



“ No fish is an island ”

Ecopath with Ecosim[®]

Joana Carolina Raposo de Brito

A spatially oriented ecosystem-based model to evaluate ecosystem impacts of fisheries

Tese de mestrado em Ecologia, orientada por Doutor João Carlos Marques e Doutor Telmo Morato e apresentada ao Departamento de Ciências da Vida da Faculdade de Ciência e Tecnologia da Universidade de Coimbra

Junho, 2016



UNIVERSIDADE DE COIMBRA

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**A SPATIALLY ORIENTED ECOSYSTEM-BASED MODEL TO EVALUATE
ECOSYSTEM IMPACTS OF FISHERIES**

Thesis submitted to the Department of Life Science,
Faculty of Science and Technology of
University of Coimbra
for the degree of Master in Ecology

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Junho, 2016



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Para os avós,

ACKNOWLEDGMENTS

It always seems impossible until it's done, Nelson Mandela.

In this I assert and express the most honest acknowledgements to all the people who contributed to make this thesis a realistic utopia:

To my supervisors, Doctor João Carlos Marques and Doctor Telmo Morato, for their support and incentive, without exception, provided during this thesis. To Doctor João Carlos Marques, a special thanks for the confidence, since the day I was invited to join the research team. When I decided to change the research topic, you never stopped believing in me and encouraged me to pursue my dreams. To Doctor Telmo Morato, my deepest appreciation for the honourable opportunity to establish this working partnership. Thank you for the excellent guidance, patience, suggestions, unconditional availability, sharing of knowledge and above everything, friendship.

An enormous acknowledgement to the Department of Oceanography and Fisheries; to MARE and to all the people who represent it, namely Doctor Christopher Pham and Doctor Gui Menezes for their collaboration in the present study.

My acknowledgments are extended to the Ecopath development team, especially to Jeroen Steenbeek for the cooperation in the construction of the model developed in this thesis.

To all the “Faial Family”, with special fondness to the house residents - Becky, Miguel, Jo, Ambre, João, Sílvio, Diya, Gonçalo, Teresa and Tomás – thank you for all the experiences and craziness lived on these islands of mist. To my amores de Coimbra, friends since ever and for ever, thank you so much for the hours of blowing off steam and bohemian times that were so remarkable in this phase of our lives.

Finally, to my family, thank you is not enough. Grandparents, thank you for the education, discipline and love during these 24 years. You are and always will be my biggest support. Mum, you are not just a mother. You are a father, friend, war companion... All the intellect of this thesis belongs to you. Thank you so much! Minês and Kiko, thank you for all the video calls at the most inappropriate times whilst I was writing this thesis. To Zé, I acknowledge all the posture and fundamental support, not only during my academic period, but also since you unified our family.

AGRADECIMENTOS

It always seems impossible until it's done, Nelson Mandela.

Deste modo destaco e exprimo os mais sinceros agradecimentos a todas as pessoas que de alguma forma tornaram esta tese uma realidade utópica:

Aos meus orientadores, o Doutor João Carlos Marques e Doutor Telmo Morato, pelo apoio e incentivo, sem exceção, prestado durante o decorrer desta tese. Ao Doutor João Carlos Marques um especial obrigado pela confiança, desde o dia em que me convidou para pertencer à sua equipa. Quando decidi mudar a linha de investigação, nunca deixou de acreditar em mim e me encorajar a seguir os meus sonhos. Ao Doutor Telmo Morato, o meu profundo agradecimento pela honorável oportunidade de estabelecer a presente parceria de trabalho. Obrigada pela excelente orientação, paciência, sugestões, disponibilidade incondicional, partilha de conhecimento e acima de tudo, amizade.

Um enorme obrigado ao Departamento de Oceanografia e Pescas, ao MARE e todas as pessoas que o representam, nomeadamente aos Doutores Christopher Pham e Gui Menezes pela colaboração no presente estudo.

Os meus agradecimentos estendem-se à equipa de desenvolvimento do Ecopath with Ecosim software, em especial ao Jeroen Steenbeek pela cooperação na construção do modelo desenvolvido nesta tese.

A toda a “família do Faial”, com especial carinho aos *residentes* da casa - Becky, Miguel, Jo, Ambre, João, Sílvio, Diya, Gonçalo, Teresa e Tomás - obrigada pelas experiências e loucuras vividas nestas ilhas de bruma. Aos meus amores de Coimbra, aos amigos de sempre e para sempre, obrigada pelas horas de desabafo e boémia que tão marcantes foram nesta fase das nossas vidas.

Finalmente, à minha família, obrigada não é suficiente. Avós, obrigada pela educação, disciplina e amor durante estes 24 anos. São e serão para sempre o meu pilar. Mãe, não és só mãe. És pai, amiga, companheira de guerra... Todo o intelecto desta tese te pertence. Obrigada. Minês e Kiko, obrigada por todas as videochamadas nos momentos mais impertinentes enquanto escrevia esta tese. Ao Zé agradeço toda a postura e apoio fundamental, não só durante o meu período universitário, mas desde que integrou a nossa família. É indubitavelmente uma referência para mim.

ABSTRACT

The current study consisted of the first phase in the development of the original spatial-oriented ecosystem based model of the Economic Exclusive Zone of the Azores. This focused on testing the ability of the model to evolve from a static and time-explicit representation of the ecosystem to a spatially dynamic dimension, where environmental and fishing responses drove the spatial distribution of the organisms included in the model.

The modelling approach encompassed the construction of the spatially explicit routine (Ecospace) of a previously developed Ecopath with Ecosim (EwE) model of the same area, to further address fisheries-related management questions within an ecosystem approach. The model was driven in time through a time series of fishing effort from 1997 to 2014, while Geographic Information Systems derived layers of depth and spatial distribution of primary production drove the spatio-temporal baseline dynamics. Since Ecospace introduces spatial variability in global model behaviour, it was expected that such a shift would improve the representativeness of ecosystem dynamics.

Two main Ecospace models were constructed, with different organism's foraging habitats use. The evaluation of the models in transit from Ecosim to Ecospace was performed based on the goodness of fit between model prediction and reference data of annual absolute catch and annual relative biomass for the period 1997-2014. For the reference model, organism's habitat uses were assigned based on criteria of habitat preferences in the Azores. From this model, a calibration process guided by an evaluation of goodness of fit in the end of each run was initiated, until the achievement of a final model with better fit than Ecosim. The two Ecospace models were then analysed comparing the predictions of relative biomass spatial distribution in the beginning and in the end of the simulation, of the groups of which biomass and catch contributed the most for the differential goodness of fit.

The introduction of spatial dynamics in trophic interactions enhanced the performance to predict potential impacts of fisheries in an ecosystem at a local scale. The model satisfactorily replicated the catch trends observed during the model period, while the biomass only observed a smooth increment. The results suggested that fisheries are not the main driver promoting the annual shifts of biomass. Although,

limitation of Ecospace to simulate changes in productivity regime-shifts prevents the exploration of other mechanisms responsible for the observed tendencies. The species that benefitted the most with the Ecosim - Ecospace transition include highly important commercial species, such as *Pagellus bogaraveo*, *Helicolenus d. dactylopterus* and the functional group Pelagic Large that comprises the highly exploited species *Xiphias gladius*.

The evaluation of spatio-temporal predictions between the two Ecospace models developed highlights the importance of inputting detailed local spatial information to develop spatial-temporal explicit models that consider environmental drivers, human impacts and food web effects.

Though the final model requires future analysis to formally validate the predictions, it represents a step forward in the usage of spatial-oriented ecosystem based models to support the implementation of an ecosystem-based management approach, through marine spatial planning in the archipelago of the Azores.

Key-Words: Ecosystem-based management; marine spatial planning; sustainability; spatial ecosystem models; goodness of fit; fisheries; Ecospace; marine ecosystem of the Azores

RESUMO

O presente estudo consistiu na primeira fase de desenvolvimento do primeiro modelo de ecossistema com considerações espaciais da zona económica exclusiva dos Açores. O estudo foi focado em testar a exequibilidade do modelo em evoluir de uma representação do ecossistema explicitamente estático-temporal para uma dimensão dinâmica no espaço, onde respostas ambientais e de pesca conduzem a distribuição espacial dos organismos incluídos no modelo.

A abordagem de modulação englobou a construção da rotina espacial (Ecospace) de um modelo Ecopath with Ecosim previamente desenvolvido para a mesma área, com o objetivo de explorar questões de gestão relacionadas com a pesca, numa abordagem focada no ecossistema.

O modelo foi conduzido no tempo, através de séries temporais de esforço de pesca, desde 1997 a 2014 enquanto camadas de profundidade e de distribuição espacial de produção primária, derivadas de sistemas de informação geográfica, dirigiram a dinâmica espaço-temporal de base. Uma vez que o Ecospace introduz variabilidade espacial no comportamento global modelo global, foi previsto que a transição melhorasse a sua representatividade na dinâmica dos ecossistemas.

Dois modelos Ecospace principais foram construídos com diferentes usos de habitat para forrageamento dos organismos. A avaliação dos modelos em transitar do Ecosim para o Ecospace foi feita com base na qualidade de ajuste entre as previsões do modelo e dados de referência de apanha absoluta anual e biomassa relativa, durante o período 1997-2014. Para o modelo de referência, os usos de habitat dos organismos foram atribuídos com base num critério de preferências de habitat nos Açores. A partir deste modelo, iniciou-se um processo de calibragem guiado por uma avaliação da qualidade de ajuste no final de cada modelo, até se atingir um modelo final com um melhor ajuste do que o Ecosim. Os dois modelos de Ecospace foram analisados, comparando as previsões de distribuição espacial de biomassa relativa, no início e no fim da simulação, para os grupos cuja biomassa e apanha contribuíram mais para a diferente qualidade de ajuste. A introdução de dinâmica espacial nas interações tróficas, melhorou a performance em prever potenciais impactos da pesca num ecossistema à escala local. O modelo replicou satisfatoriamente as tendências das apanhas observadas

durante o período do modelo, enquanto a biomassa apenas observou um melhoramento suave. Os resultados sugerem que as pescas não são o principal impulsionador das oscilações anuais de biomassa. No entanto, a limitação do Ecospace em simular alterações de regimes de produtividade impedem a exploração de outros mecanismos responsáveis pelas observações observáveis. As espécies que beneficiaram mais com a transição Ecosim - Ecospace incluem espécies de interesse comercial elevado, tais como *Pagellus bogaraveo*, *Helicolenus d. dactylopterus* e o grupo funcional de grandes pelágicos que inclui a espécie altamente explorada, *Xiphias gladius*.

A avaliação das previsões espaço-temporais entre os dois modelos de Ecospace desenvolvidos, salientam a importância de introduzir informação espacial local detalhada para desenvolver modelos orientados espacialmente que considerem condutores ambientais, impactos humanos e efeitos na cadeia trófica.

Embora o modelo requeira futuras análises para validar formalmente as previsões, o presente estudo representa um passo na utilização de modelos de ecossistema com considerações espaciais para apoiar a implementação de uma gestão baseada no ecossistema no arquipélago dos Açores.

PALAVRAS-CHAVE: gestão baseada no ecossistema; planeamento espacial marítimo; sustentabilidade; modelos espaciais de ecossistema; qualidade de ajuste; pescas; Ecospace; ecossistema marinho dos Açores

ABBREVIATIONS

EU – European Union

CFP – Common Fisheries Policy

TAC – Total Allowable Catches

ICES – International Council for the Exploration of the Sea

EBM – Ecosystem-based management

EBFM – Ecosystem-based fisheries management

MSFD – Marine Strategy Framework Directive

GES – Good Environmental Status

MSP – Marine Spatial Planning

MPA – Marine Protected Areas

RS – Remote Sensing

GIS – Geographic Informatics System

EM – Ecosystem Models

EwE – Ecopath with Ecosim

EEZ – Economic Exclusive Zone

VMS - Vessel Monitoring System

FAO – Food and Agriculture Organization of the United Nations

FC – Forcing Catch

FF – Forcing Functions

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1. INTRODUCTION

1.1 Towards an ecosystem-based management in Europe

For decades the scientific community has minutely described serious threats that global oceans face (MEA 2005; FAO 2009; Branch et al. 2010; Gutiérrez et al. 2011) and how it debilitates its capacity to provide goods and services on which all forms of life depend (Armstrong, 2012; Dell'Anno, 2005; Pratchett, 2014; Worm, 2006). Fisheries have become one of the most exploiting human activities in the world to attend the increasing demand for food resources (FAO, 2014) and have been consequently driving profound and in some instances irreversible ecological changes (Baum, 2009; D. Pauly, 1995; Daniel Pauly, 2012). Globally, 28.8% of assessed fish stocks are being overfished with some showing complete depletion (FAO, 2014), a value that highlights the lack of sustainable vision of fishery activities management and ecological awareness around the world. Nevertheless, the political recognition of ocean conservation as a first order priority issue is a recent, regional and under developing process (Ardron, 2008; Boyes, 2007; Day, 2008; Fanny Douvere, 2008, 2009; Halpern, 2012; Micheli, 2013).

The European Union (EU) fisheries sector has been regulated under a single-species perspective for the last 30 years supported by the Common Fisheries Policy (CFP) (Daw, 2005a). This political framework establishes catch limits for most of commercial fish stocks of European waters, under the form of total allowable catches (TACs) for target species and a quota management system (Karagiannakos, 1996; Sebastián Villasante, 2011). Additionally, the CFP allows EU fishermen to explore Member States' jurisdictional waters, although in specific cases imposes miles restrictions that guarantee exclusivity to local fishing fleets (e.g., Western Waters Regulation EC 1954/2003).

Although the CFP proposes to comply with principles of sustainability and to ensure economic competitiveness regarding fish stock exploitation, its nonfulfillment it is well documented facing biological, economic, legal and political issues (Daw, 2005b; Rainer Froese, 2011; Gray, 2005; Katsanevakis, 2011; Khalilian, 2010). The framework inconsistencies outset on the existent gap between the scientific TACs proposed and those approved by the European Council (Khalilian et al. 2010). For instance, during the period 2002 and 2011, in 60% of the deep-sea fisheries cases, scientific advice was not being plainly considered and catches were 3.5 times higher than suggested (Sebastian Villasante, 2012). Moreover, the Green Paper Reform of CFP affirms that 88% of

stocks are overfished while fishing industry profits show a continuous decline trend (Commission 2009; Merino et al. 2014).

These results underlined that in the long term, CFP was failing to ensure sustainability, because of disregarding the ecosystem as a whole in the decision-making process. This points out the need for a more holistic perspective of marine resources management (Curtin, 2010; Espinosa-Romero, 2011; McLeod, 2005; Salomon, 2013; Tallis, 2010), a globally consensual idea recognized as an ecosystem-based management approach (EBM) (Gavaris, 2009; Levin, 2009; Jason S. Link, 2011; Pikitch, 2004). To reach this challenging goal, the new EU reform of CFP (agreed by Council and Parliament for the period 2014-2020) commits to implement an ecosystem-based approach to fisheries management, defined 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” (EU, 2013b).

The European awareness regarding the accomplishment of an EBM is enhanced with the implementation of the science-driven European Marine Strategy Framework Directive (MSFD) in 2008 (Ounanian, 2012; Rätz, 2010). This Directive intends to achieve a Good Environmental Status (GES) in the marine environment by 2020 for the benefit of current and future generations and considers fisheries as a pressure and a descriptor (Piha, 2011; The European Parliament and the Council of the European Union, 2008).

Controversial perspectives arise when it comes to define the principles to follow on the implementation of an EBM and choose the appropriate tools to support the decision-making process, creating a gap between the theory and applicability (Espinosa-Romero et al., 2011; Katsanevakis et al., 2011). Such incongruity naturally delays and commits the successful achievement of EBM purposes (Leslie, 2011).

1.2 Marine Spatial Planning as a process to achieve EBM

Marine Spatial Planning (MSP) is a public and future-oriented process, within the EBM approach, to sustainably manage human activities in the ocean space by allocation of spatial and temporal distribution of human uses (Fanny Douvere, 2008; Maes, 2008). The aim is the ultimately achievement of ecological, economic and social objectives, normally defined through a political process (Ardrón et al., 2008; F. Douvere, 2007; Fanny Douvere, 2008). A marine spatial plan identifies and addresses conflicts among human uses (user-user) and between human uses and the marine environment (user-environment) to further design appropriate strategies capable to reduce these divergences and therefore safeguard the ability of the ocean in provide goods and services (Ehler, 2009; Lester, 2012). The origin of conflicts is cored on the growing demand for human use of ocean space that generally leads to no compatible uses and overlapping objectives within given areas (e.g., wind farms development and fisheries) and results in critical pressures on the marine environment (Pomeroy, 2008; Salomon et al., 2013).

