al. 2013).	2	2009–2013
	<i>Length structured model</i>	Length structured approach can be used in multi-species population models as an alternative to size-structured approach. One of the features of the model is that predator–prey interactions are specified in terms of body length ratios applicable across all species, thereby reducing the need for complex dietary parameterisation (e.g., Speirs et al. 2010).	2	2010–2016
2	Bioeconomic models	Fundamentally, bioeconomic model is a mathematical representation of biological and economic systems, which typically links economic and biological components and parameters together. For example, a combination of a multi-species and multi-fleets model integrating Lotka-Volterra trophic dynamics and profit functions can be used (Cissé et al. 2013). The ecological and economic performances of contrasting management strategies can be examined.	11	2009–2016
	<i>Viability modelling</i>	Viability modelling is a bio-economic model that strives to identify 'viable' paths that ensure the simultaneous fulfilment of several desirable objectives over time (Béné et al. 2001). These objectives, represented through a series of constraints that need to be satisfied throughout time, capture the multi-dimensional nature of sustainability (Doyen et al. 2012). It considers uncertainties.	3	2007–2015
3	Management strategy evaluation	Management strategy evaluation is both an approach and a set of tools to support decision making under uncertainty for complex natural resource and environmental management systems. It involves assessing the consequences of a range of management strategies or options and presenting the results in a way	7	2000–2014

		that they indicate trade-offs in performance across a range of management objectives (Fulton et al. 2014).		
4	Integrated models	Real life questions in fisheries are diverse therefore answering them requires a diversity of models. Integrated models combine into one modelling framework a variety of tools including ecosystem, bio-physical, biogeochemical and bioeconomic models (e.g., Mullon et al. 2016; Ortiz et al 2016).	4	2012–2016
Total			118	
Spatial				
5	GIS	GIS allows integration of various spatial information and performance of spatially explicit analyses. It provides a broad spectrum of mapping and analytical functions that can be applied for a range of fishery needs e.g., habitat mapping, analysis of species distribution and abundance, fisheries oceanography, monitoring of fishers' activities and fisheries management (Carocci et al. 2009).	10	2007–2016
6	MPA	Many examples from around the world illustrate the potential of using marine protected areas (MPAs) as a tool for ecosystem and fisheries management. Spatial techniques allow designing marine protected areas in the way that they protect important components of the ecosystem while minimize economic impacts to local communities (Douvere 2008).	9	2003–2015
7	VMS	EU Vessel Monitoring System (VMS) data combined with sales note and logbook information can be a valuable tool to determine fishing intensity and to identify spatial and temporal overlap between fisheries and sensitive habitats. This can help in identifying the priority areas and seasons for conservation and management (Geritssen et al. 2013).	3	2014–2016
8	Remote sensing	Satellite remote sensing (SRS) of the marine environment has become instrumental in ecology for environmental monitoring and it is a promising tool for conservation issues. In the context of an ecosystem approach to fisheries management (EAFM), global, daily, systematic, high-resolution images obtained from satellites provide a good data source for elucidating the relationships between exploited marine organisms and their habitat (Chassot et al. 2011).	2	2010–2011
Total			24	
Indicators				
9	Indicators	There is a scientific consent that the indicators can be used as a tool in EAFM. Indicators and reference points have been increasingly used in the late twentieth century to advise on stock management. Use of indicators allowed advice to be more formal and standardized. For single species management, two main indicators have been widely used: fishing mortality and spawning stock biomass, relating to objectives of keeping fishing pressure at a sustained level and maintaining stock reproductive capacity. Moving to an ecosystem approach implied a broadened view of the components to be considered therefore a long list of indicators have been proposed by scientists. Now the challenge is to shrink this list and standardized the approach by providing criteria and frameworks how	23	2006–2016

and which indicators should be used in the context of EAFM (Jennings 2005).

Socio-ecological					
10	Stakeholder participation / co-management	An important component of the Ecosystems Approach to Fisheries is the involvement of stakeholders in the decision-making process (the co-management approach). It can be performed through the performance of questionnaires or organisation of knowledge building workshops and trainings. Co-management (Co-M) emerges naturally as a promising governance mode to accomplish EAF principles and objectives. Co-M is an institutional arrangement in which responsibility and authority is shared between the government and stakeholders for managing common pool resources (Armitage et al 2009).	10	2006–2016	
11	Fishers'/local ecological knowledge (FEK, LEK)	Fishers ecological knowledge (FEK) has been recognized as an information bridge through which resource managers and fisheries scientists can gain a fuller understanding of a fish stock, population, or grounds by seeking the local knowledge of fishers. FEK may lack in empiricism, but on the other side it provides great volume of knowledge along both spatial and temporal scales. It could be complementary for fisheries scientists' scientifically sounded information (Begossi 2008).	5	2012–2016	
12	DPSIR	Driver-pressure-state-impact-response (DPSIR) framework is a socio-ecological framework that allows for the determination of the underlying causes of pressures on the ecosystem. It also describes the changes in ecosystem health, impacts of these changes and the response of people to the changes in the ecosystem. The framework is appropriate for analysing fisheries ecosystems (Martins et al. 2012).	3	2015–2016	
Total			18		
Bio-economic					
13	Portfolio-management theory	A portfolio management theory has been proposed to manage multi-species fish stocks in terms of a portfolio of economic assets (Edwards et al. 2004). In context of EAFM a portfolio framework systematically combines fish stocks that are joined by ecology (e.g., predation, competition) and unspecialized fishing technologies (e.g., mixed-species trawls) into a portfolio which balances expected aggregate returns against the risks associated with stock-attribute and other uncertainties (Edwards et al. 2004).	4	2004–2016	
14	Bio-economic models	Description of bio-economic models was included in a group “modelling” above.	11	2009–2016	
Total			15		
Risk assessment					

15	Risk assessment	Methods of Ecological risk assessment (ERA) has recently been proposed to contribute to implementing an ecosystem approach (Hobday et al. 2011). Quantitative ecological risk assessment generally uses mathematical models to describe relationships between harvest levels and various parameters of the fish stocks and/or ecosystem. This type of risk assessment is only possible in data-rich fisheries. On the other hand, qualitative ecological risk assessment uses a combination of attributes of the ecosystem, target stocks and fishery and can be used for data-deficient fisheries in many developing countries (Astles et al 2006).	11	2006–2017
Network analysis				
16	Network analysis	Ecological network analysis (ENA) is a modelling technique used for understanding the structure and flow of material within ecosystems and is most commonly used for evaluation food webs (Wulff et al. 1989). ENA incorporates several separate analyses and output includes matrices and indices that quantify trophic structure organic matter recycling and ecosystem size and organization. For each analysis, a series of mathematical algorithms is used to analyse the network model and make inferences about the corresponding ecosystem (Dame and Christian 2006).	3	2011–2016
Total			209	

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ANNEX 2

Supplementary material for chapter 2

Annex 2 – Supplementary material for chapter 2

Additional information

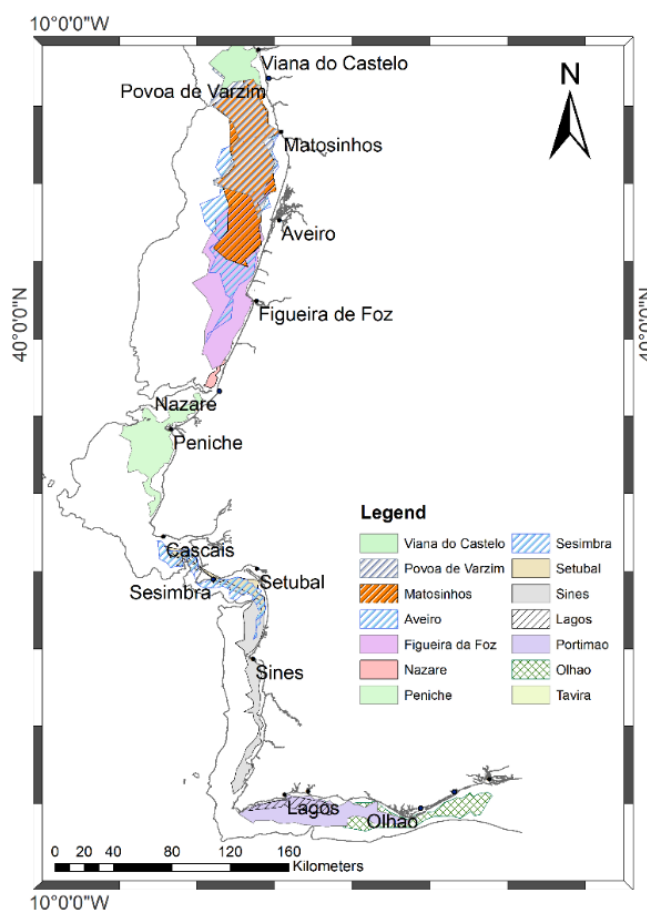
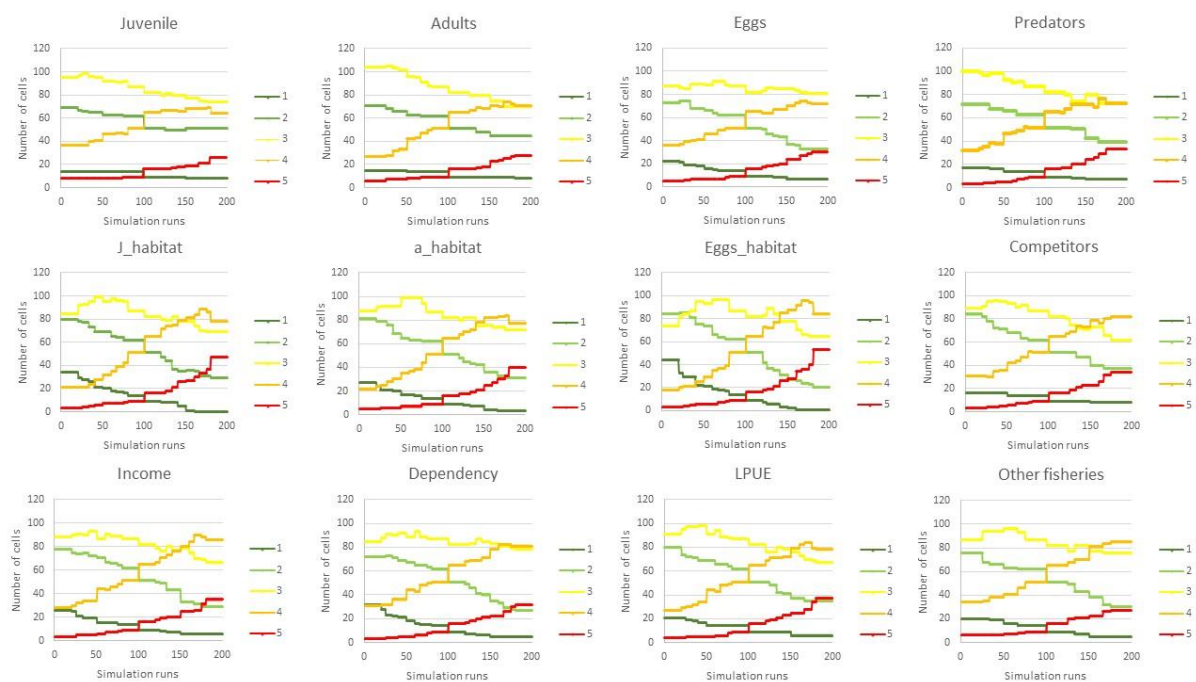


Figure A2.1. Fishing grounds attributed to ports based on VMS logbook data 2006–2010. Fishing grounds at each port were defined by connecting all VMS data points from trips with departure at the same fishing port and converting the obtained net into a polygon and then raster using ArcGis data management tool. Each cell of the obtained raster (representing fishing grounds of the port) received the value that correspond to total landings at respective port divided by the number of VMS data points used to produce each polygon. As a result, each data point received equal value that when summed corresponded to total landings at that port.



Suitability classes

1 – very low	Simulation 1 – -99% change
2 – low	Simulation 100 – Base run (0% change)
3 – moderate	Simulation 200 – +100% change
4 – high	
5 – very high	

Figure A2.2 Summary results of sensitivity analysis for each criterion (200 simulation runs for each criterion).