The main output of MSP is a comprehensive spatial plan, often implemented in the form of a zoning plan, that sets out the priorities and spatial and temporal management measures that specify how, where and when human activities are more suitable to occur in a particular marine area or ecosystem (Ehler et al., 2009). Those spatio-temporal oriented measures are for instances, zoning of areas for specific uses (e.g. marine transportation, wind farms, offshore aquaculture) or by objective (e.g. conservation areas, multiple use areas), specification of areas closed to human activities (e.g. fisheries) and designation of marine protected areas (MPAs) (F. Douvere et al., 2007; Gimpel, 2013; Metcalfe, 2015; Stelzenmüller, 2013). Within the fisheries sector, the actions normally encompass the establishment of spatial zonation, defining areas accessible by specific/pre-determined fleets, the delimitation of a harvesting threshold for particular fish stocks, the local banning of specific fishing gears (e.g., bottom trawling) and the implementation of totally protected areas in which no fishing effort is allowed (termed no-take MPAs) (Colloca, 2015; Edgar, 2014; Klein, 2010).

Therefore, MSP proposes integrated management strategies that should cover multiple sectors and scales and be guided by ecological principles to further implementation of ecosystem approaches in the area where it is based (Crowder, 2008; Foley, 2010). These concerns entail that functions supported by ecosystem such as

biodiversity, resilience, connectivity, productivity and food web stability have to be carefully contemplated along with social, economic and governance aspects (Foley et al., 2010; Gutiérrez et al., 2011). Though desirable, the commitment to embrace multiple sectors enhances the complexity to put in practice a marine spatial plan, due to inherent difficulty to find an equilibrium point where all the objectives of the process are met (Lester et al., 2012).

Although being a challenge process, the spatial management of maritime activities following an ecosystem approach is possible to be conducted, and several European initiatives have recently started to publish the major achievements and challenges faced along the process (Buhl-Mortensen, 2016; Gimpel et al., 2013; Jones, 2016; Salomon et al., 2013). Encompassing different areas and contexts, the experiences commonly identify the limited knowledge of ecosystem structure and functioning as the principal obstacle to implement MSP. Such recognition highlights the importance to support the several phases of MSP development with tools designed to describe key ecosystem processes and evaluate the potential impact of management scenarios in the natural dynamic of marine ecosystems (Villy Christensen, 2009; Metcalfe et al., 2015; Stelzenmüller, 2012).

1.3 Tools to support the implementation of ecosystem-based management approaches – The example of whole ecosystem models

Broadly, ecosystem models are mathematical tools designed and developed over the last decades to expand the knowledge on marine ecosystems dynamics (V. Christensen, 1992; Fulton, 2010). Through abstract simulations, EMs aim to describe underlying mechanisms that represent ecosystem structure and functioning and to ultimately predict future effects that anthropogenic pressures might drive in these natural processes (Fulton, 2015). Within the EBFM, EMs might be particularly useful to explain the numerous impacts associated to the (over) exploitation of marine resources and explore trade-offs as well as the performance of alternative management actions in achieve defined ecosystem-level goals (reviews in Plagányi 2007a; Collie et al. 2014).

There is a wide range of ecosystem model types designed and applied in several fishing area contexts until date (Foden, 2008). Nowadays, and thanks to computational

improvements, the ability of a model in represent spatial variability is for some authors the feature that mostly separates model types (Espinoza-Tenorio, 2012; J. S. Link, 2012). These discrimination criteria's, creates a division between models founded on its complexity and natural uncertainty and has been the main principle followed by some authors to test the performance of each model category in achieve EBFM goals. A good example of this effort is the review conducted by Espinoza-Tenorio et al. 2012. The results showed that despite no modeling approach has been robust enough to fully meet the defined EBFM objectives, Whole Ecosystem Models are the most closely to achieve them. Besides, this category, presents high levels of success regarding considerations on spatio-temporal variability, capturing the three issues established to define this goal (long-term periods; spatial variability; and drivers of change operating both between geographic scales).

Whole Ecosystem models focus on the energy flows between the trophic levels that define a food web and might include socioeconomic variables into the analysis to provide scenarios of added value (V. Christensen et al., 1992; Coll, 2009; Polovina, 1984). A representative instance of a whole ecosystem model is the Ecopath with Ecosim (EwE) and the spatial module Ecospace toolbox (Villy Christensen, 2004), worldwide used to explore future trends in marine biodiversity under fishing scenarios as well as the trade-offs associated to management actions (Plagányi 2007; Coll et al. 2009; Fulton 2010; Piroddi et al. 2011; Heymans et al. 2011).

Despite the consensual recognition of ecosystem models as potential tools to support strategic management decisions in EBFM contexts, there is not yet an agreement concerning on how these models may be directly used within the framework (Robinson & Frid 2003; Espinoza-tenorio et al. 2011 and 2012). The reasons mainly point the natural levels of uncertainty existent in modelling something as complex as an ecosystem, that requires considerations on all its components, spatial and temporal variability and human drivers (Collie et al., 2014; J. S. Link et al., 2012). In fact, uncertainty is one of the most important features to deal with in modelling since, whether neglected, model predictions can easily be under or over estimated, committing its use for management advice. According to (J. S. Link et al., 2012) the sources of uncertainty that mostly influence the development of ecosystem models and ultimately its application for EBFM purposes are cored on the natural variability presented in biological systems and on observation error in processes measurements or estimations. Although apparently challenging, these major uncertainty sources might be addressed

and be satisfactorily overcome if for instances, analytical analysis are applied (J. S. Link et al., 2012).

1.4 Context of the present study – Towards the implementation of an ecosystem approach to manage the exploitation of marine resources in the Archipelago of the Azores

The present study emerges as an integrant part of the process towards the implementation of an ecosystem-based management of the Azores marine resources, biodiversity and habitats, until 2020. As a fragile open and deep-sea ecosystem under exploitation of resources, the ecosystem approach aims to provide an analysis of human impacts and device suitable policies to mitigate and reverse harmful trends, ensuring economic and social benefits of sustainable fisheries.

The project commits to integrate in a single framework the range of relevant information regarding key ecological, fisheries, physical, social and economical attributes of the Azores, develop ecosystem models and evaluate its performance with respect to its role in ecosystem-based fisheries management and finally, apply those models to simulate and quantify the effect of different management scenarios at the whole ecosystem level. Particularly, the models seek to quantify the effect of a new Common Fisheries Policy regulation on the marine ecosystem of the Azores, explore management questions related to the impact of fishing on vulnerable marine ecosystem (such as corals and sponges) and predict outcomes derived from the establishment of no-take areas, in the ecosystem.

In doing so, the current study consisted in the first phase of the development of the first spatial-oriented ecosystem based model of the Azores, focus on test the ability of the model to evolve from a static and time-explicit representation of the ecosystem to a spatial dynamic dimension, where environmental and fishing responses drive the spatial distribution of the living organisms included in the model.

The final goal is to expand the spatial model developed here to support the implementation of an ecosystem approach to manage the exploitation of marine resources through marine spatial planning, in the archipelago of the Azores.

2. MATERIALS AND METHODS

2.1 The ecosystem modelling approach

2.1.1 Ecopath with Ecosim (EwE)

Nothing is lost, nothing is created, everything is transformed. This is the fundamental principle of Ecopath, the static mass balanced module of the EwE modelling approach (Polovina 1984, Christensen and Pauly, 1993, 1992). An Ecopath model quantitatively describes an aquatic or terrestrial ecosystem for a given period of time by providing a snapshot of trophic flows and interactions that occur between functional groups (FG) in a food web (Christensen and Pauly, 1993, 1992; D. Pauly, 2000). In practice, the mass equilibrium assumed by Ecopath means that due to predation or fishing, whether the energy of a given FG is removed, the balance has mandatorily to be found within the ecosystem.

The basic parameterization of Ecopath relies in two master linear equations – one to describe and ensure the energy balance within each group (production term, equation 1) and one for the energy balance between groups (consumption term, equation 2). The production of a group is then expressed as:

$$\text{Production} = \text{Catch} + \text{Predation} + \text{Net Migration} + \text{Biomass Accumulation} + \text{other Mortality}$$

or formally,

$$B \left(\frac{P}{B} \right)_i = Y_i + \sum_j B_j \left(\frac{Q}{B} \right)_j DC_{ij} + E_i BA_i + B_i \left(\frac{P}{B} \right)_i (1 - EE_i) \quad (1)$$

where $(P/B)_i$ is equivalent to the total mortality (Allen, 1971) and indicates the production of group i in terms of unit of biomass. Y_i is the total fishery catch rate of group i . The ratio $(Q/B)_i$ is the equation term for consumption of i per unit of biomass and DC_{ij} represents the proportion of group i consumed by predator j in weight units. E_i is the net migration rate (emigration – immigration) of group i . BA_i the biomass accumulation rate for group i . Other mortality rate for group i is here presented as $(1 - EE_i)$, where the term EE_i is the ecotrophic efficiency and represents energy exports from the system due to fishery or natural reasons.

By its principle, Ecopath solves as many linear equations as there are groups in

the modelled system. Nevertheless, the model incorporates several algorithms in the parameterization routine to estimate missing parameters, before setting up the linear equations (Villy Christensen, 2008). It is thought mandatory to enter three of the basic parameters (biomass, production/biomass ratio, consumption/biomass ratio, ecotrophic efficiency) plus fishery yields and diet composition for each group in the model. Whether the user inserts all these parameters, the program automatically estimates the biomass accumulation term or the net migration rate (Villy Christensen et al., 2008).

The mass balance is then achieved in the system when the consumption by group i equals the terms presented in Equation 2:

$$\text{Consumption (} Q_i \text{)} = \text{Production (} P_i \text{)} + \text{Respiration (} R_i \text{)} + \text{Unassimilated food (} U_i \text{)}$$

The model units are expressed in terms of energy related currency by unit of surface ($\text{tonnes}^{-1} \text{ km}^{-2} \text{ yr}^{-1}$).

In sum, the master equations of Ecopath parameterization can be seen as mass balance filters whether one is interested to observe the energetic flows, biomass and its utilization within a given ecosystem, by gathering a set of information about its components, exploitation and interactions. The amount of input information along with its inherent quality, naturally mould the reliability of the output (É. E. Plagányi, 2004).

As an ecosystem modelling approach, the functional groups included in Ecopath must range from low to high trophic levels (primary producers to top predators) and contain at least one detritus group (natural detritus and arising from fishing activities). Each FG encompasses living organisms that share the same ecology (e.g. habitat, feeding habits) and population dynamics, although it is also possible to define groups as single species that, for instances, play a key role in the ecosystem or have a high commercial interest in the modelled area.

According to (Villy Christensen, 2005), an Ecopath balanced model is found when a) estimates of $EE < 1$; b) P/Q values for the majority of FG are between 0.1 and 0.35; and c) R/B values are low for top predators and high for small organisms. This process can be done by manually changing parameters within their range of uncertainty. Balance an Ecopath model requires precaution and expert knowledge on the data that is assembled and adjusted in the model in order to make the flows meet the mass conservation criteria but at the same time stay reliable (Ainsworth, 2015).

To deal with the uncertainty associated with the information on the mass balance

estimates, a Pedigree routine included in Ecopath allows the user to attribute a confidence interval to data according to their origin and inherent quality (Villy Christensen et al., 2008; D. Pauly et al., 2000). For example, whether the input data of the consumption/biomass ratio for a given FG directly derives from an experimental estimation performed in the system being modelled and for exactly the same group/species, a pedigree index of 1 is attributed to that group parameter. On the other hand, if the same parameter is left to be estimated by Ecopath or another model, the index is 0.

The Ecopath model outcomes are examined in the form of ecological and trophodynamic indicators that express the status of the ecosystem based on the trophic flows in the food web (Villy Christensen et al., 2004, 2005; Cury, 2005; Müller, 1997).

The addition of a predictive routine module to Ecopath enables the software to evaluate trade-offs in fisheries management. This shift from a static to a dynamic representation of the ecosystem is ensured by Ecosim - the temporal component of the modelling approach (Villy Christensen et al., 2004; C. Walters, 2000; Carl Walters, 1997).

The key assumption of Ecosim modulation is that prey behaviour limits predation rates, based on the relationship expressed in Equation 3:

$$\frac{dB_i}{dt} = g_i \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - (M0_i + F_i + e_i) \quad (3)$$

where dB_i/dt is the rate of change in biomass of group i during the interval dt , g_i is the net growth efficiency, F_i is the fishing mortality rate, $M0_i$ is the natural mortality rate (excluding predation), e_i is the emigration rate and I_i is the immigration rate. The terms Q_{ji} and Q_{ij} , respectively, represent the consumption of prey i by predator j and predation of j by i . Based on foraging arena theory (Ahrens, 2012; C. J. Walters, 2004), Ecosim model behaviour is highly shaped by predator-prey interactions, formed on the vulnerability of prey i to be consumed by predator j . Preys under the threat of predation naturally adopt defence behaviours that spatially and temporally restrict the availability of their biomass for a predator. Therefore, in the foraging arena, the biomass of prey i is either available (or vulnerable, V_{ij}) or non-available (or invulnerable, $B_i - V_{ij}$) for predator j . Consequently, the transfer rate (v) between both prey biomass availability

states establishes the flow control of consumption rates at a time interval dt (Equation 4).

$$\frac{dV_{ij}}{dt} = v_{ij} (B_i - V_{ij}) - v_{ij} \cdot V_{ij} - \frac{a_{ij} V_{ij} B_j}{1 + h_j a_j V_{ij}} \quad (4)$$

In the formula, a_{ij} represents the rate of effective search for i by predator j and h_j is handling time for the predator. Low vulnerability ($v_{ij} = 1$) reflects a bottom up control since an increment of predator biomass does not proportionally increase prey mortality, owing to predator avoidance behaviour. Whereas, high vulnerability stages (e.g., $v = 100$) reveal a linear response of prey mortality due to predation, in response to predator biomass enhancement (top-down control, Lotka-Volterra). Based on the formula, it implies that a large proportion of prey i biomass is available for predator j and thus, $V_{ij} = B_j$.

Despite Ecopath parameters, other variables such as fishing effort and environmental factors drive Ecosim predictions for each time step. Furthermore, time series data of biomass and catch can be input into the Ecosim routine to calibrate and tune the model to real data. This feature is particular relevant to explore how different sources of perturbation impact the ecosystem along a specific period of time (e.g., explore the role of a specific fishing fleet in the mortality rate of a group) and ultimately address management related questions.

A statistical measure of goodness-of-fit between model predictions and reference (observed) data is estimated per each run, in the form of weighted sum of squared (SS) deviation of log biomasses and catches from log predicted biomass and catches (Villy Christensen et al., 2004; C. J. Walters et al., 2004). For relative abundance data (D), the log predictions are scaled by the maximum likelihood estimate of the relative abundance scaling factor q , according to the equation $y=qB$ (y = relative abundance, B = absolute abundance) (Villy Christensen et al., 2008). Statistically, the goal of fitting the model to real data is to reduce the SS estimation, without losing the modelling and context realism. The fitting process encompasses individual analytical steps and initiates with a sensitivity search for the most critical predator-prey vulnerabilities by smoothly changing each parameter to observe how it affects the SS estimation. Moreover, using the most sensitive predator-prey interactions, the user can perform a search for the best-fitted vulnerability estimates of functional groups. Finally,

it is possible to perform an automated searching run for time series values of forcing functions (FF). These FF represent changes in productivity regimes shifts (e.g., primary production anomalies) that, for instance, impact biomasses stability throughout the ecosystem and change production and/or consumption rates. The input of such forces normally increases the model fit since the introduction of environmental parameters influencing trophic interactions help in simulating and explaining seasonal variations of system biomass during the modelled period (Villy Christensen et al., 2008).

Ideally, a final Ecopath with Ecosim model is able to reproduce historical responses to fishing pressures along a period of time and predict from a policy point of view, which measures could potentially promote the achievement of healthy ecosystem status.