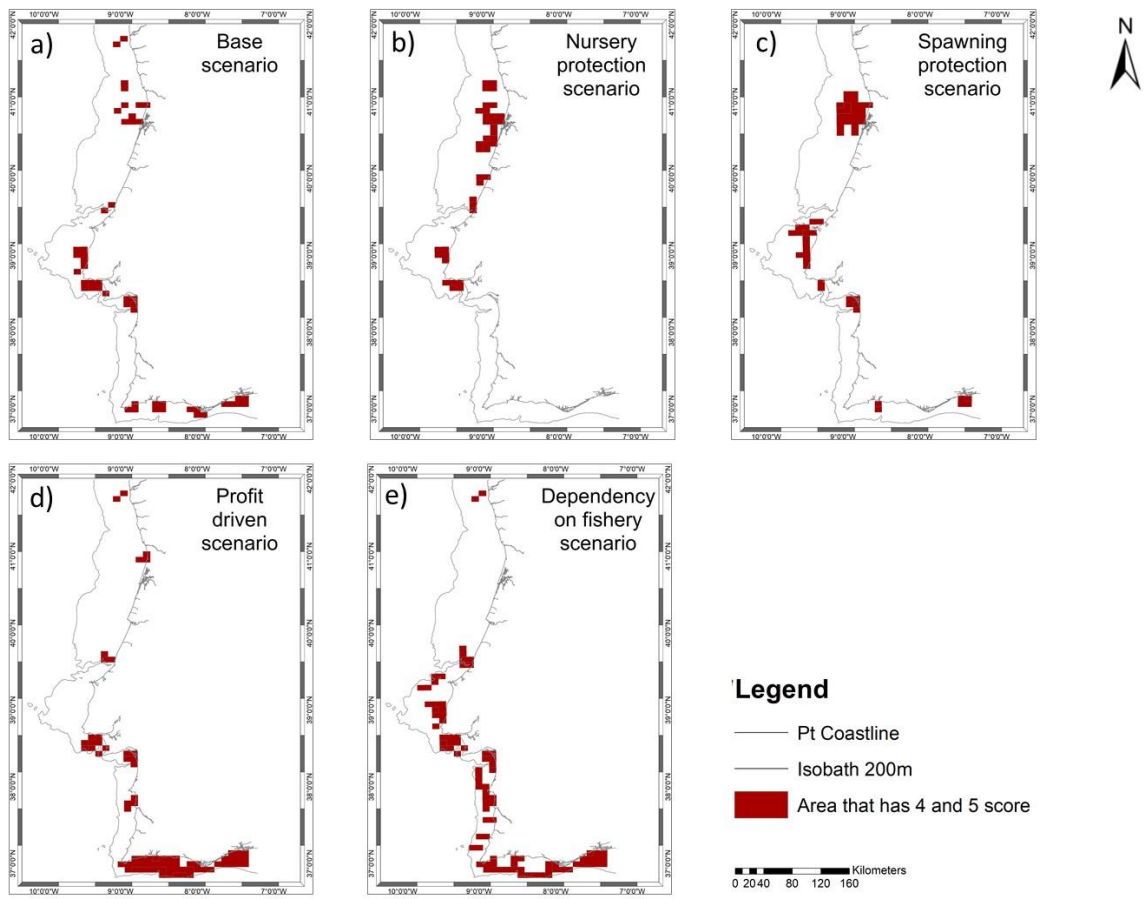


Figure A2.3 Areas that indicate the highest suitability for conservation: high (4) and very high (5) suitability score.

ANNEX 3

Supplementary material for chapter 3

Annex 3 – Supplementary material for chapter 3

Additional information

Table A3.1 Sources of the parameters used by functional group for the Portuguese continental shelf ecosystem model. Percentages before each species scientific names represent the relative abundance of each species within a group. When no relative abundance is given, such information was not available, or the functional group has only one species.

Species / Parameters	B	P/B	Q/B	EE	Mean weight	Diet
1. Seabirds [2.7% <i>Alca torda</i> (Linnaeus, 1758), 7.9% <i>Calonectris diomedea borealis</i> (Cory, 1881), 86.8% <i>Morus bassanus</i> (Linnaeus, 1758), 1.6% <i>Puffinus mauretanicus</i> (Lowe, 1921), 0.9% <i>Uria aalge</i> (Pontoppidan, 1763)]	0.009	0.1	57.64	0		
	From 2010 to 2012, Araújo et al. 2014	Christensen et al. 2009	Nilsson and Nilsson, 1976		Spring 1971, Wanless et al. 1985, Granadeiro, 1991, Genovart et al. 2003, Langston and Teuten 2013	Beja 1990, Käkälä et al. 2010, Paiva et al. 2010
1. Minkie whale [<i>Balaenoptera acutorostrata</i> (Lacépède, 1804)]	0.061	0.03	35.113	0.371		MarPro database
	From 2010 to 2012, Araújo et al. 2014	Christensen et al. 2009	From Markussen et al. 1992 daily food consumption estimates and mean weight in the area	Estimated by model	MarPro database	
3. Common dolphin [<i>Delphinus delphis</i> (Linnaeus, 1758)]	0.038	0.080	31.293	0.2		

	From 2010 to 2012, Araújo et al. 2014	Christensen et al. 2009	From Santos et al. 2014 daily food consumption estimates and mean weight in the area	Estimated by model	Fernández 2003	Stomach content analysis from stranded animals
4. Striped dolphin [<i>Stenella coeruleoalba</i> (Meyen, 1833)]	0.005	0.080	30.977	0.105		
	From 2010 to 2012, Araújo et al. 2014	Christensen et al. 2009	From Begona Santos et al. 2014 daily food consumption estimates and mean weight in the area	Estimated by model	Fernández 2003	Stomach content analysis from stranded animals
5. Bottlenose dolphin [<i>Tursiops truncatus</i> (Montagu, 1821)]	0.006	0.080	32.056	0.868		
	From 2010 to 2012, Araújo et al. 2014	Christensen et al. 2009	From Begona Santos et al. (2014) daily food consumption estimates and mean weight in the area	Estimated by model	Fernández (2003)	Stomach content analysis from stranded animals
6. Harbor porpoise [<i>Phocoena phocoena</i> (Linnaeus, 1758)]	0.004	0.080	14.166	0.013		
	From 2010 to 2012, Araújo et al. 2014	Christensen et al. 2009	From Begona Santos et al. (2014) daily food consumption estimates and mean weight in the area	Estimated by model	MarPro Stranding database (2015)	Stomach content analysis from stranded animals
7. Tunas [<i>Auxis rochei</i> (Risso, 1810), <i>Sarda sarda</i> (Bloch, 1793), <i>Thunnus</i> <i>thynnus</i> (Linnaeus, 1758)]	0.200	0.420	4.211	0.096		
	Sanchez and Olaso 2004, Coll et al. 2006 (considering that only a portion of this tuna migrates through the Portuguese continental shelf ecosystem)	Pauly 1980, F assumed 0.1	Pauly et al. 1990	Estimated by model	Santos et al. 2002, Relini et al. 2005, Rooker et al. 2007, Zaboukas and Megalofonou 2007, Kahraman et al. 2011, ICCAT 2011	Campo et al. 2006, Coll et al. 2006, Logan et al. 2011 Bănaru et al. 2013, Fletcher et al. 2013,

8. Rays [<i>Leucoraja naevus</i> (Müller and Henle, 1841), <i>Raja brachyuran</i> (Günther, 1880), <i>Raja clavata</i> (Linnaeus, 1758), <i>Raja montagui</i> (Fowler, 1910)]	0.136	0.729	4.826	0.850		
	Estimated by model	ICES 2012, Pauly 1980	Pauly et. 1990	Sanchez and Olosa 2004, Torres et al. 2013	ICES 2012	Farias et al. 2006
9. Hake [<i>Merluccius merluccius</i> (Linnaeus, 1758)]	0.389	1.300	6.070	0.934		
	Bottom trawl surveys 2006-2009	ICES 2013	Pauly et. 1990	Estimated by model	Mendes et al. 2004, Mellon-Duval et al. 2010	Cabral and Murta 2002
10. Squids [<i>Alloteuthis</i> sp. <i>Illex coindetii</i> (Vérany, 1839), <i>Loligo vulgaris</i> (Lamarck, 1798), <i>Todaropsis eblanae</i> (Ball, 1841)]	0.962	2.800	8.000	0.950		
	Estimated by model	Sanchez and Olosa 2004, Torres et al. 2013	Sanchez and Olosa 2004, Torres et al. 2013	Sanchez and Olosa 2004, Torres et al. 2013	Bidder 1950, Rocha et al. 1994, Rasero et al. 1996, Coelho et al. 1997, Sanchez and Olosa 2004, Torres et al. 2013	Bidder 1950, Rocha et al. 1994, Rasero et al. 1996, Coelho et al. 1997, Sanchez and Olosa 2004, Torres et al. 2013
11. Benthic cephalopods [<i>Eledone cirrhosa</i> (Lamarck, 1798), <i>Octopus vulgaris</i> (Cuvier, 1797), <i>Sepia officinalis</i> (Linnaeus, 1758), <i>Sepioloa</i> sp.]	1.154	2.300	6.500	0.950		
	Estimated by model	Sanchez and Olosa 2004, Torres et al. 2013	Sanchez and Olosa 2004, Torres et al. 2013	Sanchez and Olosa 2004, Torres et al. 2013	Sanchez and Olosa 2004, Lassalle et al. 2011, Torres et al. 2013	Sanchez and Olosa 2004, Lassalle et al. 2011, Torres et al. 2013
12. Horse mackerel [<i>Trachurus trachurus</i> (Linnaeus, 1758)]	2.841	0.512	7.607	0.935		
	Acoustic survey 2008-2009	Pauly 1980, F from official landings information for the study area and period (2006-2009)	Pauly et al. 1990	Estimated by model	Costa 2004, Mendes et al. 2004	Cabral and Murta 2002
13. Blue jack mackerel [<i>Trachurus picturatus</i> (Bowdich, 1825)]	0.784	0.536	7.208	0.901		

	Bottom trawl surveys 2006–2009	Pauly 1980, F from official landings information for the study area and period (2006–2009)	Pauly et al. 1990	Estimated by model	Mendes et al. 2004, Vasconcelos et al. 2006	Deudero, 2001, Hirsch, 2009, www.fishbase.org
14. Chub mackerel [<i>Scomber colias</i> (Gmelin, 1789)]	6.578	0.655	6.816	0.915		
	Acoustic surveys 2007–2009	Pauly 1980, F from official landings information for the study area and period (2006–2009)	Pauly et al. 1990	Estimated by model	Mendes et al. 2004, Velasco et al. 2011	Garrido et al. 2015
15. Mackerel [<i>Scomber scombrus</i> (Linnaeus, 1758)]	0.448	0.804	7.137	0.942		
	Bottom trawl surveys 2006–2009	Pauly 1980, F from official landings information for the study area and period (2006–2009)	Pauly et al. 1990	Estimated by model	Mendes et al. 2004, Villamor et al. 2004	Cabral and Murta 2002
16. Demersal piscivorous fish [<i>Chelidonichthys lucernus</i> (Linnaeus, 1758), <i>Conger conger</i> (Linnaeus, 1758), <i>Dicentrarchus labrax</i> (Linnaeus, 1758), <i>Helicolenus dactylopterus</i> (Delaroche, 1809), <i>Lophius budegassa</i> (Spinola, 1807), <i>Lophius piscatorius</i> (Spinola, 1807)]	0.531	0.644	3.575	0.950		
	Estimated by model	Pauly 1980 and considering the models from neighbour areas (Lassalle et al. 2011, Sanchez and Olaso 2004, Torres et al. 2013)	Pauly et al. 1990	Sanchez and Olaso 2004, Torres et al. 2013	Gonçalves et al. 1997, Landa et al. 2001, Mendes et al. 2004, García- Rodríguez et al. 2005, Olim and Borges 2006, Cicek et al. 2008, Correia et al. 2009, Sequeira et al. 2009, ICES 2013, www.fishbase.org	Sanchez and Olaso 2004, Preciado et al. 2006, Xavier et al. 2010, Neves et al. 2012, Castro et al. 2013, Spitz et al. 2013, Torres et al. 2013

17. Demersal invertivorous fish [<i>Callanthias ruber</i> , <i>Callionymus lyra</i> , <i>Cepola macrophthalma</i> , <i>Chelidonichthys</i> <i>cuculus</i> , <i>Lepidotrigla cavillone</i> , <i>Mullus</i> <i>barbatus</i> , <i>Mullus surmuletus</i> , <i>Serranus</i> <i>hepatus</i> , <i>Synchiropus phaeton</i> , <i>Trigla lyra</i> , <i>Ammodytidae</i> , <i>Gobiidae</i>]	5773	1.221	6.677	0.950		
	Estimated by model	Pauly 1980, F assumed 0.5	Pauly et al. 1990	Sanchez and Olaso 2004, Torres et al. 2013	Reñones et al. 1995, Borges et al. 2003, Mendes et al. 2004, Olim and Borges 2006, Dulčić et al. 2007, www.fishbase.org	Terrats et al. 2000, Mackinson and Daskalov 2007, Castro 2008, Hirsch 2009, Lopez-Lopez et al. 2011, Castro et al. 2013, Torres 2013, www.fishbase.org
18. Benthopelagic piscivorous fish [<i>Belone belone</i> (Linnaeus, 1760), <i>Lepidopus caudatus</i> (Euphrasen, 1788), <i>Phycis blennoides</i> (Brünnich, 1768), <i>Phycis phycis</i> (Linnaeus, 1766), <i>Zeus</i> <i>faber</i> (Linnaeus, 1758)]	0.336	0.833	4.098	0.950		
	Estimated by model	Pauly 1980, Sanchez and Olaso 2004, Torres et al. 2013 and Official landings information for the study area and period (2006–2009)	Pauly et. 1990	Sanchez and Olaso 2004, Torres et al. 2013	Demestre et al. 1993, Casas and Piñeiro 2000, Borges et al. 2003, Mendes et al. 2004, Vieira et al. 2014, www.fishbase.org	Demestre et al. 1993, Morato et al. 1999, Silva 1999, Morte et al. 2002, Klimpel et al. 2006, Sever et al. 2009, Torres 2013
19. Benthopelagic invertivorous fish [<i>Anthias anthias</i> (Linnaeus, 1758), <i>Argentina sphyraena</i> (Linnaeus, 1758), <i>Capros aper</i> (Linnaeus, 1758), <i>Gadiculus</i> <i>argenteus</i> (Guichenot, 1850), <i>Macroramphosus</i> spp. <i>Micromesistius</i> <i>poutassou</i> (Risso, 1827), <i>Trisopterus</i> <i>luscus</i> (Linnaeus, 1758)]	6.222	0.954	7.096	0.950		

	Estimated by model	Pauly 1980, F assumed 0.3	Pauly et al. 1990	Sanchez and Olaso 2004, Torres et al. 2013	Merayo and Villegas 1994, Borges 2000, Borges et al. 2003, Mendes et al. 2004, Hüssy et al. 2012, www.fishbase.org	Cabral and Murta 2002, Oliveira 2002, Lopes et al. 2006, Hirsch 2009, Sever et al. 2013, www.fishbase.org
20. Flatfish [<i>Arnoglossus laterna</i> (Walbaum, 1792), <i>Citharus linguatula</i> (Linnaeus, 1758), <i>Dicologlossa cuneata</i> (Moreau, 1881), <i>Lepidorhombus boscii</i> (Risso, 1810), <i>Lepidorhombus whiffiagonis</i> (Walbaum, 1792), <i>Microchirus azevia</i> (Capello, 1867), <i>Microchirus variegatus</i> (Donovan, 1808), <i>Pegusa lascaris</i> (Risso, 1810), <i>Platichthys flesus</i> (Linnaeus, 1758), <i>Scophthalmus maximus</i> (Linnaeus, 1758), <i>Scophthalmus rhombus</i> (Linnaeus, 1758), <i>Solea senegalensis</i> (Kaup, 1858), <i>Solea solea</i> (Linnaeus, 1758)]	0.908	0.940	5.687	0.950		
	Estimated by model	Pauly 1980, F assumed 0.3	Pauly et al. 1990	Sanchez and Olaso 2004, Torres et al. 2013	Santos 1995, Andrade 1998, Landa and Piñeiro 2000, Mendes et al. 2004, Teixeira et al. 2009, Teixeira and Cabral 2010, Teixeira et al. 2010, Félix et al. 2011, ICES 2013, www.fishbase.org	Cabral 2000, Cabral et al. 2002, Amezcueta et al. 2003, Šantić et al. 2009, Teixeira et al. 2009, Teixeira et al. 2010, Vinagre et al. 2011, Torres 2013, Torres et al. 2013
21. Sparids [0.01% <i>Diplodus annularis</i> (Linnaeus, 1758), 0.05% <i>Diplodus Bellottii</i> (Steindachner, 1882), 0.01% <i>Diplodus sargus</i> (Linnaeus, 1758), 26.4% <i>Diplodus vulgaris</i> (Geoffroy Saint-Hilaire, 1817), 55.9% <i>Pagellus acarne</i> (Risso, 1827), 0.73% <i>Pagellus bogaraveo</i> (Brünnich, 1768), 3% <i>Pagellus Erythrinus</i> (Linnaeus, 1758), 0.2% <i>Pagrus auriga</i> (Valenciennes, 1843), 1.1% <i>Pagrus</i>	0.599	0.725	5.425	0.858		

<i>pagrus</i> (Linnaeus, 1758), 12.5% <i>Spondyllosoma cantharus</i> (Linnaeus, 1758)]						
	Bottom trawl surveys 2006–2009	Pauly 1980, F from official landings information for the study area and period (2006–2009)	Pauly et al. 1990	Estimated by model	Gonçalves et al. 1997, Pajuelo and Lorenzo 2000, Erzini et al. 2001, Santos et al. 2002, Borges et al. 2003, Gonçalves et al. 2003, Mendes et al. 2004, Pajuelo et al. 2006, Matić-Skoko et al. 2007, Coelho et al. 2010, Lorange 2011, www.fishbase.org	Chakroun-Marzouk and Kartas 1987, Gonçalves and Erzini 1998, Pita et al. 2002, Torres 2013
22. Anchovy [<i>Engraulis encrasicolus</i> (Linnaeus, 1758)]	0.305	1.170	12.220	0.919		
	Acoustic surveys 2006–2009	Pauly 1980, F from official landings information for the study area and period (2006–2009)	Pauly et al. 1990	Estimated by model	Basilone et al. 2004, www.fishbase.org	Sanchez and Olaso 2004, Lassalle et al. 2011, Castro et al. 2013, Torres et al. 2013
23. Sardine [<i>Sardina pilchardus</i> (Walbaum, 1792)]	14.760	0.891	9.677	0.956		
	Acoustic surveys 2006–2009	Pauly 1980, F from official landings information for the study area and period (2006–2009)	Pauly et al. 1990	Estimated by model	Mendes et al. 2004, Silva et al. 2008	Garrido et al. 2008
24. Bogue [<i>Boops boops</i> (Linnaeus, 1758)]	0.794	1.246	6.201	0.950		
	Estimated by model	Pauly 1980, F from Monteiro et al. 2006	Pauly et al. 1990	Sanchez and Olaso 2004, Torres et al.	Mendes et al. 2004, Monteiro et al. 2006	Derbal and Kara 2008, Bănarău et al. 2013, Dobroslavić

				2013		et al. 2013
25. Henslow's crab [<i>Polybius henslowii</i> (Leach, 1820)]	0.526	2.100	10.640	0.950		
	Estimated by model	Coll et al. 2006, Torres et al. 2013	Cammen 1980	Sanchez and Olaso 2004, Torres et al. 2013	Acoustic and bottom trawl surveys 2006-2009	Signa et al. 2008, Torres et al. 2013
26. Shrimps [Crustacea natantia]	3.619	4.200	11.670	0.950		
	Estimated by model	Sanchez and Olaso 2004, Torres et al. 2013	Sanchez and Olaso 2004, Torres et al. 2013	Sanchez and Olaso 2004, Torres et al. 2013		Sanchez and Olaso 2004, Torres et al. 2013
27. Macrozoobenthos [Starfishes, Annelids, Sea urchins, Sea cucumbers, Bivalves, Crustaceans, Sea anemone, other benthic invertebrates]	14.540	3.555	9.727	0.842		
	López-Jamar et al. 1992, Martins et al. 2013	Sanchez and Olaso 2004, Torres et al. 2013	Sanchez and Olaso 2004, Torres et al. 2013	Estimated by model		Sanchez and Olaso 2004, Torres et al. 2013
28. Suprabenthic invertebrates [Euphausiids, Mysids, Isopods, Amphipods]	3.599	16.00	42.00	0.950		
	Sanchez and Olaso 2004, Torres et al. 2013	Sanchez and Olaso 2004, Torres et al. 2013	Sanchez and Olaso 2004, Torres et al. 2013	Sanchez and Olaso 2004, Torres et al. 2013		Sanchez and Olaso 2004, Torres et al. 2013
29. Macrozooplankton [Zooplankton length > 3 mm, width > 1 mm]	5.253	17.00	44.00	0.781		
	Spring and Autumn surveys 2006–2009, Conversion factors were used to estimate wet weight of those samples (Cushing et al. 1958, Wiebe et al. 1975, Wiebe 1988, Alcaraz et al. 2003).	Sanchez and Olaso 2004, Torres et al. 2013	Sanchez and Olaso 2004, Torres et al. 2013	Estimated by model		Sanchez and Olaso 2004, Torres et al. 2013

	The conversion to t/m^2 from t/m^3 was made based on information about vertical distribution of zooplankton in the western Portuguese continental shelf (L. Sobrinho-Gonçalves unpubl. Data, Sobrinho-Gonçalves et al. 2013)				
30. Meso/ Microzooplankton [Zooplankton length ≤ 3 mm, width ≤ 1 mm]	25.29	30.100	152.500	0.635	
	Mesozooplankton: Spring and Autumn surveys 2006-2009, Microzooplankton: L. Sobrinho-Gonçalves unpubl. data, 2010-2011 Conversion factors were used to estimate wet weight of those samples (Cushing et al. 1958, Wiebe et al. 1975, Wiebe 1988, Alcaraz et al. 2003). The conversion to t/m^2 from t/m^3 was made based on information about vertical distribution of zooplankton in the western Portuguese continental shelf (L. Sobrinho-Gonçalves unpubl. Data, Sobrinho-Gonçalves et al. 2013)	Sanchez and Olaso 2004, Torres et al. 2013	Sanchez and Olaso 2004, Torres et al. 2013	Estimated by model	Sanchez and Olaso 2004, Torres et al. 2013

31. Phytoplankton	18.720 chlorophyll-a satellite data from the Globcolour project (algorithm by Morel and Brethon 1989; www.globcolour.inf) Conversion factors (Jorgensen et al.1991, Dalsgaard and Pauly 1997)	350.800 Vertically Generalized Production Model (VGPM) (Behrenfeld and Falkowski 1997)	0.432 Estimated by model
32. Discards	1.003 Borges et al. 2001, Batista et al. 2009, Prista et al. 2012, Feijó 2013, Fernandes et al. 2015		0.933 Estimated by model
33. Detritus	45.230 Pauly et al. 1993		0.068 Estimated by model

Table A3.2 Diet composition matrix adjusted for the Portuguese continental shelf food web of the Ecopath model.

Preys	Predators														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1 Seabirds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2 Minkie whale	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3 Common dolphin	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4 Striped dolphin	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5 Bottlenose dolphin	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6 Harbor porpoise	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7 Tunas	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8 Rays	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9 Hake	0.1	0	0.042	0.1	0.084	0.152	0	0.012	0.02	0.01	0	0	0	0	0
10 Squids	0.01	0	0.047	0.139	0.003	0.003	0.01	0.093	0.01	0.05	0	0.005	0.01	0.02	0.01
11 Benthic cephalopods	0	0	0.008	0.037	0.011	0.001	0	0.021	0	0.004	0.03	0	0	0.03	0
12 Horse mackerel	0.014	0.2552	0.13	0.03	0.009	0.021	0.01	0.03	0.02	0	0	0	0	0	0
13 Blue jack mackerel	0	0.0888	0.025	0.005	0	0	0.01	0	0.01	0	0	0	0	0	0
14 Chub mackerel	0.126	0.108	0.233	0.104	0.007	0.023	0.09	0.002	0.059	0.163	0.083	0	0	0	0
15 Mackerel	0.25	0.002	0.047	0.038	0.004	0	0	0	0.001	0	0	0	0	0	0
16 Demersal piscivorous fish	0	0	0	0	0.673	0.073	0	0	0	0	0	0	0	0	0
17 Demersal invertivorous fish	0.122	0	0.002	0.013	0.004	0.106	0	0.227	0	0.116	0.212	0	0.01	0.01	0
18 Benthopelagic piscivorous fish	0	0	0.001	0	0	0	0	0	0.03	0	0	0	0	0	0
19 Benthopelagic invertivorous fish	0.078	0.021	0.057	0.202	0.013	0.051	0	0.172	0.51	0.183	0.015	0	0	0.02	0.1
20 Flatfish	0	0	0.003	0	0.015	0.026	0	0.025	0	0.031	0.035	0	0	0	0
21 Sparids	0	0.062	0	0	0	0	0	0	0	0.005	0.01	0	0	0	0
22 Anchovy	0.019	0.04	0.007	0.064	0	0	0.01	0	0.025	0.01	0	0	0	0	0.01
23 Sardine	0.253	0.357	0.372	0.226	0.002	0.012	0.37	0.095	0.255	0.261	0.275	0.03	0.02	0.03	0.03
24 Bogue	0	0	0.026	0.002	0.002	0.001	0	0	0.03	0.015	0.09	0	0	0	0
25 Henslow's crab	0	0	0	0	0	0	0	0.074	0	0.002	0.015	0	0	0	0
26 Shrimps	0	0	0	0	0	0	0	0.056	0.005	0.022	0.026	0	0	0	0
27 Macrozoobenthos	0	0	0	0	0	0	0	0.124	0	0.025	0.065	0.1	0.1	0.02	0
28 Suprabenthic invertebrates	0	0	0	0	0	0	0	0.014	0.005	0.034	0.066	0.44	0.32	0.097	0.16
29 Macrozooplankton	0	0	0	0	0	0	0	0.055	0.02	0.069	0.078	0.385	0.24	0.325	0.141
30 Meso and Microzooplankton	0	0	0	0	0	0	0	0	0	0	0	0.04	0.3	0.446	0.549
31 Phytoplankton	0	0	0	0	0	0	0	0	0	0	0	0	0	0.002	0
32 Discards	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33 Detritus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
34 Import	0.018	0.066	0	0.04	0.173	0.531	0.5	0	0	0	0	0	0	0	0

Table A3.2. (Continued)

Preys	Predators														
	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
1 Seabirds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2 Minkie whale	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3 Common dolphin	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4 Striped dolphin	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5 Bottlenose dolphin	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6 Harbor porpoise	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7 Tunas	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8 Rays	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9 Hake	0.016	0	0.017	0	0.001	0	0	0	0	0	0	0	0	0	0
10 Squids	0.008	0	0.019	0.002	0.081	0.051	0	0	0	0.03	0	0	0	0	0
11 Benthic cephalopods	0.04	0.002	0.02	0	0.042	0.022	0	0	0	0	0	0	0	0	0
12 Horse mackerel	0.033	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13 Blue jack mackerel	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
14 Chub mackerel	0.076	0	0.032	0	0	0	0	0	0	0	0	0	0	0	0
15 Mackerel	0.012	0	0	0	0	0	0	0	0	0	0	0	0	0	0
16 Demersal piscivorous fish	0.02	0	0.019	0	0	0	0	0	0	0	0	0	0	0	0
17 Demersal invertivorous fish	0.166	0.01	0.086	0.029	0.215	0.05	0	0	0	0	0	0	0	0	0
18 Benthopelagic piscivorous fish	0.078	0	0.004	0	0	0	0	0	0	0	0	0	0	0	0
19 Benthopelagic invertivorous fish	0.249	0	0.241	0.01	0.021	0	0	0	0	0	0	0	0	0	0
20 Flatfish	0.026	0	0.016	0	0.01	0.033	0	0	0	0	0	0	0	0	0
21 Sparids	0	0	0.001	0	0	0	0	0	0	0	0	0	0	0	0
22 Anchovy	0.004	0	0.011	0	0	0	0	0	0	0	0	0	0	0	0
23 Sardine	0.035	0	0.142	0.014	0.009	0	0	0	0	0	0	0	0	0	0
24 Bogue	0	0	0.014	0	0	0	0	0	0	0	0	0	0	0	0
25 Henslow's crab	0.01	0.015	0	0.001	0.003	0	0	0	0	0.038	0	0	0	0	0
26 Shrimps	0.115	0.115	0.211	0.079	0.139	0.022	0	0	0.4	0	0.005	0.017	0	0	0
27 Macrozoobenthos	0.037	0.368	0.085	0.069	0.366	0.588	0	0	0.15	0.41	0.28	0.02	0	0	0
28 Suprabenthic invertebrates	0.009	0.197	0.082	0.37	0.063	0.062	0.007	0	0.15	0.01	0.12	0.044	0	0	0
29 Macrozooplankton	0.066	0.174	0	0.265	0.05	0.152	0.021	0	0.25	0.255	0.05	0.091	0.04	0	0
30 Meso and Microzooplankton	0	0.094	0	0.161	0	0.02	0.97	0.833	0.05	0.163	0.09	0.021	0.2	0.7	0
31 Phytoplankton	0	0.01	0	0	0	0	0.002	0.167	0	0	0.03	0.079	0.08	0.3	0.95
32 Discards	0	0	0	0	0	0	0	0	0	0.01	0.004	0.005	0	0	0
33 Detritus	0	0.015	0	0	0	0	0	0	0	0.084	0.421	0.723	0.68	0	0.05
34 Import	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Formulas used to calculate Production/Biomass (P/B) and Consumption/biomass (Q/B) ratio for the functional groups included in the model.