2.1.2 Ecospace

The EwE modelling approach assumes that ecosystems present a spatial homogenous behaviour, a deficiency that limits its ability to fully represent natural ecosystems dynamics. Ecospace has thus been developed as the spatially explicit time dynamic module of EwE to address spatial-oriented ecosystem questions, such as the impact of the establishment of marine protected areas in the spatial distribution of modelled groups and fishing effort (Fouzai, 2012; Carl Walters, 2000, 1999, 2010).

The biomass balanced in Ecopath for each functional group is allocated through Ecospace to a two-dimensional grid of equally sized cells, wherein groups execute random and symmetric movements, following an Eulerian approach. In each grid cell, Ecosim differential equations are computed to simulate biomass temporal changes and species consumption that impact predator-prey relationships at the local scale, in monthly time steps. Although Ecospace generically relies on the EwE approach (e.g., fishing effort time-series, predator-prey vulnerabilities) its parameterization requires additional data to regulate functional groups and fishing effort spatial distribution patterns (Villy Christensen et al., 2004, 2008; Martell, 2005; Carl Walters et al., 1999).

Ecospace basic input parameterization entails the construction of several initialization grid maps, each one representing distinct features of the study area that play a considerable influence in the spatial distribution of living organisms and fishing effort. Environmental-related maps encompass layers of depth, primary productivity and habitats features. Normally, habitats are set based on depth intervals, bottom type or

salinity, although the user is allowed to establish habitats attending own modelling purposes and available data. Marine protected areas may be assign as habitats closed to fishing for all or specific times of the year. The routine also includes fishing-related maps, which can be constructed based on fleets sailing cost.

The most recent Ecospace software version (v6.5) enables the input of spatial data to fill model layers and therefore build each initial cell map (Steenbeek et al. 2013). This new facility constitutes a step forward towards the use of Geographic Informatics System (GIS) with spatial-oriented models. Once coupled, they constitute a powerful tool to explore spatio-temporal patterns of the ecosystem, access cumulative human pressures in the marine ecosystem and ultimately design and evaluate the impact of alternative management actions (Lewis, 2016; Steenbeek, 2013).

Additionally to the initialization maps, Ecospace requires the input of i) organisms movement rates between spatial cells to estimate changes in FG distributions, ii) habitat preferences for each FG to reproduce the influence of environmental variables in spatial distribution patterns and iii) specification of which fishing gears occur in each created habitat, as well as the relative cost and/or attractiveness of fishing in each cell to drive the spatial dynamic of fishing mortality (Carl Walters et al., 1999).

A fraction of the biomass of each FG (B_i) is constantly moving between grid cells once an Ecospace run initiates. The rate at which the biomass fraction moves is known as the Base Dispersal Rate (expressed in *km/year*) and must be understood as a result of random movements executed by a given species within an ecosystem.

Ecospace discriminates each grid cell as being a “preferred” or “non-preferred” habitat for a given functional group, by setting differential dispersal rates. Habitats are computed as sets of cells that share features that affect the survival, movements and feeding rates of Ecopath groups occurring therein. Thus, unsuitable or non-preferred habitat cells for a given group are associated with high emigration rates (high dispersal rate), high vulnerability to predation and reduced feeding rates, while the opposite is processed for preferable habitat cells. These differential consumption and dispersal rates between suitable and non-suitable habitats are user-defined and drive the initial spatial distribution patterns of the functional groups, within the study area.

Currently, Ecospace is forging the link between ecosystem modelling and species distribution models, given its ability to explore how changes in habitat quality might influence the spatial distribution of living organisms (Villy Christensen, 2014). This capacity was recently introduced in the software (v6.5) under the form of a habitat

foraging capacity model (HFCM) to capture the fact that predator-prey interactions gradually lose local impact as the size of their foraging arena increases.

In practise, the introduction of the new HFCM re-structures the computed vulnerable prey density V_{ij} in each spatial cell. A variable that represents the fraction of the cell available for a FG to forage (named continuous relative habitat capacity, C_{rcj}) was then added to the predation rate term of the foraging arena equation, which now assumes the following simplified form:

$$V_{ij} = \frac{v_{ij} \cdot B_i}{2 \cdot v_{ij} + \frac{a_{ij} \cdot B_j}{C_{rcj}}} \quad (6)$$

The C_{rcj} fluctuates in response to environmental factors that limit the ability of the species to thrive and assumes values between 0 and 1. As result, whether the foraging arena (C) is small, predation activities are locally intensified, so as the vulnerable prey density V_{ij} are driven down more rapidly as B_j increases. Because the cell habitat capacity is calculated per functional group at every time step, the new Ecospace model is dynamic both in space and time. Finally, the inclusion of the C_{rcj} as a modifier of trophic interactions occurring in a cell, results in spatial biomass patterns of consumers, proportional to their cell foraging capacity, a feature that helps in understand why species are where they are and reflects its habitat preferences. In the software the user can either create environmental responses to the drivers that within the modelled area cumulatively constraint the most the foraging capacity of the species (e.g.: depth, salinity, temperature, bottom type) or, specify the fraction of each habitat/grid cell that is available to the species to forage.

Until this point in the model, the spatial behaviour of functional groups within the modelled area is merely being influenced by its biology and ecology, without the direct intervention of anthropogenic actions. Once Ecosim fishing fleets are assigned to the defined habitats, the spatial distribution of groups changes as a response to the presence of fishery fleets on their natural habitat, a factor that might dramatically modifies the cells habitat capacity (recall that Ecosim equations assume fisheries as a predator). The fishing effort distribution is initially conducted by the differential attribution of fleets to habitat cells. Closing cells to fishery can execute MPA simulation at this point. A “gravity model” is afterwards responsible to spread Ecosim fishing effort values across the fleet allocated cells, based on the assumption that the

“attractiveness” of each cell is proportional to the total effort allocated per cell. Here, “attractiveness” resumes the sum over groups of the product of biomass, catchability and profitability of fishing the target groups (Villy Christensen et al., 2008).

2.1.3 Goodness of fit in Ecospace

The most recent versions of the EwE software do not include an interface to show a statistical measure of goodness of fit for each Ecospace run, like Ecosim does per time-step. To overcome that limitation, a routine was developed during the present study to estimate the sum of squares deviation of log time series of biomass (y_B) and catch (y_C) from log biomass and catch Ecospace predictions (\hat{y}). The routine is based on the formula used in Ecosim to estimate the goodness of fit of each run (Villy Christensen et al., 2008):

$$SS = \sum [Ln(y_C - \hat{y}_C)^2] + \sum [Ln(q y_B - \hat{y}_B)^2] \quad (7)$$

The scaling factor q used for relative abundance data (biomass) was obtained using the Excel tool Solver, which determines the minimum possible value for the SS formula, based in a smooth nonlinear optimization algorithm. For the catch term, such scaling factor that minimizes the differences between predictions and observed data is not required since both model results and time series data are expressed in absolute values of $t^{-1}km^{-2} year^{-1}$.

The routine was firstly tested for a hypothetical Ecosim model to authenticate its capability in estimate the same SS calculated by the software and then used to estimate the goodness of fit of the Ecospace runs. The reference data used in this test corresponds to a time series from 1997-2013.

2.2 Application of the EwE and Ecospace modelling approach for the Azores deep-sea ecosystem

2.2.1 Study area

The archipelago of the Azores is a Portuguese isolated group of islands situated in the central North Atlantic (33° 44' N–42° 57' N, 35° 45' W–21 05' W), with an Economic Exclusive Zone (EEZ) of 953 633 km² (Figure 1). Being an integrant archipelago of the Macaronesia, the Azores had a recent volcanic origin (\approx 20 million years), resultant from the continuous activity of the Mid Atlantic Ridge (MAR) (Azevedo, 1991). MAR forms the boundary between the North American and Eurasian/Nubian plates, creating the Azores Triple Junction Area that is reflected in the spatial distributions of the nine islands that compose the archipelago (Azevedo et al., 1991). Its origin designed the oceanic archipelago of the Azores as a predominantly deep-sea environment. In fact, the EEZ has an average depth of 3000 meters and merely 1% of the total area is shallower than 600 meters (Menezes, 2006). The peak of seamounts (a common submarine feature in the mid North Atlantic but particularly abundant in the Azores), the narrow island shelves and a portion of the MAR account for these shallow parts (Morato et al. 2008; 2013). The irregular topography of the region seems to promote the existence of enigmatic ecosystems that occur in deep seafloor such as deep-water coral gardens and reefs (Sampaio et al. 2012; Braga-Henriques et al. 2013; De Matos et al. 2014, Tempera et al. 2015), sponge grounds (Tempera, 2012, 2013) and hydrothermal vents (Cardigos, 2005; Cuvelier, 2009). Moreover, the existence of seamounts has a remarkable role in make the Azores a very important transitional habitat for large mammals as whales and dolphins, sharks, large pelagic fish and sea turtles (Morato et al. 2008; Silva et al. 2013; Vandeperre et al. 2014).

The climate in the region is oceanic subtropical to temperate. The sea surface temperature (SST) presents defined patterns of seasonal variations, exhibiting higher values during the summer (maximum of 22.7 ± 0.4 °C) in opposition to the winter (minimum of 16.1 ± 0.3 °C) (Amorim et al., in press). Such discontinuity is due to the existence of a deep mixed layer at 150 meters deep in the winter while thermocline develops at 40 to 100 m during summer time.

Regarding ocean circulation currents, the waters of the Azores are subjected to

different fronts, which create dynamic and complex patterns. The eastward-flowing Gulf Stream jet, the cold North Atlantic Current and the warm Azores Current in the south side, form the large-scale circulations (Alves, 1999; Bashmachnikov, 2009; Santos, 1995).

All the features described above conceive the archipelago of the Azores as a unique and fragile hotspot of biodiversity that requires holistic management contemplations to ensure the integrity and dynamism of the diverse ecosystem that characterize it, along with the exploitation of its resources.

The study area of the present study is confined to the marine territory of the Azores' EEZ.

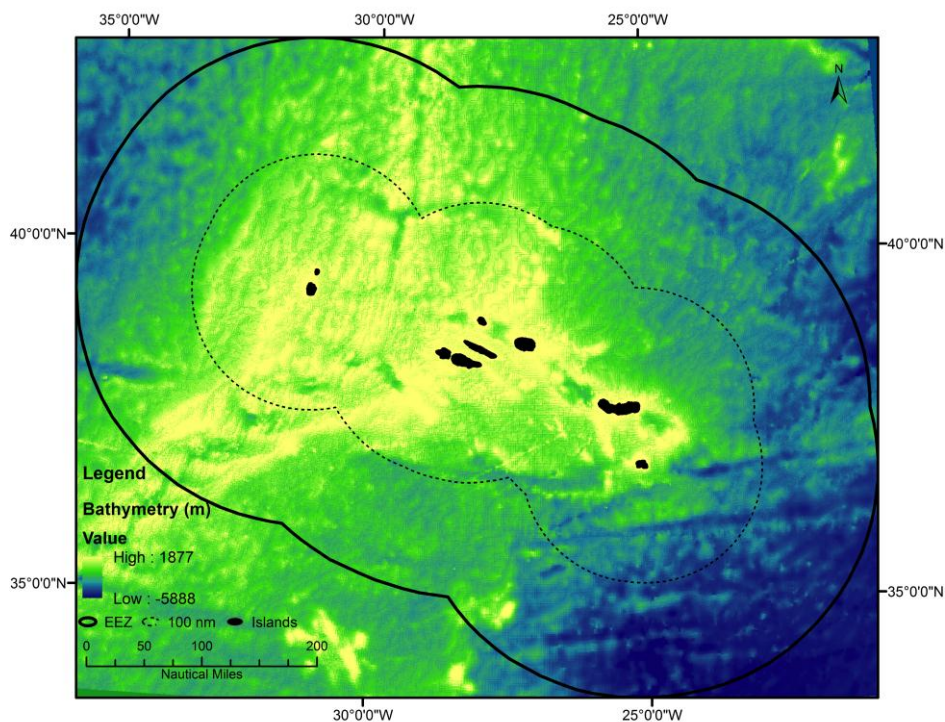


Figure 1 – Bathymetry map of the 200 nm of Economic Exclusive Zone of the Azores (study area). The dashed line illustrates the limit of the 100 nautical miles.

2.2.2 Brief description of fisheries in the Azores and its current management

The exploitation of marine resources is a vital sector for the local economy of the Azores (Da Silva and Pinho, 2007). Despite the vast area of the EEZ, the topographic features that characterize the archipelago constraint the fishing grounds to the island

slopes and seamounts (Da Silva and Pinho, 2007, Morato and Machete, et al. 2008).

The fishery of the Azores is predominantly a small-scale fisheries, that comprise several gear-types (hooks and line gears) and target multi-species. In total, the small fleets land considerably more catch than its larger counterpart, a semi-industrial fishing fleet (10-20%) (Carvalho, 2011).

The industry is divided in four principal components: the high valued pole-and-line tuna fishery, the bottom longline and handline targeting demersal species, normally to 700 meters (e.g., blackspot seabream (*Pagellus bogaraveo*), alfonsinos (*Beryx* spp.), blackbelly rosefish (*Helicolenus dactylopterus*), wreckfish (*Polyprion americanus*)), the fishery of small pelagic species that mostly targets the blue jack mackerel (*Trachurus picturatus*, and chub mackerel (*Scomber colias*) and the pelagic longline targeting swordfish, *Xiphias gladius* (Menezes et al. 2006; Da Silva and Pinho, 2007; Menezes et al. 2013; Pham et al. 2013). The artisanal fisheries sector of the Azores also embraces a small component of coastal invertebrates harvesting and squid fishery, targeting patellid limpets (*Patella candei* and *Patella aspera*), the common octopus (*Octopus vulgaris*), spiny lobster (*Palinurus elephas*), the giant barnacle (*Megabalanus azoricus*), the slipper lobster (*Scyllarides latus*), some crabs (e.g. *Maja squinado* and *Grapsus grapsus*) and *Loligo forbesi* (Blanchard, 2012).

During the last 50 years, the number of species landed in the Azores has increased, mirroring the exploitation of new grounds and introduction of new gears (Pham et al., 2013). Two representative examples of this trend are the experimental drifting deep-water longline, targeting the black scabbardfish (*Aphanopus carbo*) that started in 1998 (Machete, 2011) and the exploratory bottom trawling fishing towards orange roughy (*Hoplostethus atlanticus*) during the period 2001-2002 (Melo, 2002). Both experiments explored depth ranges between 700 and 1500 meters and the total bycatch of both fisheries accounted for 4 – 7.5%.

Currently, the management of marine resources of the Azores is in accordance with the CFP, with the implementation of TACs for commercial important species (e.g. *Pagellus bogaraveo*, *Beryx splendens* and *B. decadactylus*, and deep-water sharks such as *Deania* spp., *Centrophorus* spp., *Etmopterus* spp., *Centroscymnus* spp., and kitefin shark *Dalatias licha*; EC Reg. 2340/2002; EC Reg. 2270/2004). The legislation also establishes the legal boundaries within the EEZ for foreign fleets exploitation, which is set on the 100 nautical miles (Western Waters Regulation, EC 1954/2003). To complement the European legislation, the local government imposes several restrictions,

mostly to specify minimum landing sizes or weights, limitations of licences for specific gears and closure areas and gears bans. The main guidelines dictating the fishery using hooks and line restrict fishing operations of longlines until three nautical miles from coast and specify that boats longer than 30 meters (bow and stern) can not explore the waters within the 12 nautical miles of each island (Portaria N° 7/2000 de 27 de Janeiro; Decreto-Lei N° 383/98, de 27 de Novembro). In 2012, temporal restrictions on the utilisation of longlines around the coast were also introduced (Portaria N° 50/2012 de 27 de Abril). Recently, the regulation of the Azores to prohibit bottom trawling was officialised by the European Commission (EC 1568/2005).

2.2.3 The food web Ecopath with Ecosim model of the Azores EEZ

The ecosystem model used to construct the spatially oriented model of the Azores is based on a previous developed Ecopath with Ecosim model for the Economic Exclusive Zone of the Azores, fitted to time series data from 1997 to 2014 (Morato *et al.* in preparation). The model is centred on intermediate and deep-water species of the Azorean waters, wherein biomass pools (or functional groups) were established founded on ecological and biological similarities.

Particularly the non-fish groups were defined based on a previous Ecopath model of the Azores (Guenette and Morato, 2001) and a hypothetical seamount Ecopath model in the North Atlantic (Morato *et al.*, 2009). Smooth updates were done to include recent biodiversity assessments of the Azores. The fish species incorporated in the model, arise from a check list of marine fishes of the Azores (Santos *et al.*, 1995), an updated list of commercial species caught in the Azores between 1950–2010 (Pham *et al.*, 2013), a list of fish species caught on fisheries research cruises (Gui Menezes, unpublished data), a list of deep-pelagic fishes compiled during mesopelagic trawling survey's (Sutton *et al.*, 2008), and a list of coastal species sighted during a sub-aquatic visual census program (Afonso, 2002). The division of the fish groups was done based on diet composition, length and average habitat depth (R Froese, 2015; Menezes *et al.*, 2006).

Finally, the model encompasses 45 functional groups, from low to high trophic levels – one detritus group, two primary producer groups, eight invertebrate groups, 29 fish groups, three marine mammal groups, one sea turtle and one seabird group (detailed description available in Appendix I). Due to its high commercial interest in the Azores

and to moreover perform management simulations, 11 of the 29 fish groups consist in single species: *Helicolenus dactylopterus*, *Conger conger*, *Pontinus kuhlii*, *Raja clavata*, *Phycis phycis*, *Pagrus pagrus*, *Beryx splendens*, *Beryx decadactylus*, *Pagellus bogaraveo*, *Mora moro*, *Lepidopus caudatus*. The functional group of Tunas also represents a high importance commercial value in the Azores.

The parameterization of the model (P/B, Q/B and P/Q) was accomplished focus on local studies, although in the absence of data, the estimates were originated from similar deep areas and using empirical equations (Appendix II, Table I) (Palomares, 1998; Daniel Pauly, 1980). The habitat fraction occupied by each biomass pool was established according to habitat depth ranges of the Azores converted into surface areas using a bathymetric grid (Appendix II, Table I) (Medeiros, unpublished data). The diet matrix was constructed based on local stomach content analyses and when necessary, derived from other literature sources and adapted to empirical knowledge (Appendix II, Table II). The biomass was expressed in tonnes of wet weight per square kilometre of species habitat.

Concerning fishery inputs, the reference marine catch data consisted on official fishery statistics and estimated illegal, unreported and unregulated (IUU) catch in the EEZ of the Azores in 1997 (expressed in tonnes of wet weight per square kilometre of the model area) (Pham et al., 2013), which was afterwards differentially assigned to the 12 fishery fleets and functional groups included in the model (Appendix II – Table III). In the present model discards, as being the fish returned to the sea, were not individually analysed. The model reference year is 1997 since most of the parameterization data (functional group's diet and growth parameters) result from that year.

The static model was then calibrated in Ecosim to validate the model and perform temporal dynamic simulations. In the calibration process, the model was fitted to time series data of biomass and fisheries catches for the period 1997–2014, which were used as historical (or reference) comparison data. The time series of catch (Appendix III – Figure 3) consisted in the same marine catch data as explained above, extended to 2014 (Pham et al. 2013; C.K. Pham, unpublished data). Only the groups Algae and *Lepidoups caudatus* did not contain reference time series of catch in the modulation. The reference biomass (Appendix III – Figure 2) entailed an index of relative abundances from the Azores Spring deep-water bottom longline surveys, in the form of catch per unit of effort (CPUE) in weight standardized by depth and fishing ground (Menezes et al., 2006, 2013). The groups *large demersal fish group*, *large shallow-water fish group*,

medium shallow-water fish group, and *benthic sharks and rays*, respectively assumed *Polyprion americanus*, *Serranus atricauda*, *Pagellus acarne*, and *Galeorhinus galeus* as representative species of the group and thus the relative population number is referred to those species.

The model was driven in time (1997-2014) by a time series of fishing effort (Appendix III – Figure 2). To 1997, the relative fishing effort was calculated as the number of landing events in the official database per fleet for the following fleets: pole and line, commercial coastal invertebrates, squid fisheries, small pelagic and local pelagic longline and drifting deep-water longline. For the bottom longline and handline, the fishing effort was estimated as the number of hooks per year and for the mainland and foreign pelagic longline fleets, the effort was estimated based on unpublished vessel monitoring system (VMS) data. The effort of the recreational fleet was estimated according to local population oscillations.

Currently, there are three Ecosim models of the Azores driven by the same time series of fishing effort, for the same period of time. One was calibrated to exhibit a good fit of catch (hereafter, “best model for catch”) and another one to replicate the biomass oscillations observed between 1997 and 2013 (hereafter, “best model for biomass”). The improvement of goodness of fit of both models implied the input of forcing functions for primary producers and forced catches of algae and shrimps. Forcing the catch of a given groups consists in removing the reference catch in each year from the ecosystem of group(s) whose predicted catch is heavily under or overestimated, promoting a bad fit (Villy Christensen et al., 2008). Those FG were chosen due to its low importance in the Azores in terms of commercial interest and biomass. The third model developed for the Azores EEZ consisted in an intermediate model that aimed to balance the fit of biomass and catch in a single model. Nonetheless, the catch and biomass of some groups in this model remained under or overestimated.

2.2.4 The underlying Ecosim of the Ecospace model of the Azores EEZ

Although Ecospace generically relies in an Ecopath with Ecosim model, the forcing functions applied in Ecosim to simulate temporal changes in system productivity, are not inherited in Ecospace (Villy Christensen et al., 2009). According to

the same author there is not to date sufficient knowledge concerning how time varying productivity can be spatially distributed, to incorporate the same routine in Ecospace.

It was hypothesized whether Ecospace would be able to incorporate forced catches in the modulation and how the absence of such forces in an Ecosim model, as well as forcing functions, further influence Ecospace predictions and affect the goodness of fit. To test the hypothesis, the annual relative biomass and catch predicted by two hypothetical Ecospace models^[1] was compared. The hypothetical Ecospace models relied on the Ecopath and Ecosim Azores model, however, they consisted in models wherein none habitat preference of organisms was introduced and all fishing fleets were set to all habitats; and depth is the only environmental driver input. A designated “Ecospace A” had an underlying Ecosim model without forcing functions and forced catches, while “Ecospace B” relied in the third Ecosim model developed for the Azores, with forcing functions influencing the biomass of primary producers and forced catches for the algae and shrimps groups.

^[1]The two hypothetical Ecospace models consisted in models which depth was the only baseline space-time dynamic driver, the functional groups were allocated to all habitats and all fishing fleets were allowed to operate in all habitats.

2.3 Development of the Ecospace model of the Azores EEZ

2.3.1 Initialization maps construction

The Ecospace model of the Azores EEZ was developed under the most recent Ecopath with Ecosim software version beta 6.5, freely available in www.ecopath.org.

The spatially explicit data used to construct initial Ecospace maps derived from SIGMAR Azores, a platform that integrates geo-referenced information of the marine ecosystem of the Azores and includes environmental, human and legal aspects. The SIGMAR layers of interest for the present modelling approach were processed in ArcGIS® software to later feed Ecospace layers in the form of ASCII grid files.

Firstly, a basemap to delineate spatial boundaries and grid map dimensions was created. The process encompassed two major steps – the construction of a reference grid to define the extension of the map and the delimitation of the Azores EEZ within the grid map. This reference grid derived from a fishing effort GIS layer converted to a

raster file that geographically limits the basemap borders. Because the study area presents an oval form, the reference grid raster was then clipped to have the extension of the EEZ limit coordinates and the same grid cell size. The cells located outside the EEZ were excluded from the modulation, as well as the cells correspondent to the nine islands that form the Archipelago of the Azores. The basemap had 108 rows and 130 columns, considering a cell size of 10 kilometres length. It resulted in a total of 631.800 differential equations per time step, a huge equation system to be computed but required at the same time to obtain a sound representation of the study area.

Subsequently, environmental-related layers were produced to create the baseline space-time dynamics. Primarily, a depth layer of the model area was built through a GIS bathymetry raster of the EEZ, projected to the reference grid coordinate system and resampled afterwards to have the same cell size as the reference grid (Figure 2). The module assumes depth as positive, non zero values and is expressed in meters (Carl Walters et al., 1999). The second environmental-layer, expressed variations in primary productivity relative to the baseline Ecopath, affecting the P/B values of primary producers while Ecospace ran (Figure 3). The respective GIS layer had the same ArcGIS treatment as the depth layer.

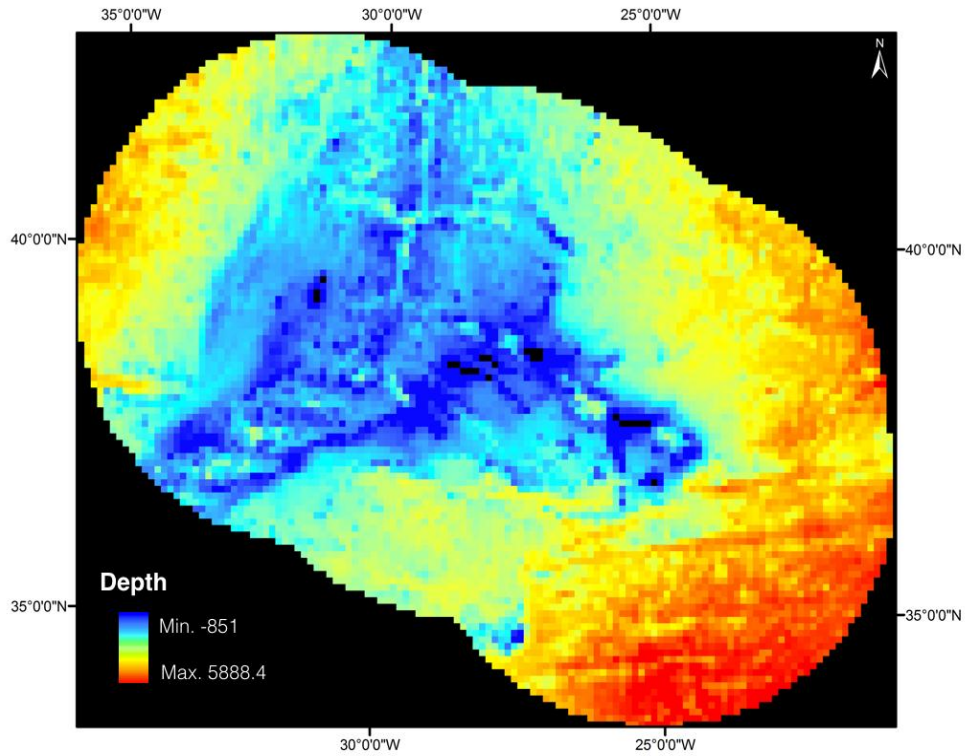


Figure 2 – Depth initialization map in the Ecospace model of the Azores EEZ. The red color cells display the deepest areas of the EEZ, representing a maximum of 5884 meters.

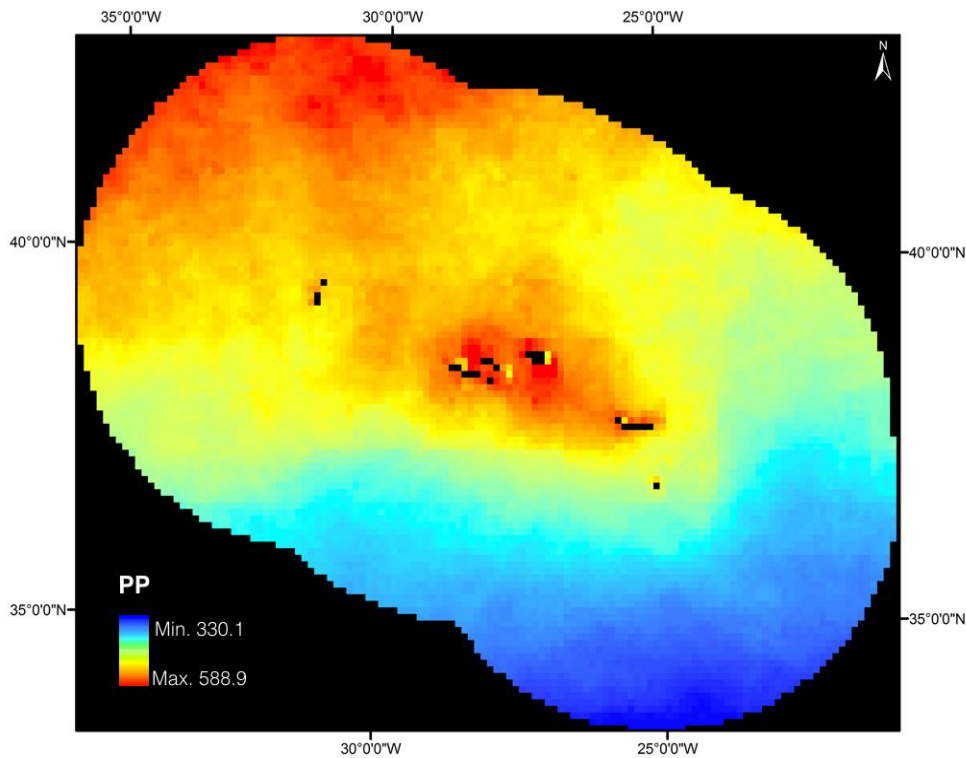


Figure 3 – Relative primary production initialization map of the Ecospace model of the Azores. Red indicates the highest concentration levels of chlorophyll-a in a cell (588.9 mgC/m²/day).

The spatial model of the Azores gathered seven different habitat types (Figure 4). Depth plays a determinant role in explaining most of the spatial distribution of living organisms, and catch densities in the Azores (Menezes et al., 2006; Parra, 2016; Pham, 2015). Based on this fact, five habitat types were assigned as depth intervals (in meters) in the Ecospace model: <150; 150-400; 400-900; 900-1500; <5000 (for illustration reasons the depth ranges might also appear in the form of: <150; <400; <900; <1500 and <5000). The depth ranges approximate where the different functional groups are most likely to occur. To create the depth-based habitats, conditions were imposed to the projected bathymetry raster (created for the depth layer) using the raster calculator tool, in order to establish the depth intervals that define each habitat. The block statistics tool was lately resorted to generate a raster that incorporates blocks of cells with mean depth values of each interval. Every originated depth profile was resampled to bring the raster to the 10 km cell size.

Two distance-based habitats were also created. One was a buffer of 20 km around each island, designated “20 km B”. This habitat was generated to represent the foraging arena of species that prefer island shores (Afonso, 2008; Menezes et al., 2006; T. Morato, 2001). The second habitat was the marine protected area of 100 nautical miles (nm) where foreign fishing fleets are not allowed to operate in accordance to the Western Waters Regulation under the Common Fisheries Policy (EC 1954/2003). The 100nm buffer was available as a polygon, which was projected to the grid coordinate system and converted to a 10km cell size raster.

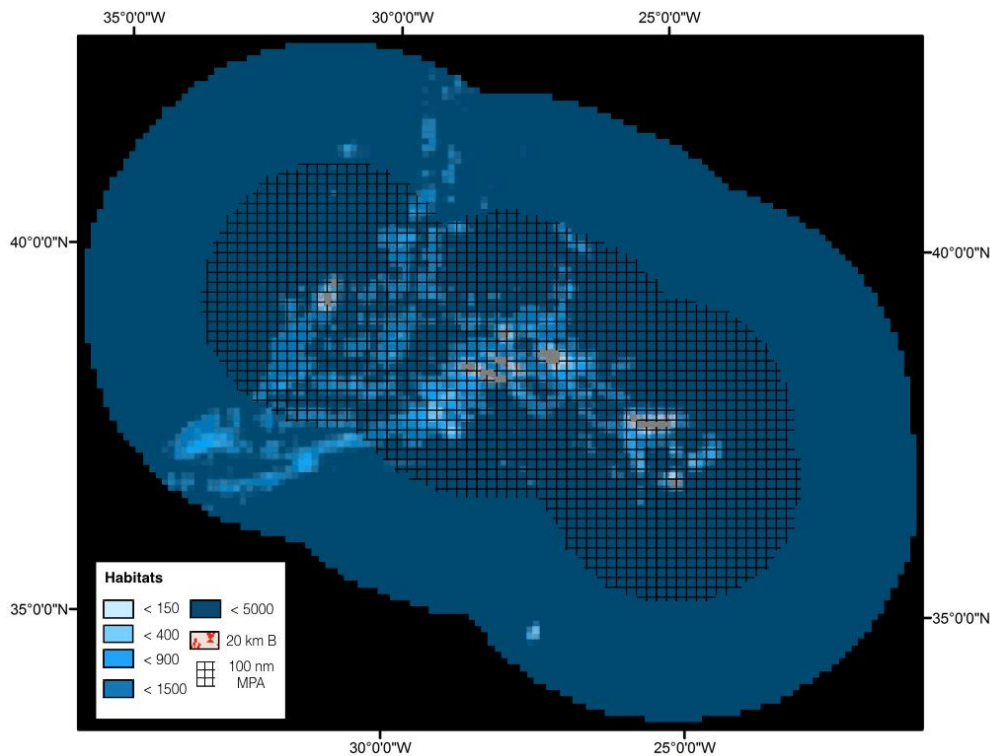


Figure 4 – Spatial distribution of habitats created to drive the Ecospace model of the Azores EEZ

2.3.2 Functional groups habitat preferences and fishery fleets allocation per habitats

The attribution of habitat preferences is a key phase in the construction of an Ecospace model, since it regulates the trophic interactions occurring at each cell and consequently the spatial distribution of organisms, catch and fishing effort. In doing so, to ensure the input of habitat preferences were as much as possible close to reality, at the local scale, four main criteria were established to accompany this part of model development process.