Production/Biomass (P/B) ratio

Fish groups

It was calculated using assumption by (Allen 1971) that assumes that in a steady-state ecosystem:

$$P/B = Z = M + F$$

where Z = total mortality, M = natural mortality, F = fishing mortality. Natural mortality (M) was calculated using Pauly (1980) empirical equation:

$$\log(M) = -0.0066 - 0.279 \times \log(L_{inf}) + 0.6543 \times \log(k) + 0.4634 \times \log(T)$$

where L_{inf} and k are parameters of the von Bertalanffy growth equation and T is the mean environmental temperature (°C). F was calculated as catch/biomass. When no biomass estimates were available, a mean F for the group was assumed based on literature and expert knowledge.

Consumption/biomass (Q/B) ratio

Seabirds

Daily ration for seabirds (DR) in g day^{-1} was calculated using the empirical equation (Nilsson and Nilsson 1976):

$$\log(DR) = -0.293 + 0.85 \times \log(W)$$

where W is the mean body mass of birds expressed in g. DR was multiplied by 365 days and divided by the mean weight of the species to provide the Q/B ratio.

Fish groups

For fish groups Q/B was calculated with the empirical equation from Pauly et al. (1990):

$$\text{Log}(Q/B) = 6.37 - 1.5045 \times T' - 0.168 \times \log(\text{Winf}) + 0.1399 \times Pf + 0.2765 \times Hd$$

where $T' = 1000/T$ is mean water temperature in Kelvin ($K = ^\circ\text{C} + 273.15$), Winf is the asymptotic body weight (g), Pf and Hd express feeding types: Pf = 1 for apex and/or pelagic predators and/or zooplankton feeders and 0 for all others, and Hd = 1 for herbivores and Hd = 0 for carnivores (Pauly et al. 1990). Pf and Hd of benthic carnivores are assumed to be zero. Winf was estimated by replacing L by Linf in length-weight relationships compiled from literature (Table A3.1 in the annex 3).

Henlow's swimming crab

For Henlow's swimming crab, Q/B was calculated using the empirical equation for the daily consumption rate of invertebrates (Cammen 1980):

$$C = 0.381 \times W^{0.742}$$

being C the daily consumption rate and W the mean body weight.

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ANNEX 4

Supplementary material for chapter 4

Annex 4 – Supplementary material for chapter 4

Additional information related to model parametrization and calibration

Table A4.1 Multi-stanza parameters. Underlined values were estimated by the model. Parameter: P/B for adult sardine were adopted from Report of the Working Group on Southern Horse Mackerel, Anchovy and Sardine (WGHANSA), estimated based on age-based analytical assessment (ICES 2018), K was taken from the study by Silva et al. (2008) while Wmat and Winf parameters necessary to calculate ratio, were adopted from FishBase (Froese and Pauly 2018). Wmat/Winf is a ratio of weight at maturity to maximum weight.

	Juvenile sardine	Adult sardine
Age start (months)	0	12
Leading	-	+
Biomass (t km ⁻²)	<u>3.07</u>	31.3
P/B	3.00	0.83
Q/B	<u>25.9</u>	8.78
K		0.46
Wmat/Winf		0.64

Table A4.2 Species included in the functional group Sharks.

Common name	Latin name
Blackmouth catshark	<i>Galeus melastomus</i>
Shortfin mako	<i>Isurus oxyrinchus</i>
Lesser spotted dogfish	<i>Scyliorhinus canicula</i>
Nursehound	<i>Scyliorhinus stellaris</i>
Knifetooth dogfish	<i>Scymnodon ringens</i>
Smooth-hound	<i>Mustelus mustelus</i>
Portuguese dogfish	<i>Centroscymnus coelolepis</i>

1 Table A4.3 Diet composition

o.	Prey \ predator	Bottle nose dolphin	Harbor porpoise	Striped dolphin	Dem.f ish.p	Seabirds	Hake	Common dolphin	Rays	Sharks	Squids	Mink le whale	Benthic cephalopods	Bp.fish_p	Tunas	Flatfish	Sparids	Bogue	Horse mackerel	Bp.fish.i	Chub mackerel	Dem.f ish.i	Mackerel	Blue jack mackerel	Henslow's crab	Anchovy	Juvenile sardine	Adult sardine	Shrimps	Macrozoobenthos	Suprabenthic invertebrates	Macrozooplankton	Meso/Microzooplankton
1	Bottlenose dolphin	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
2	Harbor porpoise	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
3	Striped dolphin	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
4	Seabirds	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
5	Dem.fish_p	0.673	0.073	0.000	0.020	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.019	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
6	Hake	0.084	0.152	0.100	0.016	0.100	0.020	0.042	0.012	0.004	0.010	0.000	0.000	0.017	0.000	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
7	Common dolphin	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
8	Rays	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
9	Mink whale	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
10	Squids	0.003	0.003	0.139	0.008	0.010	0.010	0.047	0.093	0.000	0.050	0.000	0.000	0.019	0.010	0.081	0.051	0.000	0.005	0.002	0.020	0.000	0.010	0.010	0.030	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
11	Bp.fish.p	0.000	0.000	0.000	0.078	0.000	0.030	0.001	0.000	0.000	0.000	0.000	0.000	0.004	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
12	Benthic cephalopods	0.011	0.001	0.037	0.040	0.000	0.000	0.008	0.021	0.042	0.004	0.000	0.030	0.020	0.000	0.042	0.022	0.000	0.000	0.000	0.030	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
13	Tunas	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
14	Sharks	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
15	Flatfish	0.015	0.026	0.000	0.026	0.000	0.000	0.003	0.025	0.000	0.031	0.000	0.035	0.016	0.000	0.010	0.033	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
16	Sparids	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.005	0.062	0.010	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
17	Bogue	0.002	0.001	0.002	0.000	0.000	0.030	0.026	0.000	0.000	0.015	0.000	0.090	0.014	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

18	Bp.fish.i	0.013	0.051	0.202	0.249	0.078	0.510	0.057	0.172	0.392	0.183	0.021	0.015	0.241	0.000	0.021	0.000	0.000	0.000	0.010	0.020	0.000	0.100	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
19	Dem.fish.i	0.004	0.106	0.013	0.166	0.122	0.000	0.002	0.227	0.075	0.116	0.000	0.212	0.086	0.000	0.215	0.050	0.000	0.000	0.029	0.010	0.010	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
20	Mackere l	0.004	0.000	0.038	0.012	0.250	0.001	0.047	0.000	0.003	0.000	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
21	Horse mackere l	0.009	0.021	0.030	0.033	0.014	0.020	0.130	0.030	0.034	0.000	0.255	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
22	Chub mackere l	0.007	0.023	0.104	0.076	0.126	0.059	0.233	0.002	0.005	0.163	0.108	0.083	0.032	0.090	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
23	Blue jack mackere l	0.000	0.000	0.005	0.000	0.000	0.010	0.025	0.000	0.000	0.000	0.089	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
24	Henslow 's crab	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.074	0.036	0.002	0.000	0.015	0.000	0.000	0.003	0.000	0.000	0.000	0.001	0.000	0.015	0.000	0.000	0.038	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
25	Anchovy	0.000	0.000	0.020	0.004	0.010	0.010	0.007	0.000	0.000	0.010	0.030	0.000	0.011	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
26	Adult sardine	0.002	0.012	0.260	0.025	0.209	0.240	0.300	0.075	0.000	0.251	0.367	0.275	0.142	0.300	0.090	0.000	0.000	0.005	0.014	0.000	0.000	0.030	0.020	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
27	Shrimps	0.000	0.000	0.000	0.115	0.000	0.005	0.000	0.060	0.089	0.022	0.000	0.026	0.211	0.000	0.139	0.022	0.400	0.000	0.079	0.000	0.115	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.005	0.017	0.000	0.000
28	Juvenile sardine	0.000	0.000	0.010	0.010	0.053	0.030	0.072	0.015	0.000	0.030	0.000	0.000	0.000	0.070	0.000	0.000	0.060	0.033	0.000	0.045	0.000	0.000	0.000	0.000	0.001	0.006	0.011	0.000	0.000	0.000	0.000	0.000	
29	Suprabenthic inv.	0.000	0.000	0.000	0.009	0.000	0.005	0.000	0.014	0.095	0.034	0.000	0.066	0.082	0.000	0.063	0.062	0.150	0.487	0.370	0.097	0.197	0.160	0.320	0.010	0.007	0.000	0.000	0.140	0.044	0.000	0.000	0.000	
30	Macrozoobenthos	0.000	0.000	0.000	0.037	0.000	0.000	0.000	0.120	0.226	0.005	0.000	0.065	0.085	0.000	0.285	0.588	0.150	0.007	0.069	0.020	0.368	0.000	0.100	0.410	0.000	0.000	0.000	0.240	0.025	0.000	0.000	0.000	
31	Macrozooplankton	0.000	0.000	0.000	0.066	0.000	0.020	0.000	0.060	0.000	0.069	0.000	0.078	0.000	0.000	0.050	0.152	0.200	0.424	0.265	0.000	0.174	0.000	0.240	0.255	0.000	0.000	0.000	0.060	0.090	0.040	0.000	0.000	
32	Meso/Microzooplankton	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.020	0.040	0.040	0.161	0.756	0.094	0.690	0.300	0.163	0.990	0.597	0.822	0.100	0.021	0.200	0.100	0.000	
33	Phytoplankton	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.010	0.000	0.000	0.000	0.002	0.397	0.167	0.030	0.079	0.080	0.900	1.000	
34	Discards	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.004	0.001	0.000	0.000	
35	Detritus	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.015	0.000	0.000	0.084	0.000	0.000	0.000	0.421	0.723	0.680	0.000	0.000	

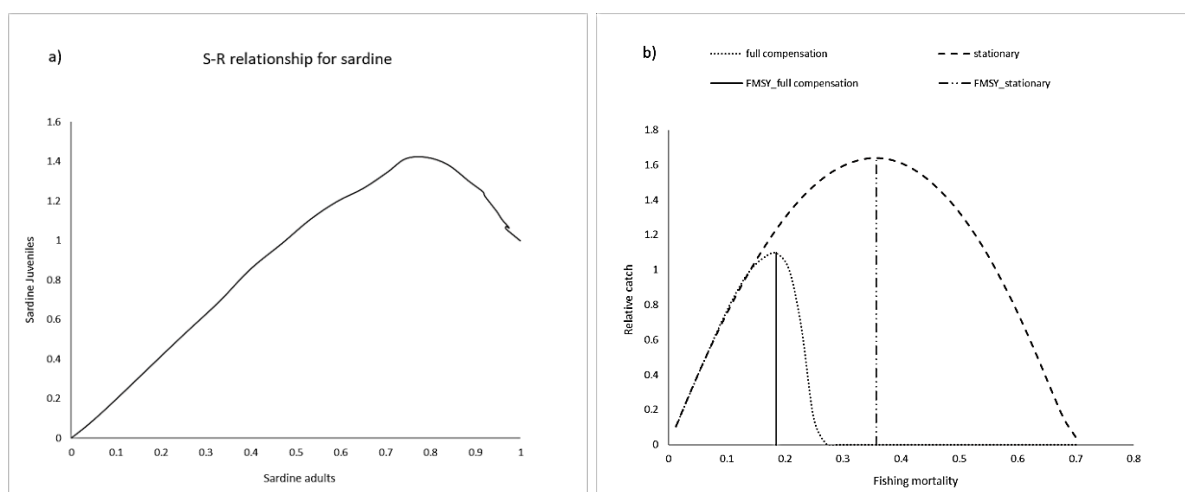


Figure A4.1 Emergent stock-recruitment relationship predicted by the Ecosim model. It was obtained by applying a V-shaped fishing pattern as demonstrated in the Report of the Working Group on Multispecies Assessment Methods (WGSAM) (ICES 2017) (a); Relative catch as a function of F from Ecosim equilibrium calculations for stationary (when only the biomass of the targeted stanza reacts to changes in fishing mortality and biomasses of all other species are maintained constant) and full compensation conditions (take into account indirect effects on the biomass of the targeted stanza resulted from the trophic link (b)).

Prebal - a pre-balance diagnostic (link et al. 2010)

In order to check if model parameters followed the general ecological principles, a pre-balance (PREBAL) diagnostic (Link 2010) was executed. Performed diagnostics included the slopes of biomass ratios, vital rates, total production and consumption based on trophic levels. The results of the diagnostic were used as a guide for the balancing procedure and to ensure the integrity of the input data. The PREBAL procedure revealed that for some functional groups, B , P/B and Q/B values were low (underestimated, below slope line) or high (overestimated, above slope line; Figure A.2). Before initiating mass balance of the model and running Ecosim simulations, these values were checked for data integrity.