The first criteria assumed that functional groups encompassing pelagic species and both shallow and deep water species, should not have depth preferences and so the C in all habitats equal to 1 (FG: phytoplankton, small and large zooplankton, shrimp, cephalopods, crabs, benthic filter feeders, benthic worms, other benthos, pelagic small, medium and large, mesopelagic, pelagic sharks, tunas, baleen and toothed whales and detritus).

Secondly, was recognized that since depth shapes the spatial distribution of demersal species (Menezes et al., 2006; Parra et al., 2016), the foraging capacity of those groups should be modelled under the influence of responses to depth. The input of such effect can be done applying one of two different methods: i) creating response curves that relate the habitat capacity of a species along a depth range (depth profiles); or ii) defining the fraction of each habitat type suitable for a group to forage, according to their depth preferences.

Hence, depth profile curves for demersal groups and mainly targeted by the Azorean bottom longline fishing fleet were designed in the form of local catch per unit effort (CPUE) (here defined as the number of individuals in a given depth stratum of longline surveys, relative to 1000 hooks), as an indirect abundance measure (Maunder, 2006), along depth (FG: Shallow Water Small, Medium and Large, Demersal Small, Medium and Large, *Helicolenus d. dacylopterus*, *Conger conger*, *Pontinus kuhlii*, *Raja clavata*, *Phycis phycis*, *Beryx splendens*, *Beryx decadactylus*, *Pagellus bogaraveo*, *Mora moro*, *Lepidopus caudatus*, Benthic Sharks and Rays and Deep-water Sharks). Later, the CPUE values were converted to a continuous scale from 0 to 1, in order to represent how depth impacts the habitat capacity of each functional group (environmental responses to depth available in Appendix IV – Figure 3).

The third criterion was focus on the habitat “20 km B”. Afonso et al. 2008 showed that Azorean populations of *Pagrus pagrus* have a particular habitat preference for island’s shores, regardless whether suitable habitat exists in offshore seamounts, mainly due to ontogenetic segregation in habitat use of local populations (Menezes et al., 2006). Therefore, it was settled that this species should have a full habitat capacity in the “20 km B” habitat, and none in the other habitat types.

Finally, the last criterion embraces the remained functional groups, on which depth profiles were not possible to define due to the lack of CPUE data (FG: algae, bathypelagic, bathydemersal small, medium and large, seabirds, turtles and dolphins). For these groups the habitat capacity was purely estimated based on the empirical knowledge on the biology and ecology of the species (Appendix IV – Table II) (Ferreira, 2011; Machete et al., 2011; M. a. Silva, 2003).

The dispersal rates in preferable (C equal to 1) and non-preferable habitats (C equal to 0), as well vulnerability to predation were left has default Ecospace values (Base dispersal rate, 300km/year, except Detritus, 10 km/year; Relative dispersal in bad habitats, 5 km/year; Relative vulnerability to predation in bad habitats, 2; Relative feed

rate in bad habitats, 0.5 (Christensen et al. 2008). The reason relies on the assumption that at this early model development stage, it should be kept as simple as possible so one would be able to easily understand how each input parameter influences the spatial dynamics of the model.

The allocation of fishing fleets over the modelled habitats was set based on empirical knowledge on fisheries operations, and local legislation, in accordance with the description provided in chapter 2.2.2 (Table II). The models developed in the present study, had the fishery input configuration as showed in Table II, with the exception of model baseline.

Table II – Allocation of fishery fleets operating in the EEZ of the Azores per each model habitat (the symbol indicates the fleet operates in the respective habitat)

Fleet\ Habitat	All Habitats	<150	<400	<900	<1500	<5000	20 km B	MPA 100nm
Bottom longline/Handline		<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>			<input type="checkbox"/>	<input type="checkbox"/>
Pole and line tuna and live bait	<input type="checkbox"/>							
Small pelagic fishery		<input type="checkbox"/>					<input type="checkbox"/>	<input type="checkbox"/>
Pelagic longline regional		<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>		<input type="checkbox"/>
Recreational fishing		<input type="checkbox"/>					<input type="checkbox"/>	<input type="checkbox"/>
Coastal invertebrate fishery		<input type="checkbox"/>					<input type="checkbox"/>	<input type="checkbox"/>
Squid fishery		<input type="checkbox"/>	<input type="checkbox"/>				<input type="checkbox"/>	<input type="checkbox"/>
Pelagic longline mainland		<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>		<input type="checkbox"/>
Pelagic longline foreign		<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>		
Bottom trawling				<input type="checkbox"/>	<input type="checkbox"/>			<input type="checkbox"/>
Drifting deep-water longline					<input type="checkbox"/>	<input type="checkbox"/>		<input type="checkbox"/>
Whaling	<input type="checkbox"/>							

2.3.3 Step-by-step approach in model calibration - adjustment of functional groups habitat preferences guided by the goodness of fit

Plausibly, an Ecospace model is a more robust representation of an ecosystem than Ecosim, given the introduction of spatial considerations into the modulation (Villy Christensen et al., 2014; Carl Walters et al., 1999). In doing so, it was expected that the Ecospace model of the Azores would have a better ability to predict the overall trends of catch and biomass observed in the Azores between 1997 and 2014, than the underlying Ecosim. Thus, such improvement should be reflected in the overall goodness of fit of the Ecospace model.

Firstly was developed a spatial model (hereafter designated “Baseline”) in which none of the functional groups had a preferable habitat and therefore equally forage along the study area (Appendix IV, Table I). All fishery fleets were assigned to all habitats, including the foreign fleets in the 100nm MPA. Additionally, depth was the only initialization map driving initial spatial dynamics. The purpose of this baseline model was to verify that the sum of squares obtained in Ecosim were similar to those obtained in Ecospace, when no spatial preferences were given, and therefore could be compared.

It was then hypothesized whether the input of the primary productivity initialization map could increase the fit of the baseline model. Although very smooth, the driver enhanced the total model fit (from 294,7 to 293,2). For that reason, it was decided to also include the primary productivity as a driver of baseline time-spatial dynamics.

A second model (Model 1) introduced spatial variability through the definition of habitat foraging usages of the functional groups. This model narrowly respected the criteria of habitats preferences attribution (Appendix IV, Table II) and for this reason was considered the reference Ecospace model of the Azores. The purpose of this model consisted in evaluate how the model would behave under the influence of the conventional criteria and evaluate its goodness of fit.

A model calibration process was consequently followed, to adjust the habitat foraging usage of FG, adopting a step-by-step approach guided by the evaluation of sum of squares at the end of each model run. This assessment was individually made in terms of overall, biomass and catch sum of squares. Such approach is pioneer in the development of an Ecospace model.

The process initiated removing all the environmental responses to depth (from Model 1) and replacing it by values of habitat cells fractions occupied per functional group. Those portions introduced in each habitat, consisted in average CPUE values in the scale of 0 to 1 at each depth-based habitat, obtained from the depth profiles previously generated. The average CPUE value in each habitat type was then weighted by the highest average estimated for a given habitat. In doing so, it implied whether the depth profile assigned the maximum habitat capacity at depth x , in this new approach, the functional group would have 100% of the habitat type, that comprised that value x , to forage. This model was named “initial Azores Ecospace model” and the input habitat capacity is available in Appendix II, Table III. From this point, smooth changes in the foraging arena size of some species were made, until obtaining the final Azores Ecospace model (Appendix II, Table IV). In the last step of the calibration process, the environmental response to depth was again input for the group Demersal Large, since it improved the global fit results. Nonetheless, although the conventional criteria to attribute habitat foraging use to FG had to be broken in some cases, the new inputs were based in the ecology and biology of the species, giving preference to local studies data (Abramov, 1993, Morato et al. 2001, Menezes et al. 2006, Menezes et al. 2013, Pinho et al. 2014).

3. RESULTS

3.1 The underlying Ecosim of the Ecospace model of the Azores EEZ

Both Ecospace models A and B predicted exactly the same annual relative biomass and catch between 1997 and 2013, confirming that forced catches were not underlined in Ecospace. Analysing the annual estimates of relative biomass, it is clear that Ecospace is limited in replicating seasonal oscillations of biomass promoted by external environmental factors to the model that affect system productivity, as the straight lines revealed (Figure 5).

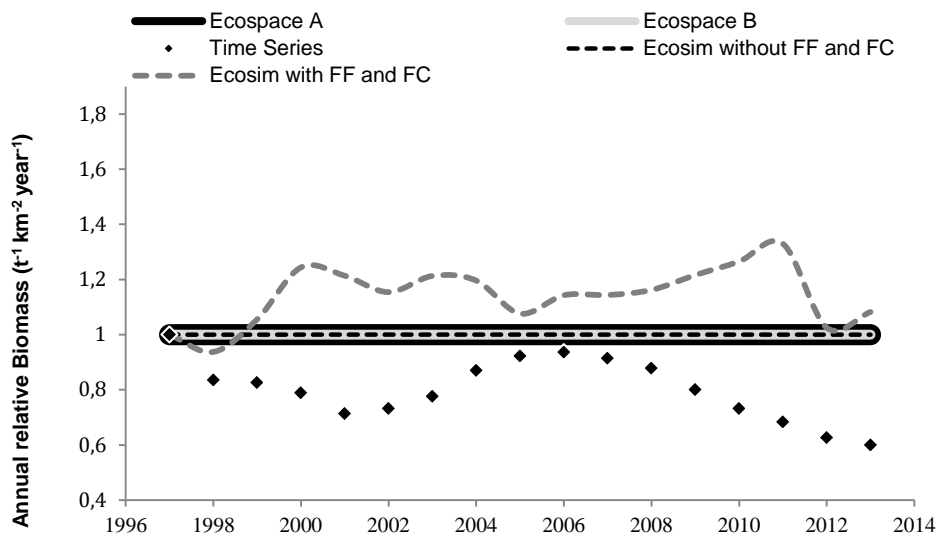


Figure 5 – Annual relative biomass predicted by Ecospace model A (black line), derived from an Ecosim without forcing function (FF) and forced catches (FC) (black dashed line) and Ecospace B (grey line), which underlying Ecosim contains both forcing functions and forced catches of algae and shrimps (grey dashed line). The black dots represent biomass time series data for the period 1997-2013.

On the other hand, the results of the Ecosim model with forcing functions featured the existence of regime shifts of productivity moving the biomass along the modelled period, introduced by the forcing functions. Regarding catch predictions, the same pattern was observed comparing the results of Ecospace model A and B (Figure 6). The Ecosim model with forcing functions and forced catches estimations were closer to the reference data, in comparison to the remaining models in the analysis. An evaluation of the goodness of fit also highlighted how the input of forcing functions and forced catches increases the fit of an Ecosim model (Figure 7).

Concluding, due to the mentioned restrictions of the spatial routine of EwE, the time dynamic model employed in each cell grid by Ecospace presented a basic form, that did not include forcing functions and forced catches and in doing so did not have the most possible goodness of fit (Figure 6).

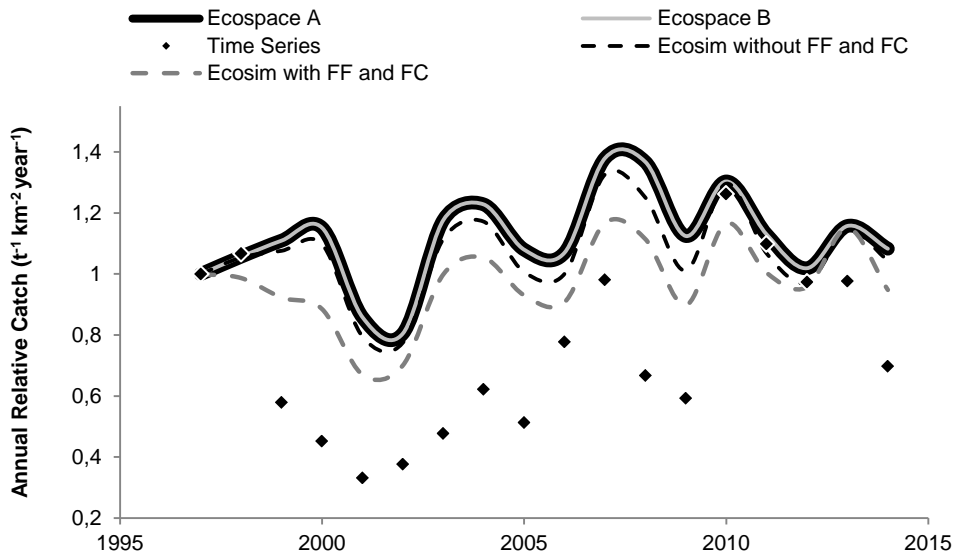


Figure 6 – Comparison of annual relative catch predicted by Ecospace model A (black line), derived from an Ecosim without forcing function (FF) and forced catches (FC) (black dashed line) and Ecospace model B (grey line), which underlying Ecosim contains forcing functions and forced catches of algae and shrimps (grey dashed line). The black dots represent catch time series data for the period 1997-2014

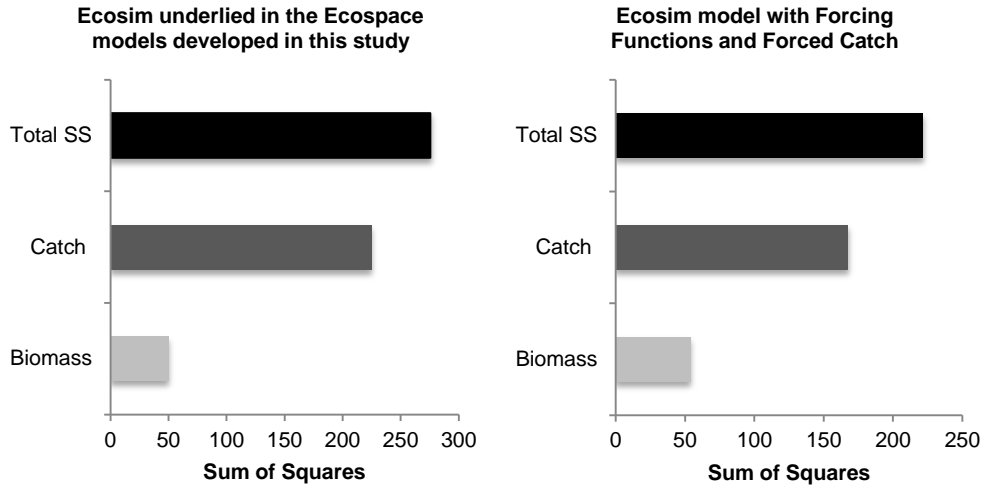


Figure 7 – Goodness of fit (in the form of Sum of Squares) comparison between the Ecosim model inherited to the Ecospace models developed in this study with the Ecosim model with forcing functions and forced catches.

3.2 Performance of the routine developed to estimate the goodness of fit of Ecospace

The results showed that the developed routine satisfactory guesses a value of biomass SS equal to the one displayed in Ecosim’s interface, for each functional group with time series data (Figure 8). It was though assumed that the smooth differences observed arise from the inherit software failure in standardize decimal places and/or from the method executed by the software to estimate the scaling factor.

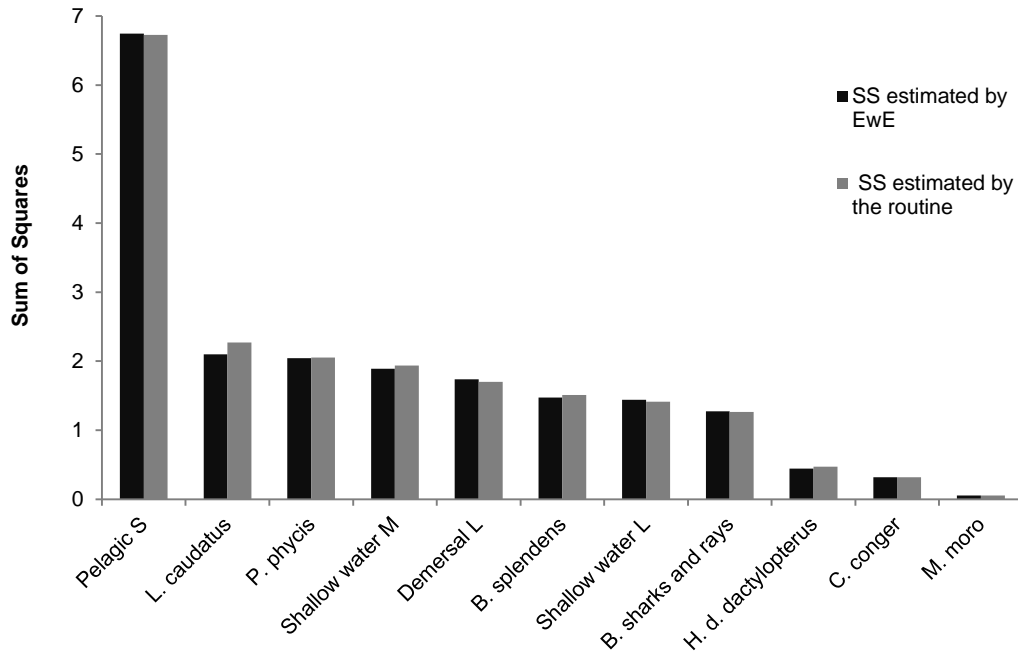


Figure 8 – Goodness of fit of biomass of an Ecosim run estimated by the developed routine and by Ecosim’s interface, per each functional group with reference data from 1997 to 2013

Regarding the SS of the catch, a huge discrepancy was observed between the SS estimated by the routine and Ecosim’s interface (Figure 9). It was thus hypothesised that the scaling factor could be minimizing the fit of catches in the EwE’s software routine that calculates the SS. To test the assumption, the scaling factor was introduced in the routine, according to the formula:

$$SS = \sum [Ln(q y_C - \widehat{y}_C)^2] + \sum [Ln(q y_B - \widehat{y}_B)^2] \quad (8)$$

The SS estimated per each group were identical to Ecosim's results, showing that a bug was present in software's SS interface (Figure 9). The EwE development team was informed about the problem and the SS interface was fixed for the official release of software beta version EwE 6.5, available in www.ecopath.org.

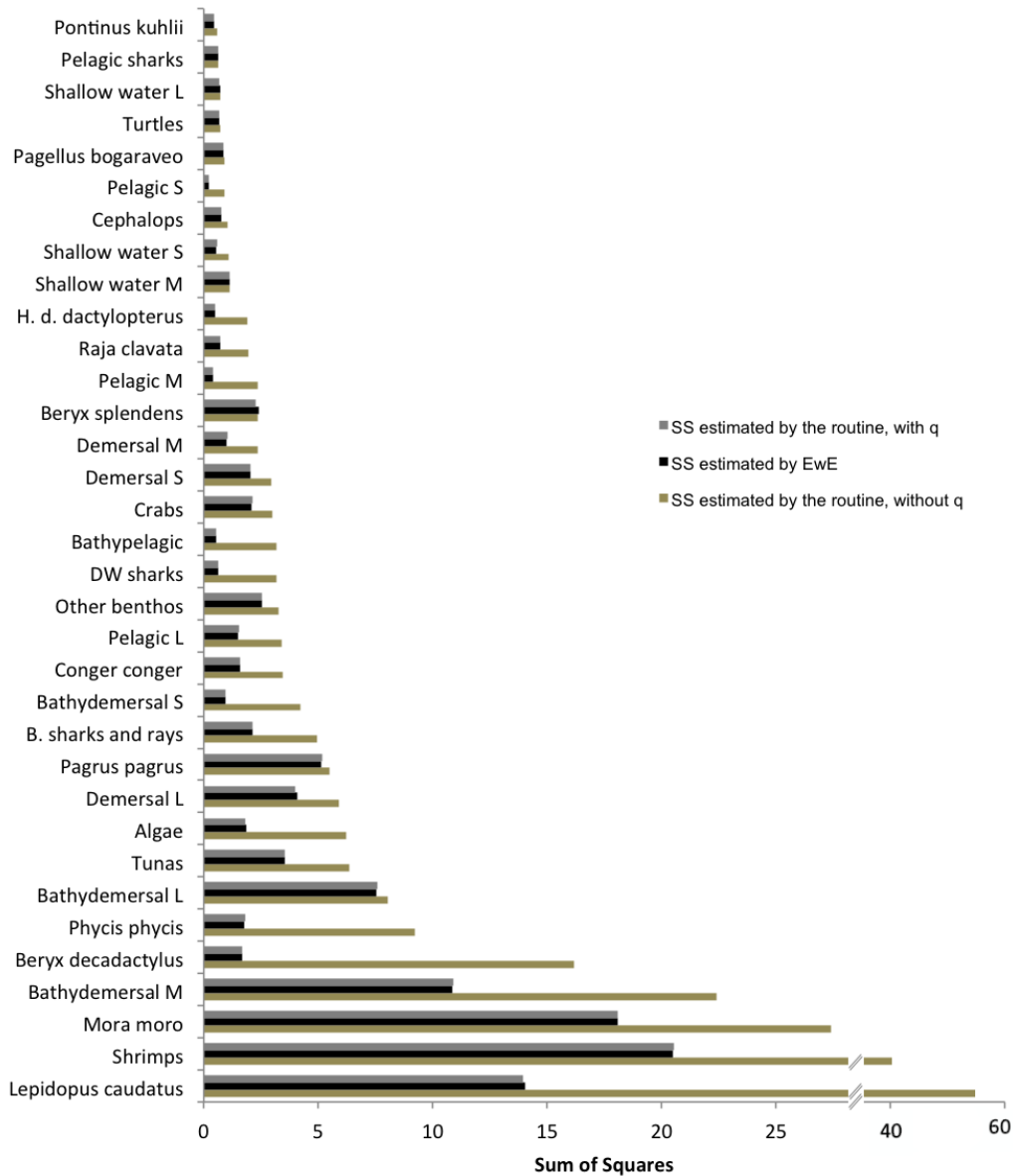


Figure 9 – Goodness of fit of catch estimated by the developed routine (under the form of Sum of Squares), with and without the scaling factor that minimizes the fit of catch, and by Ecosim's interface, per each functional group with reference data from 1997 to 2013.

3.3 Transition from Ecosim to Ecospace – evaluation of goodness of fit and models predictions

The global goodness of fit of the Ecospace baseline was very close to Ecosim (Figure 10). The fit of biomass of this spatial model improved in 8%, while the fit of catch worsened in 11%, relatively to the time-explicit model (Figure 12 and 13). It was expected that these two models would have exactly the same fit, since the spatial model was built in a way that the trophic interactions occurring in each cell would not be interfered by habitat preferences and spatial allocation of fishing fleets.

Ecospace Model 1 had an extremely bad fit, showing a value of total sum of squares equal to 1298.6 (Figure 10). In this model, the catch was the most responsible term promoting the bad fit (5.6 times higher than Ecosim) (Figure 13), while in comparison, the sum of squares of biomass was only 13.3% higher than Ecosim (Figure 12).

The total sum of squares of “Azores Ecospace model” was 248.7, a value 8% lower than the underlying Ecosim (sum of squares equal to 269.8) (Figure 10). The biggest difference between the two models was observed for the catch (Ecospace – 198.4; Ecosim – 219.4) (Figure 13), while the difference for the biomass was very smooth (Ecospace – 50.2; Ecosim – 50.3) (Figure 12). From the beginning to the end of the step-by-step calibration process, the Azores Ecospace model improved the total fit in 81% (Figure 10), with a notable improvement in both terms biomass and catch (Figure 12 and 13). The smooth changes made in the foraging usage contributed in 72% for the improvement

The groups of which global fit improved with the transition from Ecosim to Ecospace (both Model 1 and Azores Model) were the Pelagic Large, Bathypelagic, Bathydemersal Small, *Helicolenus d. dactylopterus*, *Beryx decadactylus* and *Pagellus boragaveo*. In opposition, the fit of Shrimps, Cephalopods, Crabs, Other benthos, Shallow Water Small and Large, Pelagic Medium, Demersal Medium, Demersal Large, Bathydemersal Medium and Large, *Mora moro*, Pelagic Sharks, Tunas and Turtles decreased (Figure 11).

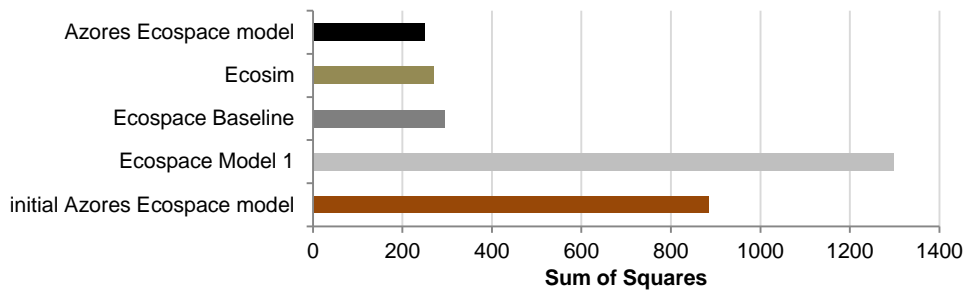
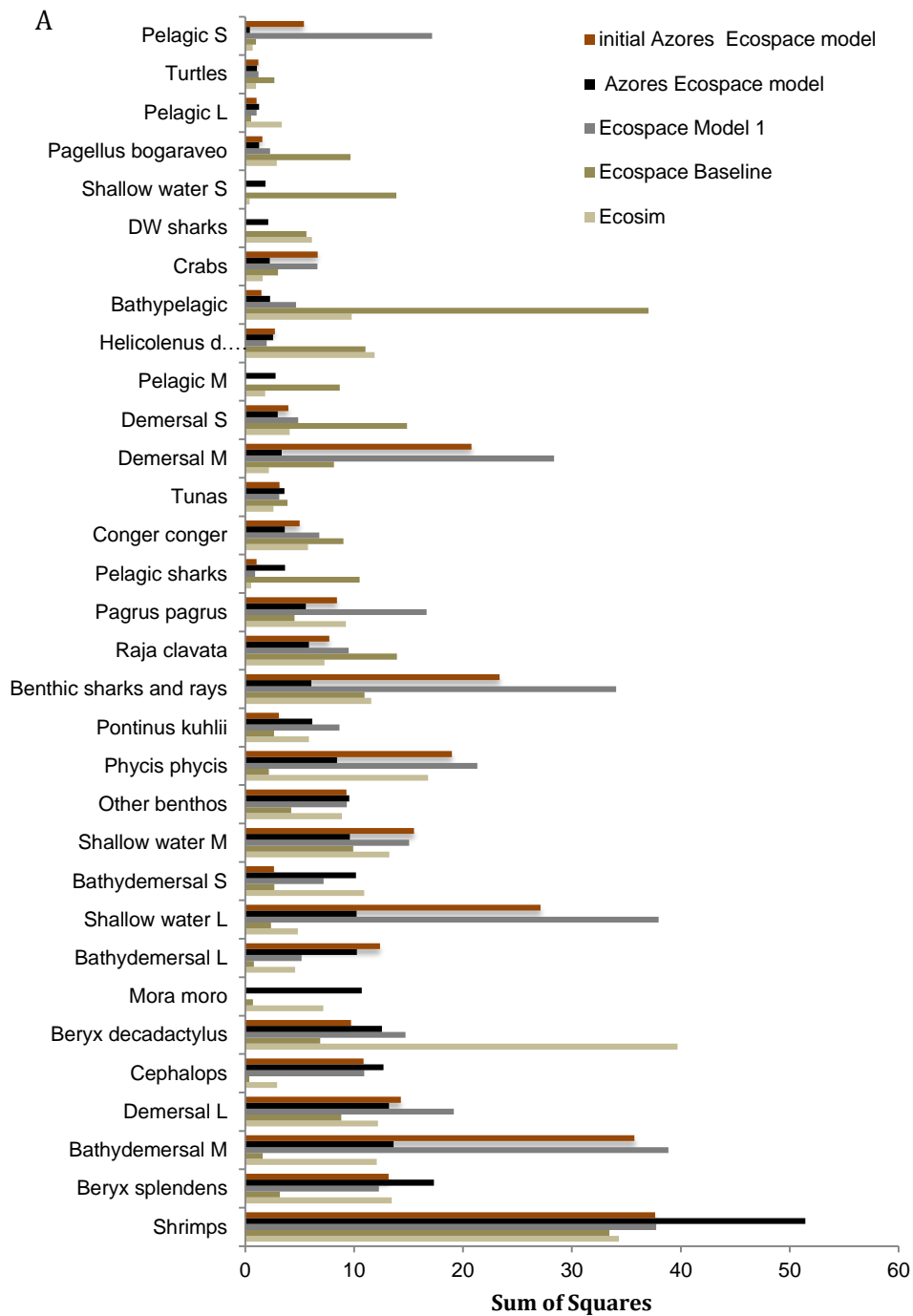


Figure 10 – Total goodness of fit between the studied models



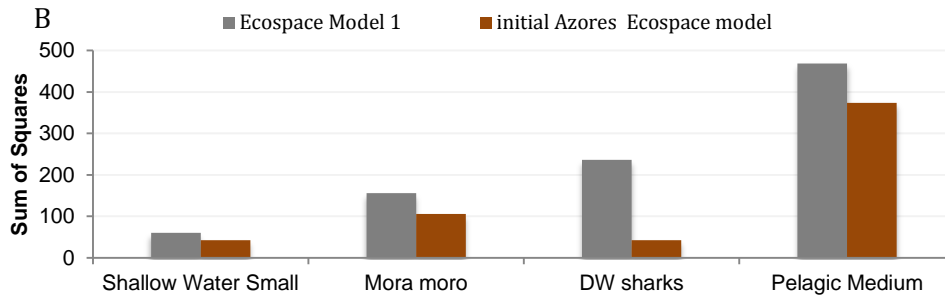


Figure 11 – Total goodness of fit (chart A and B) of each functional group with time series data (for illustration reasons, the groups of Model 1 with higher sum of squares are show in chart B)