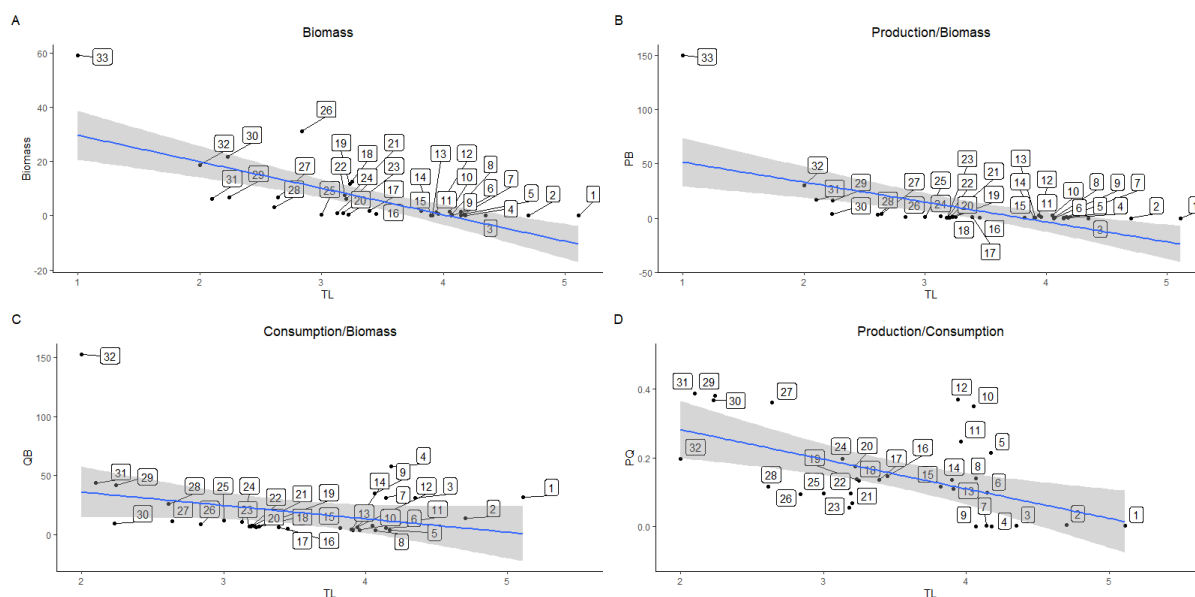


Figure A4.2 A pre-balance (PREBAL) diagnostic (Link, 2010) of the Portuguese Continental Shelf ecosystem plotting (A) biomass estimates (t/km^2), (B) production/biomass ratio (per year), and (C) consumption/biomass (per year) and (D) production/consumption (per year) vs species ranked by trophic level, from lowest to the highest trophic level. Numbers correspond to functional groups and they are explained in Table A4.3 in the annex and Table 4.1 in chapter 4.

Ecosim diagnostics

The credibility of model behaviour was checked based on the criteria proposed by the Working Group on Multispecies Assessment Methods (WGSAM) (ICES 2016, 2017) and applied in the Baltic and North Sea key runs. The following diagnostics/tests were assessed: (1) fit to historical data; (2) stock-recruitment and F-catch relationships, and (3) model stability. Firstly, we evaluated the fit of the model to historical data by assessing the contribution of each functional group SS to the total SS of the model. It was done by the rank order of SS contributions of catch and biomass as proposed by the WGSAM (ICES 2016) and applied in the North Sea key run (Table A4.4). Lower SS scores (higher rank) demonstrate that good model fits were achieved for these time-series data.

Table A4.4 Rank order of SS contributions of each functional group to the overall model fit. Lower values indicate better fits to data.

Biomass		Catch	
Functional group / species	SS contribution	Functional group / species	SS contribution
Horse mackerel	0.676	Benthopelagic invertivorous fish	1.266
Benthopelagic invertivorous fish	1.064	Flatfish	2.658
Sparids	1.207	Horse mackerel	3.025
Rays	1.736	Rays	3.516
Adult sardine	2.232	Demersal piscivorous fish	4.478
Mackerel	2.371	Sparids	4.851
Benthopelagic piscivorous fish	3.175	Anchovy	4.993
Anchovy	4.311	Benthopelagic piscivorous fish	5.058
Bogue	4.64	Bogue	7.426
Demersal piscivorous fish	5.455	Mackerel	8.373
Hake	6.472	Demersal invertivorous fish	9.513
Blue jack mackerel	8.545	Blue jack mackerel	12.97
Juvenile sardine	10.27	Benthic cephalopods	13.86
Demersal invertivorous fish	21.85	adult sardine	14.68
Flatfish	28.6	Chub mackerel	16.06
Squids	31.98	Hake	21.1
Benthic cephalopods	49.58	Squids	23.62
Sharks	58.47	Juvenile sardine	27.18
Chub mackerel	150	Sharks	248.1

Secondly, we checked if the Ecosim model has a capability to predict plausible Beverton-Holt (or Ricker) type relationship for sardine. To ascertain the shape of Stock recruitment curve, a model was forced with V-shaped fishing pattern as proposed by WGSAM (ICES 2017).

Moreover, model predictions of F_{MSY} (fishing mortality at maximum sustainable yield, MSY) were checked to ascertain if they are consistent with published ranges of F_{MSY} (ICES 2018; Table A4.5)

Table A4.5 Predictions of fishing mortality at maximum sustainable yield (F_{MSY}). Underlined values were estimated by the model. Parameter F_{MSY} (ICES); were adopted from Report of the Working Group on Southern Horse Mackerel, Anchovy and Sardine (WGHANSA), estimated based on age-based analytical assessment (ICES, 2018). F_{MSY} stationary is fishing mortality at maximum sustainable yield estimated when only the biomass of the targeted stanza reacts to changes in fishing mortality and biomasses of other species are kept constant and F_{MSY} full compensation is fishing mortality at maximum sustainable yield estimated when indirect effects on targeted stanza biomass resulted from trophic interactions are taken into account respectively.

	Sardine
F_{MSY} full compensation	<u>0.19</u>
F_{MSY} stationary	<u>0.36</u>
F_{MSY} (ICES)	0.12

Finally, we checked the model stability by applying the following steps: (1) checking if all modelled biomasses were stable when forcing functions (including fishing) were not applied and 2) we checked if biomasses returned to stability after applying fishing only for short period.

Model calibration

The model calibration process was performed by applying the hypothesis testing procedure proposed by Mackinson et al. (2009) and appended by introducing environmental forcing on sardine in form of recruitment forcing patterns (also referred to as ‘egg production’ anomalies) and through environmental response function (Table A.6).

Table A4.6 Steps of model calibration procedure applied to fit the PCSE Ecosim model to time-series, performed in order to choose the best model fit. The model fit was assessed based on the values of the weighted sum of squared deviations (SS) between log observed biomass/catch and log predicted biomass/catch values and the Akaike Information Criterion (AIC) parameter. Two types of drivers are considered: external – fishing mortality and environmental forcing on sardine, and emergent from the Ecosim model during the fitting procedure – PP anomaly and vulnerabilities representing environmental effects and trophic interactions, respectively. Vs is the number of vulnerabilities estimated; Spp is the number of primary productivity spline points estimates; Min SS is a reduction in the weighted sum of squared deviations; k is the total number of parameters estimated; AIC is an Akaike Information Criterion (AIC) parameter. The best model fit chosen based on SS and AIC value is presented in bold.

Steps/Hypothesis	Description	k	Vs	Spp	min SS	AIC
Baseline	No forcing parameters (fishing, environmental forcing and PP anomaly) were used to drive the model. Vulnerabilities (that describe trophic interactions) are set to 2 (default value, indicating mixed control).	0	0	0	1202	6.227
Baseline + vulnerabilities	A set of 27 most sensitive vulnerabilities have been identified and estimated during the calibration process.	27	27	0	1202	5.838
Baseline + pp	PP anomaly, that imitates a potential historical primary productivity time series impacting P/B of phytoplankton, is used to drive a model. Vulnerabilities are set to a default value and fishing are not considered.	5	0	5	1161	-36.3
Baseline +vulnerabilities + pp	Both vulnerabilities and PP anomaly are used. Fishing mortality is not considered.	32	27	5	1177	-19.24
Baseline + environmental forcing on sardine	Environmental forcing on sardine that consists of forcing on sardine egg production and SST effect on sardine spawning, were applied.	0	0	0	1208	12.01
Baseline + environmental forcing on sardine + vulnerabilities	Forcing on sardine, and vulnerabilities are considered.	27	27	0	1182	-13.71
Baseline + environmental forcing on sardine + pp anomaly	Forcing on sardine, and pp anomaly are considered	5	0	5	1169	-27.65
Baseline + environmental forcing on sardine + vulnerabilities + pp anomaly	Forcing on sardine, vulnerabilities and pp anomaly are considered.	32	27	5	1149	-47.92
Fishing	Fishing mortality for 12 species is used to drive a model. Vulnerabilities are reset to default, and PP anomaly is not used.	0	0	0	2262	768.6
Fishing + vulnerabilities	Fishing mortality for 12 species is used to drive a model and vulnerabilities are considered. PP anomaly is not used.	27	27	0	946	-282.2

Fishing + pp	Fishing mortality for 12 species and PP anomaly is used to drive a model. Vulnerabilities are reset to default.	5	0	5	2250	762.3
Fishing + vulnerabilities + pp	Fishing mortality, vulnerabilities and PP anomaly are considered.	32	27	5	929	-304.7
Fishing + environmental forcing on sardine	Fishing and forcing on sardine are considered.	0	0	0	2223	747.7
Fishing + environmental forcing on sardine + vulnerabilities	Fishing, forcing on sardine and vulnerabilities are considered.	27	27	0	854	-406.5
Fishing + environmental forcing on sardine + pp anomaly	Fishing, forcing on sardine and pp anomaly are considered.	5	0	5	2216	743.6
Fishing + environmental forcing on sardine + vulnerabilities + pp anomaly	Fishing, forcing on sardine, vulnerabilities and pp anomaly are considered.	32	27	5	825	-447.4

Table A4.7 The most sensitive predator-prey interactions that were identified during the search for vulnerabilities procedure. Vulnerabilities of groups not included in the table were maintained as default ($v_{ij}=2$)

Prey \ predator	Bottlenose dolphin	Hake	Benthic cephalopods	Sparids	Bogue	Horse mackerel	Benthopelagic Invertivorous Fish	Chub mackerel	Mackerel	Blue jack mackerel	Anchovy	Juvenile sardine	Adult sardine	Meso/Micro zooplankton
Dem.fish_p	1	2	2	2	2	2	2	2	2	2	2	2	2	2
Benthic cephalopods	2	2	2	2	2	2	2	1.7	2	2	2	2	2	2
Bogue	2	2	1.9	2	2	2	2	2	2	2	2	2	2	2
Benthopelagic Invertivorous fish	2	1	2	2	2	2	2	1000	1000	2	2	2	2	2
Chub mackerel	2	2	1	2	2	2	2	2	2	2	2	2	2	2
Blue jack mackerel	2	1	2	2	2	2	2	2	2	2	2	2	2	2
Anchovy	2	1	2	2	2	2	2	2	1000	2	2	2	2	2
Juvenile sardine	2	2	2	2	1000	1000	2	1.00E+10	2	2	2	2	2	2
Macrozoobenthos	2	2	2	10	2	2	2	2	2	2	2	2	2	2
Suprabenthic invertebrates	2	2	2	2	2	1000	1	1000	2	2	2	2	2	2
Macrozooplankton	2	2	2	2	1000	2	2	2	2	2	2	2	2	2
Meso/Microzooplankton	2	2	2	2	2	2	1000	26.7	2	2.2	3.6	1	5	2
Phytoplankton	2	2	2	2	2	2	2	2	2	2	2	1	1.00E+10	1.3

Table A4.8 Pearson correlations of PP anomaly (obtained during the calibration process) with environmental variables. Abbreviations: AMO, NAO, EA, SST and UI means Atlantic Multidecadal Oscillation, North Atlantic Oscillation, Eastern Atlantic pattern, Sea surface temperature and Upwelling index, respectively. Significant results ($p \leq 0.05$) are underlined.

Environmental variable	r	p-value	Source
AMO annual mean	0.22	0.22	NOAA's Earth System Research Laboratory (http://www.esrl.noaa.gov/psd/data/timeseries/AMO)
AMO winter mean	0.15	0.41	
AMO summer mean	0.22	0.22	
NAO winter mean	0.15	0.41	NOAA Climate Prediction Centre-National Weather Service (http://www.cpc.ncep.noaa.gov/data/teledoc/ea.shtml)
NAO winter mean	0.25	0.16	
NAO summer mean	-0.3	0.1	
<u>EA annual mean</u>	<u>0.56</u>	<u>0.00</u>	NOAA Climate Prediction Centre-National Weather Service (http://www.cpc.ncep.noaa.gov/data/teledoc/ea.shtml)
EA winter mean	0.34	0.06	
<u>EA summer mean</u>	<u>0.43</u>	<u>0.01</u>	
SST annual mean	0.29	0.11	KNMI Climate Explorer web application (https://climexp.knmi.nl/about.cgi?id=someone@somewhere)
SST winter mean	0.08	0.66	
<u>SST summer mean</u>	<u>0.39</u>	<u>0.03</u>	
UI annual mean	0.25	0.16	Spanish Institute of Oceanography (IEO) (http://www.ieo.esinteractivo.html)
UI winter mean	0.18	0.31	
UI summer mean	0.08	0.64	

Procedure to obtain time series data used to fit and drive the PCSE ecosim model

Stochastic stock reduction analysis

Stock reduction analysis (SRA) Kimura et al. (1984) constructs a population dynamic model with a Beverton-Holt stock-recruitment function (Beverton and Holt 1957) that simulates changes in abundance by subtracting estimates of mortality and adding estimates of new recruits from the population over time. SRA is carried out by using historical catch information to drive population models from a historical reference point near the beginning of the fishery. It is a less data-intensive method which can help to estimate how large the stock needed to be, in order to produce time series of observed landings. In the SRA the key

population parameters of the population dynamic model are adjusted until the simulation produces numbers near estimates from an independent estimate of absolute abundance. In Stochastic SRA (Walters et al. 2006) recruitment is assumed to have lognormally distributed annual anomalies (variability), that are considered by performing a large number of simulation runs with anomaly sequences chosen from normal prior distributions. In other words, Stochastic SRA determines what is the probability of obtaining the observed current population size estimate of stock i , given a mean recruitment curve by using variations and the historical catches.

Material and methods

The Stochastic SRA was performed using the Data-Limited Methods Toolkit (DLMtool) R package (Carruthers et al. 2014). To perform the analysis, the following information was required: historical catches, index of species abundance, life history information (Table B.1) and estimates of the variation in natural mortality rate mortality (M), Bertalanffy growth parameter (K) and a maximum length of the fish (Linf). Also, catch at age data could be included, however, due to lack of data, in this analysis, it was omitted. An existing operating model (OM) (obtained from De la Puente S., personal communication) has been adapted to the species of interest (appendix 1) The operating model that simulates the population dynamics based on SRA contains life-history parameters pertinent to the species of interest (Maxage -the maximum age of individuals that is simulated; M - natural mortality rate; K - Bertalanffy growth parameter that determines how fast fish approach Linf; Linf - the length of very old (infinitely old) fish, also called asymptotic length; t_0 - an initial condition parameter that is the von Bertalanffy theoretical age at length zero; L50 - length at 50 percent maturity; L50_95 - length increment from 50 percent to 95 percent maturity; a - length-weight parameter alpha; b - length-weight parameter beta and h - steepness of the stock recruitment relationship), inter-annual variability in natural mortality rate (M), growth parameter K and maximum length (Linf), and mean temporal trends in M, K, and Linf expressed as a percentage change in M, K and Linf, per year. All the parameters, excluding (Maxage, a and b) are expressed as lower and upper bounds of uniform distribution.

The life history parameters (excluding h) were obtained from FishBase online database (Froese, and Pauly 2018; FishBase) and are provided in the Table B.1 (Maxage, M, Linf, K, t_0 , L50, L50_95, a, b). Lower and upper bounds of the steepness of the stock recruitment

relationship (h) distribution were assumed to be 0.2 and 0.99 for all species. Lower and upper bounds of Inter-annual variability in M , K and $Linf$ were assumed to be 0 and 0.025 for K and $Linf$ and 0 and 0.1 for M whereas lower and upper bounds of mean temporal trends in M , K , and $Linf$ were assumed as -0.25 and 0.25.

Historical catch time-series (from 1950–2014) were obtained from the Sea Around Us project (Leitão 2014) while recent catch data (2014–2017) was provided by the Portuguese National Statistical Institute (INE). Independent estimates of abundance for all species except for anchovy were obtained from Portuguese bottom trawl surveys carried out in autumn (September–October) at predefined stations. For anchovy abundance, estimates were obtained from acoustic surveys (PELAGO survey series) performed annually in spring (April–May). Both, acoustic and bottom trawl surveys were performed by the Portuguese Institute of Sea and Atmosphere (IPMA).

In total, 100 iterations were performed for 12 species or group of species (list of species is available in Table A4.9) and the estimate of spawning stock biomass SSB representing 50th percentile (median) was used in ecosim analysis (plotted on Figure B.1). Species that are part of Rays and Sparids, for which historical catches were aggregated, were analysed jointly. With regards to the functional group Sparids, (that in Ecopath consists of *Pagellus* spp and *Pagrus* spp.) only *Pagellus* spp. were considered as there was lack of abundance data for *Pargus* spp. Seabass (*Dicentrarchus labrax*) and forkbeard (*Phycis phycis*) were excluded for the same reason. As a result, the group demersal piscivorous fish consists of European conger and anglerfish. Benthopelagic piscivorous fish consists of silver scabbardfish, while benthopelagic piscivorous fish consists of pouting and blue whiting (Table A4.9).

Table A4.9 Description of parameters, with their data sources, used to perform stochastic stock reduction analysis (SRA). Parameter Maxage is the maximum age of individuals that is simulated M is natural mortality rate; K is a curvature parameter, Bertalanffy growth parameter that determines how fast fish approach Linf; Linf is the length of very old (infinitely old) fish, also called asymptotic length; to is an initial condition parameter that is the von Bertalanffy theoretical age at length zero; L50 is the length at 50 percent maturity; L50_95 is length increment from 50 percent to 95 percent maturity; a is length-weight parameter alpha and b is length-weight parameter beta. The parameters M, Linf, K, t0, L50, L50_95 are represented as uniform distribution lower and upper bounds value range.

EwE functional group	Blue jack mackerel	Atlantic mackerel	Bogue	Anchovy	Horse mackerel	Rays	Sparids	Demersal piscivorous fish (DFP)		Benthopelagic piscivorous fish (BFP)	Benthopelagic invertivorous fish (BFI)	
Common name	Blue jack mackerel	Atlantic mackerel	Bogue	Anchovy	Horse mackerel			European conger	Anglerfish	Silver scabbardfish	Pouting	Blue whiting
Scientific name	<i>Trachurus picturatus</i>	<i>Scomber scombrus</i>	<i>Boops boops</i>	<i>Engraulis encrasicolus</i>	<i>Trachurus trachurus</i>		<i>Pagellus</i> spp	<i>Conger conger</i>	<i>Lophius</i> spp	<i>Lepidopus caudatus</i>	<i>Trisopterus luscus</i>	<i>Micromesistius poutassou</i>
Life history parameters												
Maxage	21	11	19	7	20	22	14	48	22	10	5	8
Natural mortality rate (M)	0.37–0.42	0.28–0.64	0.21–0.48	0.49–1.11	0.18–0.42	0.16–0.38	0.26–0.59	0.06–0.15	0.15–0.35	0.23–0.53	0.56–1.28	0.42–0.96
Linf	32–64	43–47	32–36	19–25	39.3–58.1	95–104	21.8–49.6	229–265	108–157	125.3–195.4	36.2–46.7	28.1–48.4
K	0.07–0.38	0.196–0.272	0.166–0.280	0.32– 1.07	0.122– 0.270	0.13–0.84	0.12–0.32	0.063–0.270	0.145–0.159	0.297–0.384	0.211–0.590	0.150–0.480
t0	-3.3– -0.2	-2.9– -2.1	-2.14– -0.96	-4.09– 0.5	-4.43– - 0.31	0.71– -0.19	-2.97– -0.45	-2.4– 0.39	-1.005– -0.48	-0.53– -0.38	-1.27– - 0.01	-3.51– -0.35
L50 (Lm)	20–36	19–34	15–27	9.2–16.5	20.6–36.9	41–74	17.2–30.9	93.5–167.9	37.4–67	66.7–119.8	15.5–31.4	13.9–25.0
L50_95 (Lopt)	1–8	0–1	2–3	0–1	0.6–5.4	9.3–19.2	1.2–12.2	40–57.2	4–12.4	4–8	2–4	2–4
a	0.00955	0.00646	0.01047	0.00468	0.00832	0.00253	0.01133	0.00046	0.01513	0.00046	0.00794	0.0038
b	2.96	3.05	3.00	3.10	2.96	3.22	3.04	3.25	2.95	3.06	3.10	3.15

Application in Ecosim	Used as relative biomass and to calculate fishing mortality	Used as relative biomass and to calculate fishing mortality	Used as relative biomass and to calculate fishing mortality	Used as relative biomass and to calculate fishing mortality	Used to calculate fishing mortality	Used as relative biomass and to calculate fishing mortality	Used as relative biomass and to calculate fishing mortality	Used as relative biomass and to calculate fishing mortality	Used as relative biomass and to calculate fishing mortality	Used as relative biomass and to calculate fishing mortality	Used as relative biomass and to calculate fishing mortality	Used as relative biomass and to calculate fishing mortality

Results

The estimates of spawning stock biomass (SSB) for analysed species are presented in Figure A4.3. Also, for reference, historical catch and available abundance indices' time-series are presented on the figure. The output of SRA expressed as the median of probability density function (considering 100 simulations) of spawning stock biomass (SSB) estimates were used as relative biomass and to obtain fishing mortality to fit and force the PCSE Ecosim model, respectively.

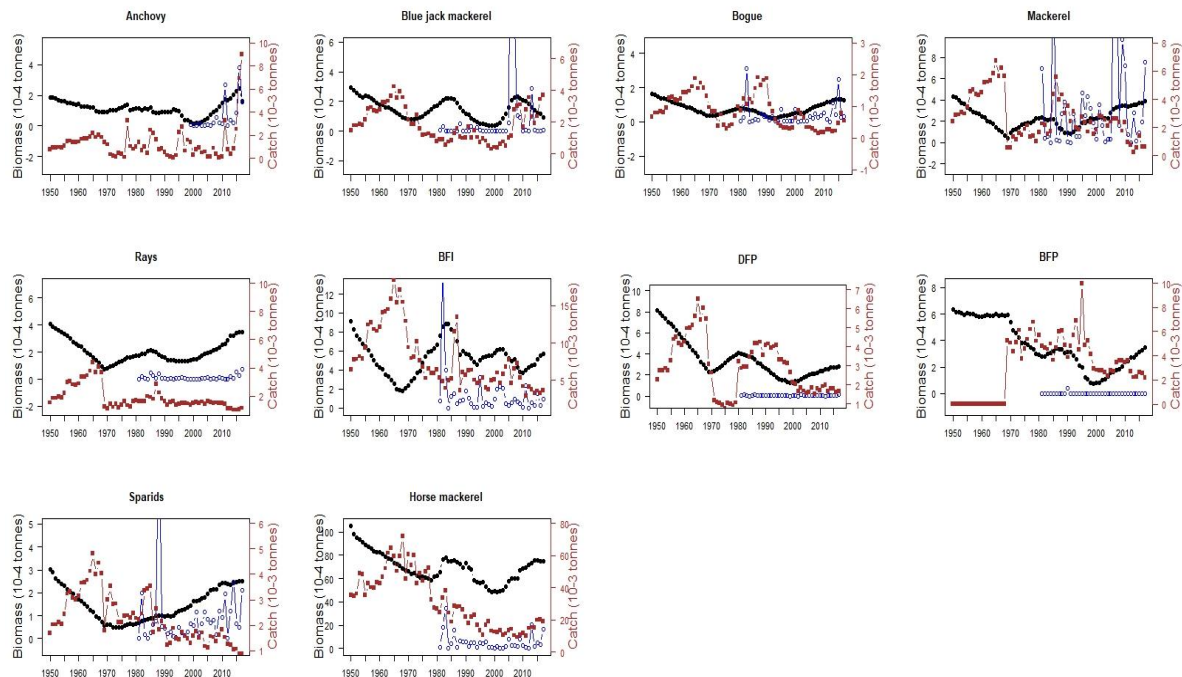


Figure A4.3 The estimates of spawning stock biomass (SSB) represented as second quartile (median) of the probability density function of (considering 100 simulations) (black line); catch (red dotted line) and abundance index (blue open points) for species in Portuguese continental shelf ecosystem.

Appendix 1

Operating model used in SRA (R Script; Example for atlantic mackerel)

```
#Initial setup#
setwd("/Users/sdlp/Dropbox/01 Documentos Personales/06 R/S-SRA")

library(DLMtool)
library(lubridate)
library(lattice)
library(dplyr)
getwd()

#### Atlantic mackerel ####

#Operating Model with parameters used in Stochastic SRA #

Bonito_OM<-new("OM")
Bonito_OM@Name<-c("Atlantic mackerel") # changed
Bonito_OM@Agency<-c("IPMA") # changed
Bonito_OM@Region<-c("Portugal_EEZ") # changed
Bonito_OM@nsim<-c(100) # number of simulations
Bonito_OM@Common_Name<-c("Atlantic mackerel") # changed
Bonito_OM@Species<-c("Scomber scombrus") #changed
Bonito_OM@maxage<-c(11) # data from Fishbase -The maximum age of individuals that is simulated (there is no 'plus group'). Single
value. Positive integer
Bonito_OM@M<-c(0.28,0.64) # data from Fishbase -Natural mortality rate. Uniform distribution lower and upper bounds. Positive real
number
Bonito_OM@Msd<-c(0,0.1) # assumption - Inter-annual variability in natural mortality rate expressed as a coefficient of variation. Uniform
distribution lower and upper bounds. Non-negative real numbers
Bonito_OM@Mgrad<-c(-0.25,0.25) # assumption - Mean temporal trend in natural mortality rate, expressed as a percentage change in M
per year. Uniform distribution lower and upper bounds. Real numbers
Bonito_OM@h<-c(0.2,0.99) # assumption - Steepness of the stock recruit relationship. Uniform distribution lower and upper bounds.
Values from 1/5 to 1
Bonito_OM@Linf<-c(43,47) #changed from Fishbase -Maximum length. Uniform distribution lower and upper bounds. Positive real
numbers
Bonito_OM@K<-c(0.196,0.272) # changed- from Fishbase -von Bertalanffy growth parameter k. Uniform distribution lower and upper
bounds. #Positive real numbers
Bonito_OM@t0<-c(-2.9,-2.1) # data from Fishbase -von Bertalanffy theoretical age at length zero. Uniform distribution lower and upper
#bounds.Non-positive real numbers
Bonito_OM@Ksd<-c(0,0.025) # assumption - Inter-annual variability in growth parameter k. Uniform distribution lower and upper
bounds.Non-negative real numbers
Bonito_OM@Kgrad<-c(-0.25,0.25) # assumption - Mean temporal trend in growth parameter k, expressed as a percentage change in k per
year.Uniform distribution lower and upper bounds. Real numbers
Bonito_OM@Linfsd<-c(0,0.025) # assumption - Inter-annual variability in maximum length. Uniform distribution lower and upper
bounds.Non-negative real numbers
Bonito_OM@Linfgrad<-c(-0.25,0.25) # assumption - Mean temporal trend in maximum length, expressed as a percentage change in Linf
per year. Uniform distribution lower and upper bounds. Real numbers
Bonito_OM@L50<-c(19,34) # data from Fishbase - (Lm)-Length at 50 percent maturity. Uniform distribution lower and upper bounds.
#Positive real numbers
Bonito_OM@L50_95<-c(0,1) # data from Fishbase -Length increment from 50 percent to 95 percent maturity. Uniform distribution lower
and upper bounds. Positive real numbers
Bonito_OM@a<-c(0.00646) # data from Fishbase -Length-weight parameter alpha. Single value. Positive real number
Bonito_OM@b<-c(3.05) # data from Fishbase -Length-weight parameter beta. Single value. Positive real number
Bonito_OM@nyears<-c(68) # The number of years for the historical 'spool-up' simulation. Single value. Positive #integer
Bonito_OM@CurrentYr<-c(68) # The current calendar year (final year) of the historical simulations (eg 2011). Single value. Positive
integer.
Bonito_OM@Cobs<-c(0.1,0.3) # assumption - Log-normal catch observation error expressed as a coefficient of variation. Uniform
distribution lower and upper bounds. Non-negative real numbers
Bonito_OM@lobs<-c(0.1,0.4) # assumption - Log-normal observational error in CPUE. Uniform distribution lower and upper bounds. Non-
negative real numbers

#Data input for Historical catches (Chist), Catch at age data (CAA) and Indices of abundance (Ind) ####
data<-read.csv ("G:/EARTHSYSTEMS_PhD/THESE/Ecopath_with_ecosim_PhD_second_step/UBC_EwE_course/SRA/SRA_other
species_to_2017/MAC.csv",header = T)
Chist<-data$Chist
Ind<-data$Ind
```