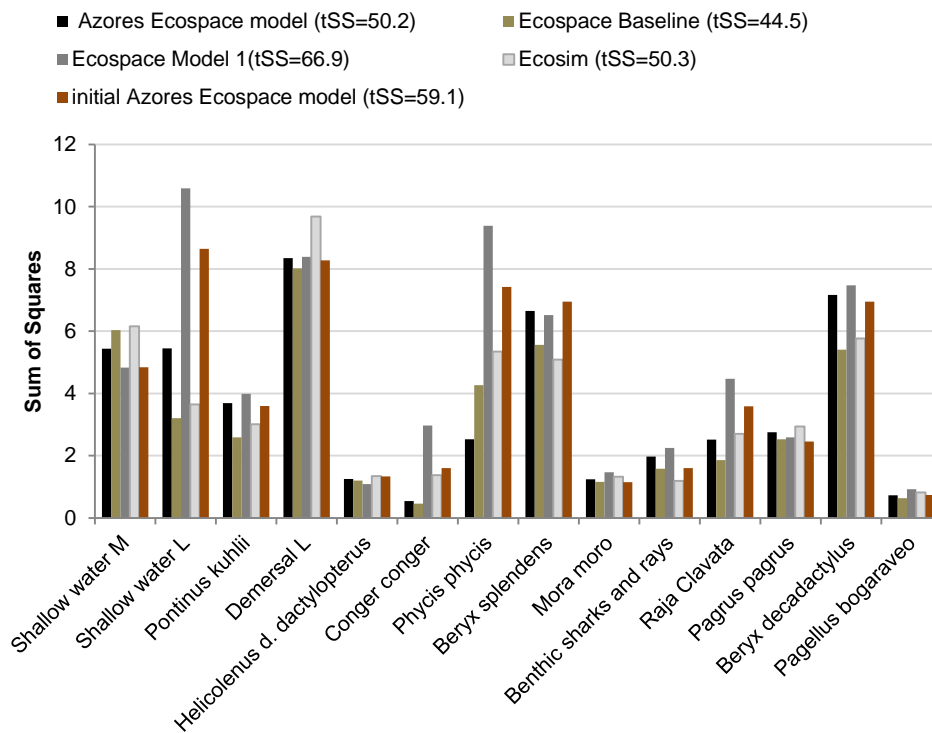
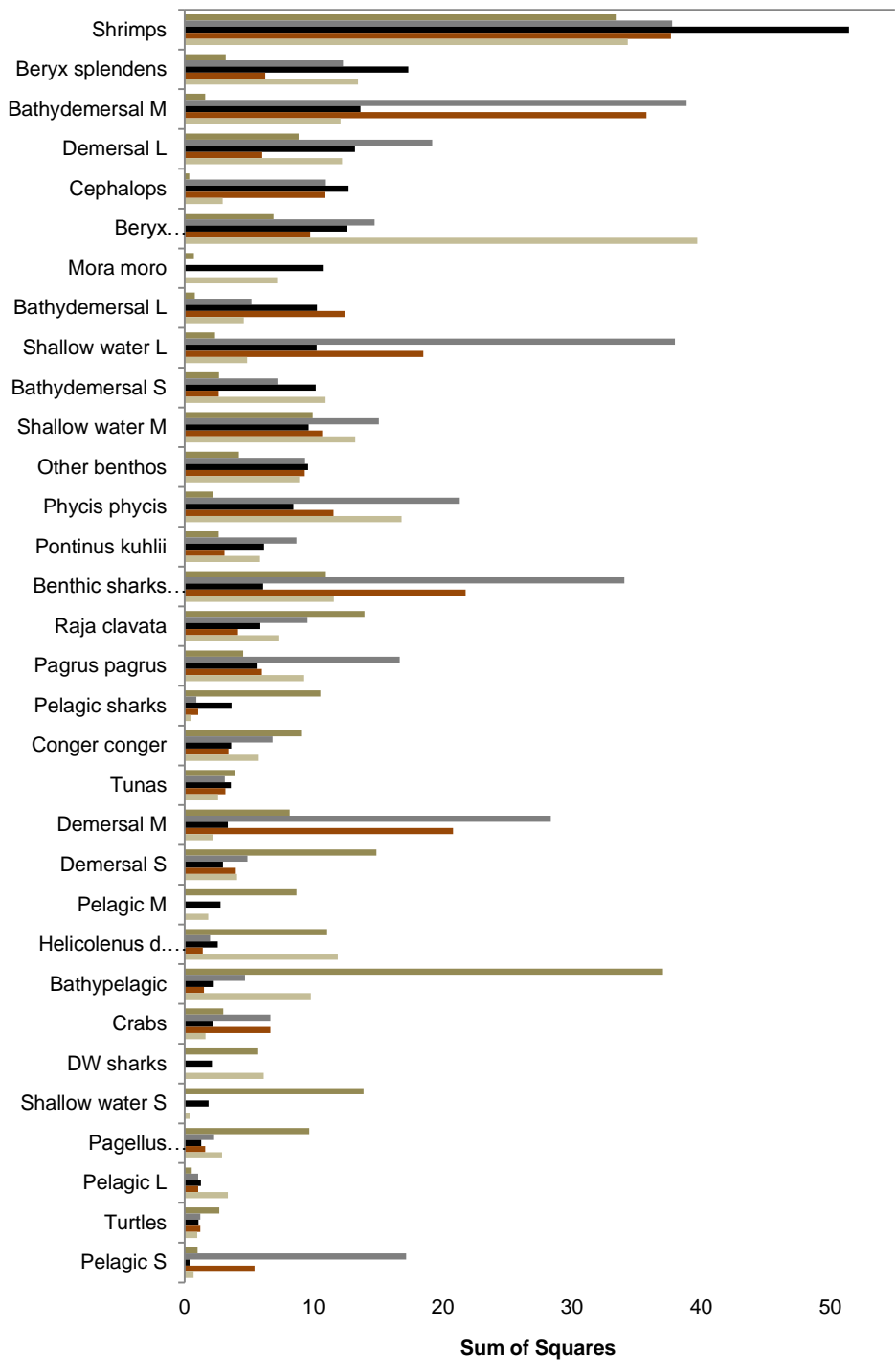


Figure 12 – Comparison of the goodness of fit of biomass between the Azores Ecospace model, Ecospace Model 1, the Ecospace baseline and the underlying Ecosim. In the legend, tSS is the total sum of squares of biomass of that model.

A

- Ecospace Baseline (tSS=248.8)
- Azores Ecospace Model (tSS=198.4)
- Ecosim (tSS=219.4)
- Ecospace Model 1 (tSS=131.7)
- initial Azores Ecospace model (tSS=825.6)



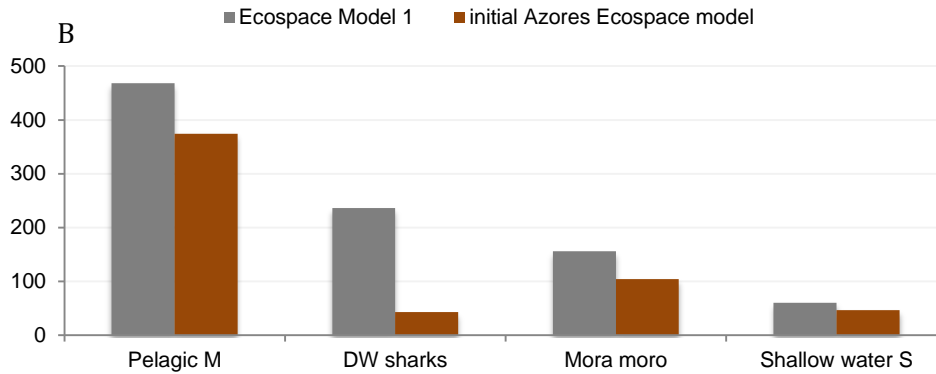


Figure 13 – Comparison of the goodness of fit of catch between the Azores Ecospace model, initial Azores Ecospace model, Ecospace Model 1, the Ecospace baseline and the underlying Ecosim (chart A and B). In the legend, tSS is the total sum of squares of catch of that model. For illustration reason, the groups that showed a very high sum of squares are represented in chart B.

A general analysis of the annual relative biomass and catch predicted by each model reflected the results of models' fit.

All the Ecospace models failed to exhibit shifts of biomass regimes, which the time series suggest exist (Figure 14). As expected, the Ecospace Baseline, like the Ecosim did not predict any changes in biomass, although Model 1 and Azores Ecospace model predicted a smooth enhancement of total biomass in the first three years of modulation that rapidly stabilized until the end. Although the predictions of the best Ecosim model for biomass of the Azores did not strictly follow the time series tendencies, it illustrated the occurrence of changes through time, which approximates it from reality. Nonetheless, the overall results showed little variation over time and consequently a very smooth response to the fishing effort driving the model in time and to depth and primary production, driving the spatio-temporal dynamics.

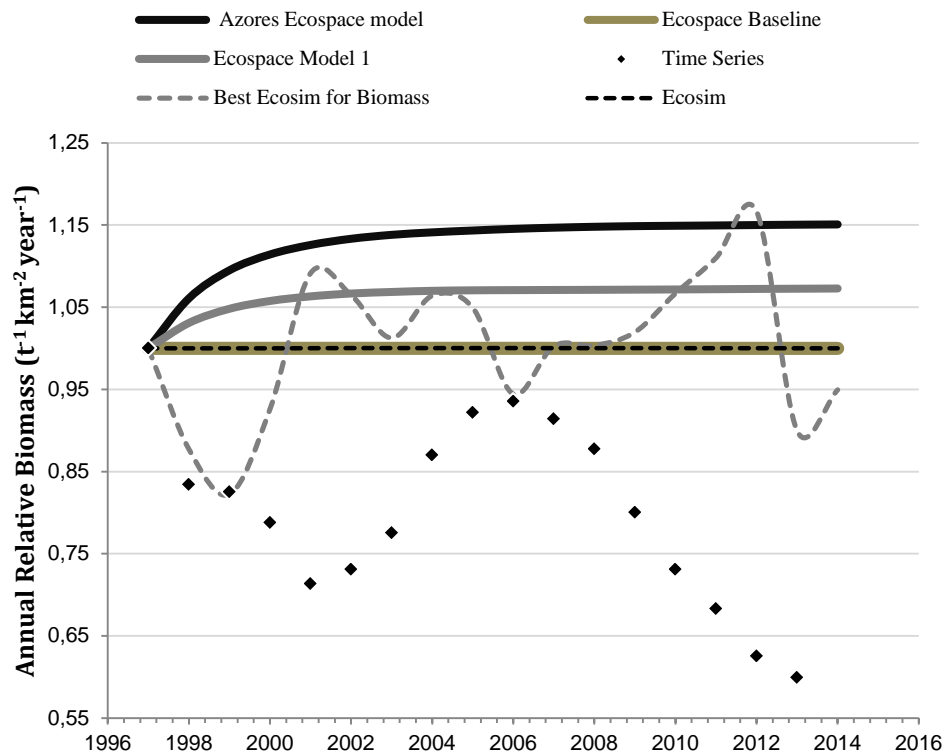
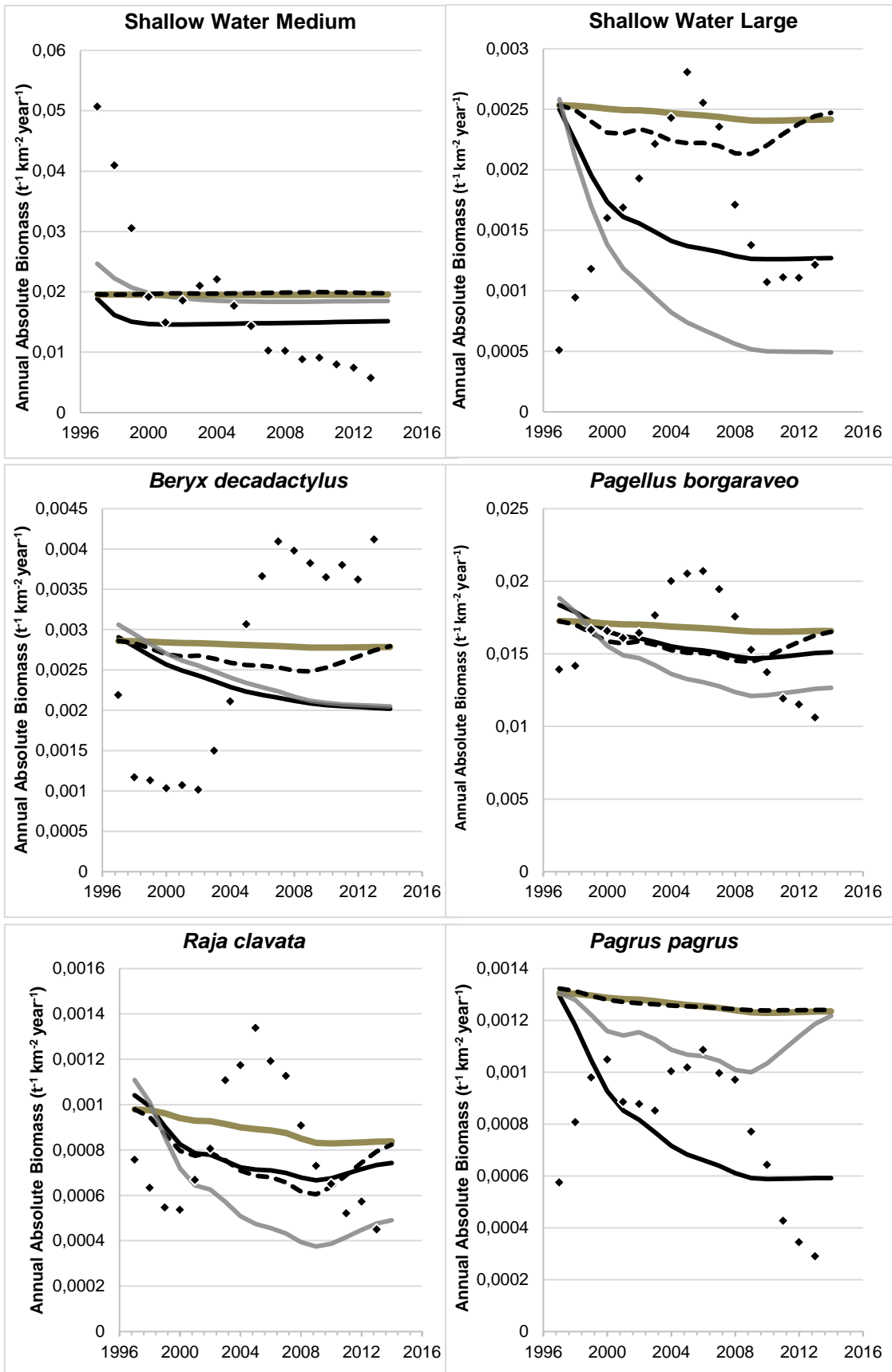
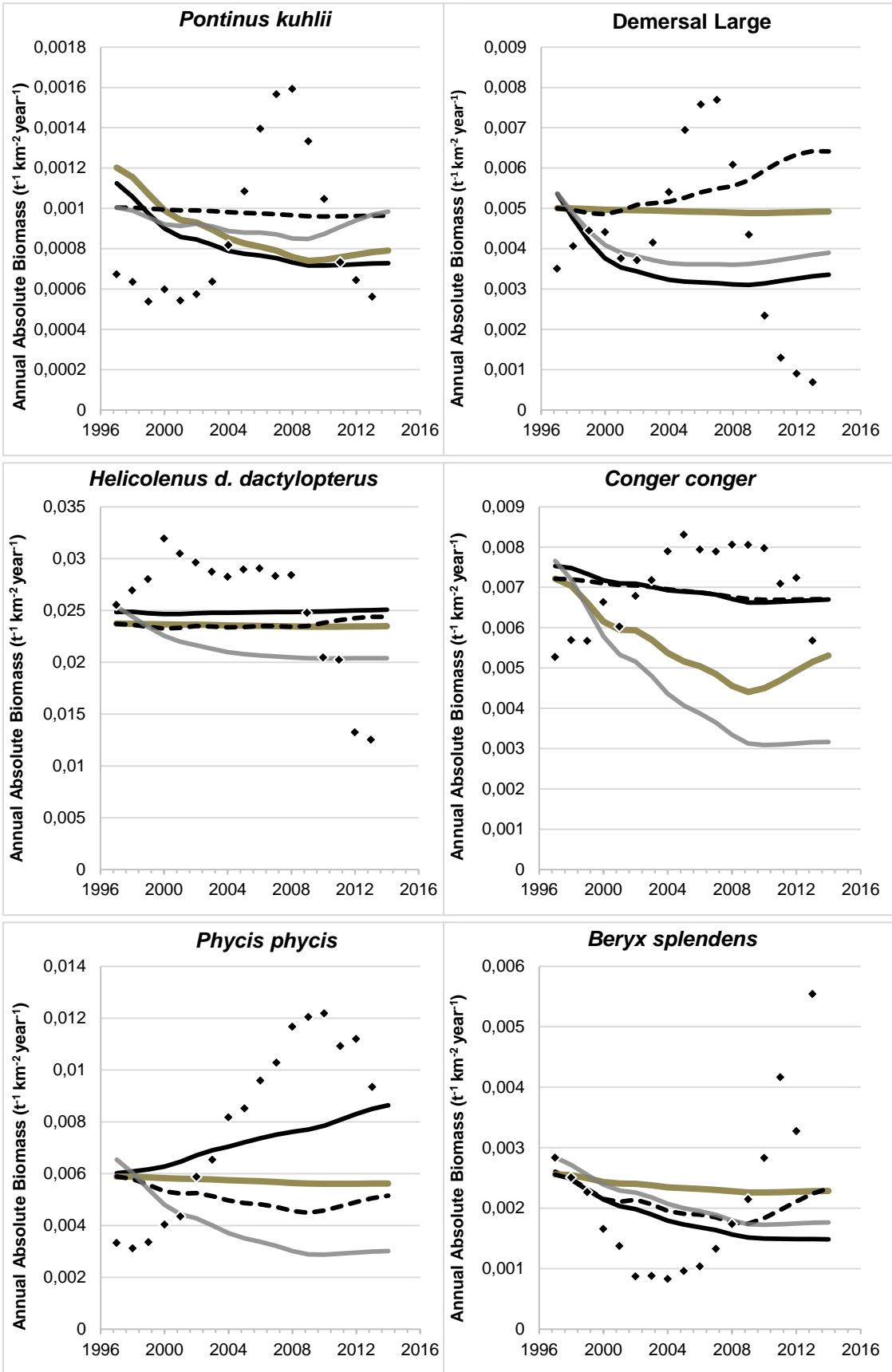


Figure 14 – Comparison of annual relative biomass between the Azores Ecospace model (black line), Ecospace model 1 (grey line), Ecospace Baseline (beige line), underlying Ecosim (black dashed line) and the best Ecosim model for Biomass (dashed grey line), for the model period. The black dots represent the reference time series data between 1997 and 2013.