[illegible]

```
#Run S-SRA#####
OMout <- StochasticSRA(Bonito_OM,CAA,Chist,Ind)
```

```
##Run boxplot to retrieve median ###
par(mfrow=c(1,1))
a<-boxplot(OMout@cpars$SSB, xlab="Year", ylab="SSB")
a
b<-a$stats
write.table(b,"G:/EARTHSYSTEMS_PhD/THESE/Ecopath_with_ecosim_PhD_second_step/UBC_EwE_course/SRA/SRA_other
species_to_2017/MAC_bp.xls", sep="\t")
###END###
```

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ANNEX 5

Supplementary material for chapter 5

Annex 5 – Supplementary material for chapter 5

Additional information

Table A5.1. List of functional groups and species within each group included in the Portuguese continental shelf ecosystem model.

Functional group	Species
Seabirds	<i>Morus bassanus</i> ; <i>Calonectris borealis</i> ; <i>Alca torda</i> ; <i>Puffinus mauretanicus</i> ; <i>Uria aalge</i>
Minke whale	<i>Balaenoptera acutorostrata</i>
Common dolphin	<i>Delphinus delphis</i>
Striped dolphin	<i>Stenella coeruleoalba</i>
Bottlenose dolphin	<i>Tursiops truncatus</i>
Harbour porpoise	<i>Phocoena phocoena</i>
Tunas	<i>Sarda sarda</i> ; <i>Auxis rochei</i> ; <i>Thunnus thynnus</i>
Sharks	<i>Galeus melastomus</i> , <i>Isurus oxyrinchus</i> , <i>Scyliorhinus canicular</i> , <i>Scyliorhinus stellaris</i> , <i>Scymnodon ringens</i> , <i>Mustelus mustelus</i> , <i>Centroscyrmnus coelolepis</i>
Rays	<i>Raja clavata</i> ; <i>Raja brachyura</i> ; <i>Leucoraja naevus</i> ; <i>Raja montagui</i>
Hake	<i>Merluccius merluccius</i>
Squids	<i>Loligo vulgaris</i> ; <i>Illex coindetii</i> ; <i>Todaropsis eblanae</i> ; <i>Alloteuthis subulata</i> ; <i>Alloteuthis media</i>
Benthic cephalopods	<i>Octopus vulgaris</i> ; <i>Eledone cirrhosa</i> ; <i>Sepia officinalis</i> ; <i>Sepiola</i> spp.
Horse mackerel	<i>Trachurus trachurus</i>
Blue jack mackerel	<i>Trachurus picturatus</i>
Chub mackerel	<i>Scomber colias</i>
Mackerel	<i>Scomber scombrus</i>
Demersal piscivorous fish	<i>Conger conger</i> ; <i>Chelidonichthys lucernus</i> ; <i>Helicolenus dactylopterus</i> ; <i>Dicentrarchus labrax</i> ; <i>Lophius budegassa</i> ; <i>Lophius piscatorius</i>
Demersal invertivorous fish	<i>Trigla lyra</i> ; <i>Serranus hepatus</i> ; <i>Callionymus lyra</i> ; <i>Chelidonichthys cuculus</i> ; <i>Synchiropus phaeton</i> ; <i>Lepidotrigla cavillone</i> ; <i>Callanthias ruber</i> ; <i>Mullus surmuletus</i> ; <i>Mullus barbatus</i> ; <i>Cepola macrophthalma</i> ; <i>Ammodytidae</i> ; <i>Gobiidae</i>
Benthopelagic piscivorous fish	<i>Zeus faber</i> ; <i>Lepidopus caudatus</i> ; <i>Belone belone</i> ; <i>Phycis blennoides</i> ; <i>Phycis phycis</i>
Benthopelagic invertivorous fish	<i>Trisopterus luscus</i> ; <i>Micromesistius poutassou</i> ; <i>Argentina sphyraena</i> ; <i>Macroramphosus</i> spp.; <i>Capros aper</i> ; <i>Gadiculus argenteus</i> ; <i>Anthias anthias</i>
Flatfish	<i>Solea solea</i> ; <i>Solea senegalensis</i> ; <i>Pegusa lascaris</i> ; <i>Microchirus azevia</i> ; <i>Microchirus variegatus</i> ; <i>Platichthys flesus</i> ; <i>Citharus linguatula</i> ; <i>Dicologlossa</i>

	<i>cuneata</i> ; <i>Scophthalmus maximus</i> ; <i>Scophthalmus rhombus</i> ; <i>Lepidorhombus boscii</i> ; <i>Lepidorhombus whiffiagonis</i> ; <i>Arnoglossus laterna</i>
Sparids	<i>Pagellus acarne</i> ; <i>Pagellus erythrinus</i> ; <i>Pagellus bogaraveo</i> ; <i>Spondylusoma cantharus</i> ; <i>Diplodus vulgaris</i> ; <i>Diplodus bellottii</i> ; <i>Diplodus annularis</i> ; <i>Diplodus sargus</i> ; <i>Pagrus pagrus</i> ; <i>Pagrus auriga</i>
Anchovy	<i>Engraulis encrasicolus</i>
Sardine (adult and juvenile)	<i>Sardina pilchardus</i>
Bogue	<i>Boops boops</i>
Henslow's crab	<i>Polybius henslowii</i>
Shrimps	Unspecified Crustacea natantia
Macrozoobenthos	Starfishes; annelids; sea urchins; sea cucumbers; bivalves; crustaceans; sea anemone; other benthic invertebrates
Suprabenthic invertebrates	Euphausiids, mysids, isopods and amphipods
Macrozooplankton	Zooplankton: length >3 mm, width >1 mm
Meso/microzooplankton	Zooplankton: length ≤3 mm, width ≤1 mm; including fish eggs
Phytoplankton	Phytoplankton

Table A5.2 Pearson cross-correlation matrix for variables included in fishing mortality data group. Variables that have cross-correlation >0.8 are in bold.

	F_DFP	F_Rays	F_BFP	F_Sparids	F_BO G	F_HO M	F_BFI	F_MA C	F_JAA	F_ANE	F_PIL	F_HKE
F_DFP	1											0.5
F_Rays	0.8	1										
F_BFP	0.7	0.6	1									
F_Sparids	0.5	0.8	0.2	1								
F_BO G	0.4	0.6	-0.1	0.8	1							
F_HOM	0.5	0.6	0.2	0.7	0.6	1						
F_BFI	-0.1	0.3	-0.1	0.3	0.2	-0.1	1					
F_MAC	0.4	0.7	0.0	0.9	0.9	0.6	0.3	1				
F_JAA	-0.1	-0.4	-0.2	-0.3	-0.2	-0.1	-0.4	-0.4	1			
F_ANE	0.2	0.1	0.5	-0.1	-0.2	0.1	-0.3	-0.2	0.3	1		
F_PIL	0.1	0.1	0.2	0.1	0.1	-0.1	-0.1	0.1	-0.3	-0.1	1	
F_HKE	0.5	0.3	0.7	-0.2	-0.3	-0.3	-0.1	-0.3	0.0	-0.1	0.1	1

Table A5.3 Pearson cross-correlation matrix for variables included in the environmental/climatic data group. Variables that have cross-correlation >0.8 are in bold.

	AMOm	AMOW	AMOs	NAOm	NAOW	NAOs	EAm	EAW	EAQs	SSTm	SSTw	SSTs	UIm	UIw	UIs
AMOm	1														
AMOW	0.9	1													
AMOs	0.9	0.8	1												
NAOm	-0.6	-0.5	-0.6	1											
NAOW	-0.3	-0.3	-0.3	0.7	1										
NAOs	-0.4	-0.3	-0.4	0.4	-0.1	1									
EAm	0.5	0.4	0.4	-0.1	0.0	-0.3	1								
EAW	0.1	0.1	0.0	0.1	0.2	-0.1	0.6	1							
EAs	0.5	0.5	0.3	-0.2	0.0	-0.2	0.8	0.3	1						
SSTm	0.5	0.5	0.4	0.0	0.2	-0.3	0.5	0.1	0.6	1					
SSTw	0.3	0.4	0.2	0.1	0.3	-0.2	0.3	0.1	0.4	0.8	1				
SSTs	0.5	0.5	0.5	-0.1	0.1	-0.3	0.6	0.1	0.7	0.9	0.6	1			
UIm	-0.2	-0.1	-0.2	0.3	0.3	0.0	-0.1	-0.2	0.1	0.1	0.2	0.1	1		
UIw	-0.3	-0.2	-0.2	0.5	0.6	-0.1	-0.2	-0.3	-0.2	0.0	0.1	0.0	0.6	1	
UIs	0.3	0.5	0.2	-0.3	-0.3	-0.1	0.3	0.2	0.4	0.1	0.1	0.1	0.3	-0.4	1

Table A5.4 Pearson cross-correlation matrix for variables included in the observed biomass data group. Variables that have cross-correlation >0.8 are in bold.

	B_ANE	B_Sardine	B_MAC	B_HOM	B_Sparids	B_Flatfish	B_HKE	B_DFP	B_JAA	B_DFI	B_MAS	B_BFI	B_Bogue	B_BFP	B_ceph	B_Squids	B_Rays	B_Tunas	B_Sharks	B_PIL_Juv
B_ANE	1																			
B_Sardine	-0.6	1																		
B_MAC	0.4	-0.8	1																	
B_HOM	0.1	-0.5	0.7	1																
B_Sparids	0.5	-0.8	1.0	0.7	1															
B_Flatfish	0.0	0.2	-0.2	0.0	-0.2	1														
B_HKE	0.4	0.0	-0.2	-0.7	-0.2	0.0	1													
B_DFP	0.7	-0.2	0.0	-0.5	0.0	0.1	0.9	1												
B_JAA	0.5	-0.2	0.4	-0.2	0.4	-0.1	0.6	0.7	1											
B_DFI	0.3	-0.3	0.0	0.0	0.1	0.7	0.1	0.3	0.1	1										
B_MAS	0.2	0.0	0.4	0.5	0.3	-0.1	-0.4	-0.2	0.0	-0.2	1									
B_BFI	-0.5	0.4	-0.5	-0.5	-0.6	0.2	0.3	0.1	-0.3	0.0	-0.5	1								
B_BPG	0.6	-0.8	0.9	0.4	0.9	-0.2	0.2	0.4	0.6	0.2	0.1	-0.4	1							
B_BFP	0.8	-0.2	-0.1	-0.5	0.0	0.1	0.8	0.9	0.5	0.3	-0.1	0.0	0.2	1						
B_ceph	-0.2	-0.1	0.1	0.2	0.1	0.4	-0.3	-0.2	-0.1	0.5	-0.2	0.1	0.1	-0.3	1					
B_Squids	0.2	0.1	-0.4	-0.7	-0.3	0.0	0.6	0.6	0.2	0.3	-0.5	0.4	-0.1	0.6	-0.1	1				
B_Rays	0.8	-0.8	0.8	0.3	0.8	-0.1	0.4	0.6	0.5	0.3	0.1	-0.3	0.9	0.5	0.0	0.1	1			
B_Tunas	-0.2	0.6	-0.7	-0.9	-0.7	0.0	0.7	0.4	0.2	-0.1	-0.4	0.5	-0.4	0.3	-0.2	0.6	-0.3	1		
B_Sharks	0.0	-0.2	0.1	0.1	0.2	0.5	0.0	0.0	-0.1	0.6	0.0	0.2	0.2	0.0	0.4	0.1	0.2	-0.1	1	
B_PIL_Juv	-0.6	0.6	-0.7	-0.5	-0.7	0.0	0.0	-0.2	-0.3	-0.1	-0.5	0.5	-0.7	-0.2	0.0	0.3	-0.7	0.4	-0.2	1

Table A5.5 Pearson cross-correlation matrix for variables included in the modelled biomass data group. Variables that have cross-correlation >0.8 are in bold.

B_Tunas	B_Bortenoselphin	B_Harbor_porpoise	B_Stripped_dolphin	B_DFP	B_Seabirds	B_Hake	B_Common_dolphin	B_Rays	B_Sharks	B_Squids	B_Minke	B_Ben_Cephalopods	B_BFP	B_Flatfish	B_Sparids	B_BOG	B_HOM	B_BFI	B_MAS	B_DEI	B_MAC	B_JAA	B_Henslow'scra b	B_ANE	B_PIL_Juv	B_PIL	B_Shrimps	B_Macro	B_Supra_Juv	B_Macrozooplankton	B_Meso_Micro	B_Phytoplankton
B_Phytoplankton	1																															
B_Meso_Micro	0.8	1																														
B_Macrozooplankton	0.9	0.9	1																													
B_Supra_Juv	0.5	0.5	0.4	1																												
B_Macro	1.0	0.8	0.9	0.6	1																											
B_Shrimps	0.9	0.8	0.9	0.7	0.9	1																										
B_PIL	-0.5	-0.9	-0.7	-0.1	-0.5	-0.5	1																									
B_PIL_Juv	-0.5	-0.7	-0.7	0.1	-0.5	-0.5	0.8	1																								
B_ANE	0.7	0.6	0.7	0.4	0.7	0.7	-0.4	-0.4	1																							
B_Henslow'scra b	0.9	0.9	1.0	0.5	0.9	1.0	-0.7	-0.6	0.7	1																						
B_JAA	0.3	-0.2	0.0	0.5	0.3	0.2	0.6	0.5	0.4	0.0	1																					
B_MAC	0.5	0.7	0.6	0.0	0.4	0.4	-0.9	-0.7	0.1	0.6	-0.6	1																				
B_DEI	0.9	0.9	0.9	0.7	0.9	0.9	-0.6	-0.4	0.7	0.9	0.2	0.5	1																			
B_MAS	0.8	0.8	0.9	0.0	0.7	0.7	-0.9	-0.8	0.6	0.8	-0.3	0.8	0.7	1																		
B_BFI	0.3	0.1	0.0	0.8	0.3	0.3	0.4	0.5	0.2	0.1	0.7	-0.3	0.4	-0.3	1																	
B_HOM	0.9	0.9	0.9	0.3	0.9	0.8	-0.8	-0.7	0.8	0.9	0.0	0.7	0.9	0.9	0.0	1																
B_BOG	0.7	0.9	0.9	0.3	0.7	0.7	-0.9	-0.8	0.5	0.8	-0.3	0.8	0.8	0.9	-0.2	0.9	1															
B_Sparids	0.8	0.8	0.9	0.1	0.7	0.7	-0.9	-0.8	0.6	0.9	-0.3	0.7	0.7	1.0	-0.3	0.9	0.9	1														
B_Flatfish	0.4	0.0	0.1	0.6	0.4	0.3	0.4	0.5	0.2	0.1	0.8	-0.3	0.3	-0.2	0.9	0.0	-0.2	-0.3	1													
B_BFP	0.7	0.4	0.6	0.2	0.7	0.6	-0.2	-0.3	0.9	0.6	0.5	-0.1	0.5	0.4	0.1	0.6	0.3	0.5	0.3	1												

[illegible]

Table A5.6 Pearson cross-correlation matrix for variables included in the ecosystem indices data group. Variables that have cross-correlation >0.8 are in bold.

	Dem/Pel B	PredB	Kempton Q	Shannon	Tot C	Dem C	Pel C	Dem/Pel C	Pred C	TLc	TLco	R	FCI	H	A/C	TotP/TotB
Dem/Pel B	1															
Pred B	-0.4	1														
KemptonQ	0.9	-0.5	1													
Shannon	0.6	-0.4	0.7	1												
Tot C	0.8	0.1	0.6	0.4	1											
Dem C	0.5	0.5	0.5	0.2	0.7	1										
Pel C	-0.8	0.8	-0.8	-0.7	-0.4	0.0	1									
Dem/Pel C	0.9	-0.2	0.9	0.6	0.8	0.7	-0.7	1								
Pred C	0.6	0.4	0.6	0.4	0.7	0.9	-0.2	0.7	1							
TLc	-0.7	0.4	-0.5	-0.5	-0.7	0.0	0.7	-0.6	-0.2	1						
TLco	-0.5	0.8	-0.4	-0.4	-0.1	0.4	0.8	-0.3	0.2	0.6	1					
R	0.3	-0.9	0.3	0.4	-0.2	-0.6	-0.7	0.1	-0.4	-0.4	-0.9	1				
FCI	0.8	-0.8	0.7	0.6	0.4	-0.1	-0.9	0.6	0.1	-0.7	-0.8	0.7	1			
H	0.3	0.7	0.2	0.1	0.7	0.8	0.2	0.5	0.8	-0.1	0.6	-0.8	-0.2	1		
A/C	-0.7	0.8	-0.6	-0.6	-0.2	0.3	0.9	-0.4	0.0	0.7	0.9	-0.9	-0.9	0.4	1	
TotP/TotB	0.7	-0.7	0.6	0.5	0.4	-0.1	-0.9	0.5	0.1	-0.7	-0.9	0.8	0.8	-0.4	-0.9	1

Table A5.6 Results of the Regime shift analysis (STARS) performed on each variable Presented STARS regime shift years were identified in time series using $p \leq 0.05$ and for values designated with * regime shift was detected at $p \leq 0.1$. Symbols $\uparrow$ and $\downarrow$ indicate increasing and decreasing trend respectively. Abbreviations and full names of the variables used in the analysis are shown.

Abbreviation	Full name	Shift mid-90s	Shift mid-2000s	Shift mid-2010s
FM	Fishing mortality			
F_DFP	Demersal piscivorous fish		2001 $\downarrow$	
F_Rays	Rays		2002 $\downarrow$	2010 $\downarrow$
F_BFP	Benthopelagic piscivorous fish	1995 $\uparrow$	2003 $\downarrow$	
F_Sparids	Sparids	1994 $\downarrow$	2004 $\downarrow$	2016 $\downarrow$
F_BOG	Bogue	1993 $\downarrow$		
F_HOM	Horse mackerel		2000 $\downarrow$	2015 $\uparrow$
F_BFI	Benthopelagic invertivorous fish			2014 $\downarrow$
F_MAC	Mackerel	1993 $\downarrow$		2011 $\downarrow$
F_JAA	Blue jack mackerel			2015 $\uparrow$
F_ANE	Anchovy	1996 $\uparrow$	2005 $\downarrow$	2016 $\uparrow$
F_PIL	Sardine			2014 $\downarrow$
F_PIL_Juv	Juvenile sardine			2015 $\downarrow$
F_HKE	Hake			2015 $\downarrow$
ENV	Environmental variables			
SSTm	Mean sea surface temperature	1998 $\uparrow$		2011 $\uparrow$
SSTw	Winter sea surface temperature	1999 $\uparrow$		2012 $\uparrow$
SSTs	Summer sea surface temperature	1998 $\uparrow$		2011 $\uparrow$
UI_m	Mean Upwelling index			2015 $\uparrow$
UI_w	Winter Upwelling index			-
UI_s	Summer Upwelling index			2016 $\uparrow$
CLIM	Climatic indices			
AMOm	Mean Atlantic multidecadal oscillation	1997 $\uparrow$		2016 $\uparrow$
AMOW	Winter Atlantic Multidecadal oscillation	1995 $\uparrow$		2016 $\uparrow$
AMOs	Summer Atlantic Multidecadal oscillation	1998 $\uparrow$		
NAOm	Mean North Atlantic oscillation	-	-	-
NAOW	Winter North Atlantic oscillation			2014 $\uparrow$
NAOs	Summer North Atlantic oscillation		2007 $\downarrow$	
EAm	Mean Eastern Atlantic pattern	1998 $\uparrow$		2014 $\downarrow$
EAW	Winter Eastern Atlantic pattern			2014 $\downarrow$
EAs	Summer Eastern Atlantic pattern	1998 $\uparrow$		2016 $\downarrow$
B_obs	Observed biomass			
B_ANE_o	Anchovy	1997 $\downarrow$	2007 $\uparrow$	
B_PIL_o	Sardine	1996 $\downarrow$	2009 $\downarrow$	
B_MAC	Mackerel	1995 $\uparrow$	2005 $\uparrow$	
B_HOM_o	Horse mackerel			2013 $\uparrow$

B_Sparids_o	Sparids	1996	2004	2014*↑
B_Flatfish_o	Flatfish	-	-	-
B_HKE_o	Hake	1993↓	2009↑	
B_DFP_o	Demersal piscivorous fish	1993↓	2007↑	
B_JAA_o	Blue jack mackerel		2004*↑	2016*↓
B_DFI_o	Demersal invertivorous fish			
B_MAS:o	Chub mackerel			
B_BFI_o	Benthopelagic invertivorous fish		2006↓	2015↑
B_BOG_o	Bogue		2004↑	2012↑
B_BFP_o	Benthopelagic piscivorous fish	1994↓	2009↑	
B_Ben_Ceph	Benthic cephalopods			
B_Squids_o	Squids	1992↓		
B_Rays_o	Rays		2005↑	2012↑
B_Tunas_o	Tunas	1992↓		
B_Sharks_o	Sharks			
B_PIL_Juv_o	Juvenile sardine		2006↓	

B_model	Modelled biomass			
B_ANE_m	Anchovy	1994↓		
B_PIL_m	Sardine	1998↓		2010↓
B_MAC_m	Mackerel			2012*↑
B_HOM_m	Horse mackerel			2010↑
B_Sparids_m	Sparids		2004↑	2013*
B_Flatfish_m	Flatfish	-	-	-
B_HKE_m	Hake	-	-	-
B_DFP_m	Demersal piscivorous fish			2014*↑
B_JAA_m	Blue jack mackerel	1992↓		
B_DFI_m	Demersal invertivorous fish			2010↑
B_MAS_m	Chub mackerel		2001↑	2011↑
B_BFI_m	Benthopelagic invertivorous fish		2003↓	
B_BOG_m	Bogue	1999↑		2010↑
B_BFP_m	Benthopelagic piscivorous fish	1995↓		2012*↑
B_Ben_Ceph_m	Benthic cephalopods		2007↑	2015↑
B_Squids_m	Squids		2003↑	2014↑
B_Rays_m	Rays			2010*↑
B_Hcrab_m	Henslow's crab		2009↑	
B_Tunas_m	Tunas	-	-	-
B_Minke_m	Minke whale			2015*↑
B_Sharks_m	Sharks	-	--	-
B_Common_dolphin_m	Common dolphin		2003*↑	2014*↑
B_Seabirds_m	Seabirds			2013*↑
B_Stripped_dolphin_m	Stripped dolphin	—	—	—
B_Harbor_porpoise_m	Harbor porpoise	1992*↓	2002*↓	
B_Phyto_m	Phytoplankton			2011↑

B_MesoMicrozoo_m	Mesozooplankton/Microzooplankton	2009↑	
B_Macrozoo_m	Macrozooplankton	2008↑	2013↑
B_Supra_Inv_m	Suprabenthic invertebrates	-	-
B_Macrozoobenthos_m	Macrozoobenthos		2012↑
B_Shrimps_m	Shrimps	2009↑	
B_PIL_Juv_m	Juvenile sardine	2000↓	2012↓
B_Bottlenose_dolphin_m	Bottlenose dolphin	2009*↑	

indices	Ecosystem indices		
Dem_Pel B	Demersal per Pelagic biomass	1999↓	2012*↓
Dem_Pel C	Demersal per Pelagic catch	1995↓	2004↓
Pred B	Predatory biomass		2012↑
Pred C	Predatory catch	1994↓	
Kempton Q	Kempton's diversity index	1998↓	2004↓
Shannon	Shannon diversity index		2012↓
Tot C	Total catch	1999↓	
Dem C	Demersal catch	1994↓	2015↑
Pel C	Pelagic catch		2011↑
mTLc	The trophic level of the catch		2012↑
mTLco	The trophic level of the community		2011↑
FCI	Fins cycling index		2011↓
A_C	Relative ascendancy		2010*↑
R	Redundancy		2011↓
H	Entropy	1992↓	2014↑
TotP_TotB	Turnover rate		2010↓

ANNEX 6

Supplementary material for chapter 6

et al. 2013) and extracted for the study area from the Royal Netherlands Meteorological Institute Climate Explorer (<https://climexp.knmi.nl>).

Table A6.1 The most sensitive predator-prey interactions that were identified during the search for vulnerabilities procedure. Vulnerabilities of groups not included in the table were maintained as default ($v_{ij}=2$)

Prey/predator	Bottlenose dolphin	Hake	Benthic cephalopods	Sparids	Bogue	Horse mackerel	Benthopelagic invertivores fish	Chub mackerel	Mackerel	Blue jack mackerel	Juvenile sardine	Adult sardine	Meso/Micro zooplankton
Demersal piscivores fish	1	2	2	2	2	2	2	2	2	2	2	2	2
Benthic cephalopods	2	2	2	2	2	2	2	1.7	2	2	2	2	2
Bogue	2	2	2	2	2	2	2	2	2	2	2	2	2
Benthopelagic invertivores fish	2	1	2	2	2	2	2	1000	1000	2	2	2	2
Chub mackerel	2	2	1	2	2	2	2	2	2	2	2	2	2
Blue jack mackerel	2	1	2	2	2	2	2	2	2	2	2	2	2
Anchovy	2	1	2	2	2	2	2	2	1000	2	2	2	2
Juvenile sardine	2	2	2	2	1000	1000	2	1000	2	2	2	2	2
Macrozoobenthos	2	2	2	10	2	2	2	2	2	2	2	2	2
Suprabenthic invertebrates	2	2	2	2	2	4	1	1000	2	2	2	2	2
Macrozooplankton	2	2	2	2	1000	2	2	2	2	2	2	2	2
Meso/Microzooplankton	2	2	2	2	2	2	1000	26.7	2	1	1	2.7	2
Phytoplankton	2	2	2	2	2	2	2	2	2	2	1	1000	1.3

References

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