Performing an analysis group-by-group, none of the Ecospace models did satisfactorily replicate the seasonal oscillations of biomass observed for the reference groups, even for those which the sum of squares highlighted a relative good fit, such as the high exploited species *Pagellus bogaraveo* (Figure 12 and 15). The results indicate that other drivers, besides those included in the model might be promoting the biomass fluctuations along the period modelled. The biomass fit of the groups Shallow Water Medium, Demersal Large, *Helicolenus d. dactylopterus* and *Pagrus pagrus* improved with the transition from Ecosim to Ecospace, exhibiting in the two spatial-temporal dynamic models a better fit than Ecosim (Figure 12). An opposite trend was observed for the groups Benthic Sharks and Rays and *Beryx splendens*, for which both Ecospace models, respectively over and under estimated the biomass (Figure 12 and 15).

— Azores Ecospace — Ecospace Model 1 — Ecosapce Baseline ♦ Time Series - - - Ecosim





— Azores Ecospace — Ecospace Model 1 — Ecosapce Baseline • Time Series - - - Ecosim

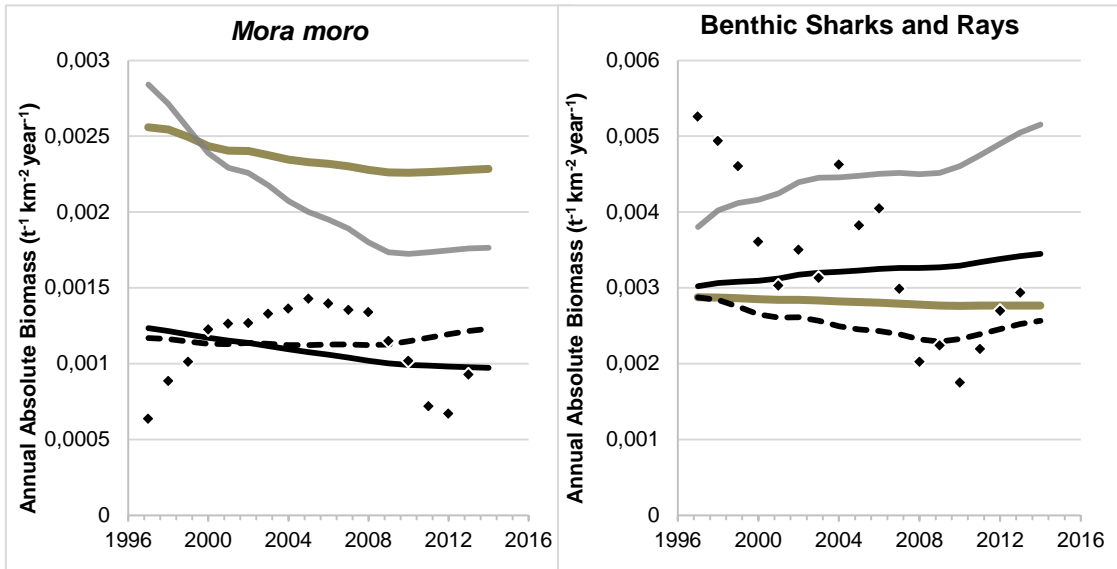


Figure 15 – Annual absolute biomass predicted by the Azores Ecospace model (black line), Ecospace model 1 (grey line), Ecospace baseline (beige line) and the underlying Ecosim (black dashed line) per each functional group with reference time-series during the model period. The black dots show the reference time series.

Regarding the Ecospace models performance in predict the total annual relative catch, the Azores Ecospace model was the one that more satisfactorily followed the tendencies observed from 1997 to 2014, particularly during the first nine years (except in 1998) (Figure 16). During the period 2005 - 2007 and 2010 - 2013, the model underestimated the catch, although in the last year it re-approximated the prediction from reality. Model 1 showed through time, exactly the same trend as the Azores Ecospace model, although with higher relative values (Figure 16). The estimates of model baseline were over estimated for the all period, following the trend of the underlying Ecosim model (Figure 16).

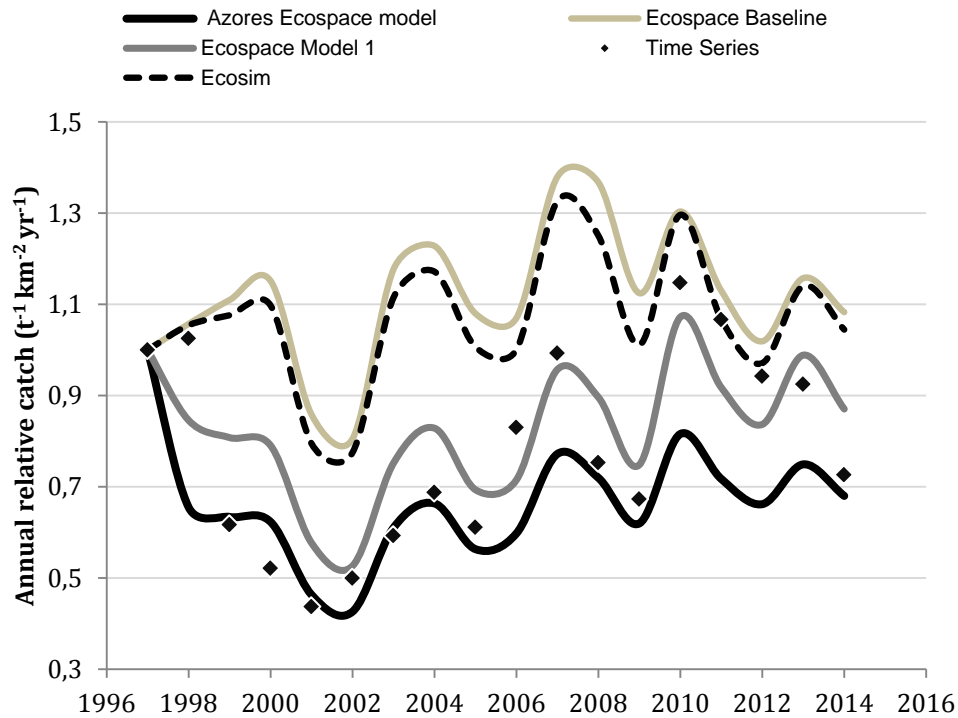
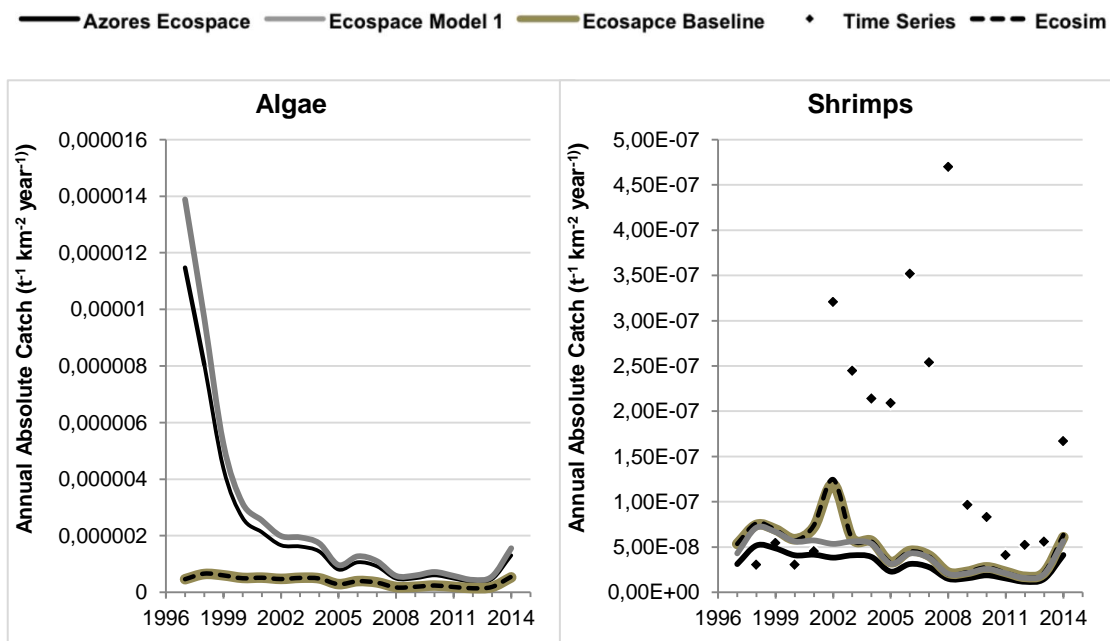


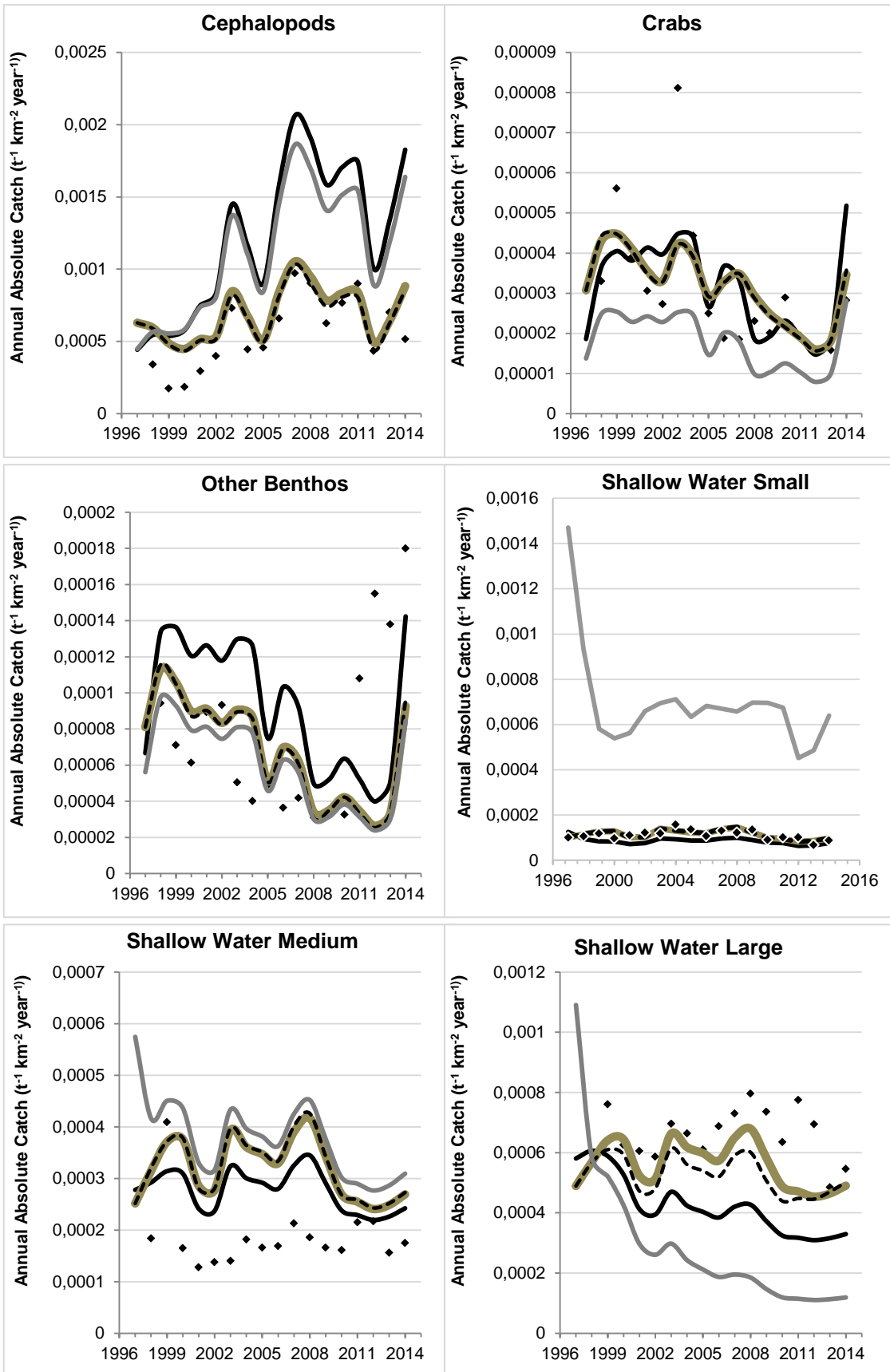
Figure 16 - Total annual relative catch predicted by the Azores Ecospace model (black line), Ecosapce Model 1 (grey line), Ecospace baseline (beige line) and the underlying Ecosim model (black dashed line) for the modelled period. The black dots represent the reference time series for the period 1997-2014.

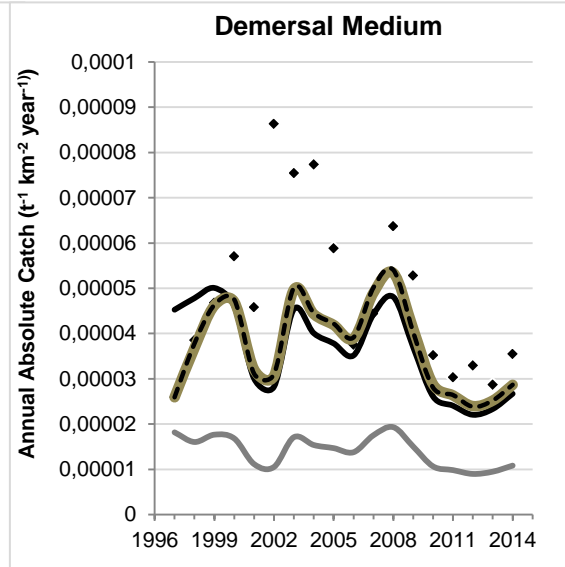
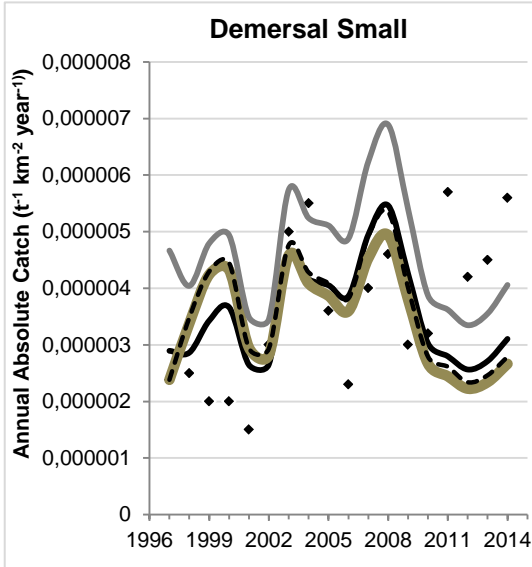
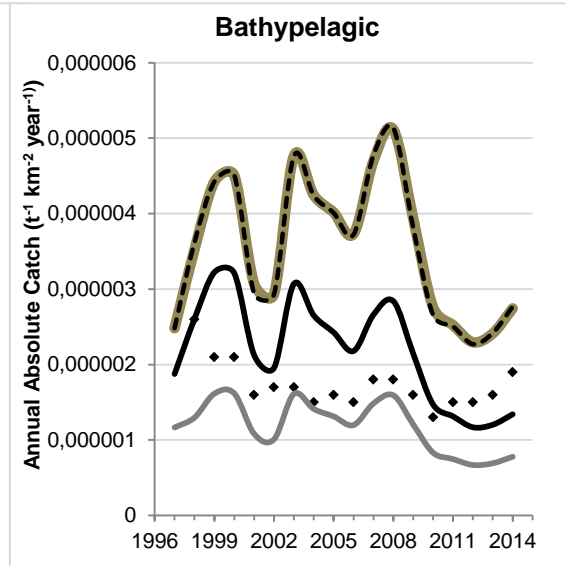
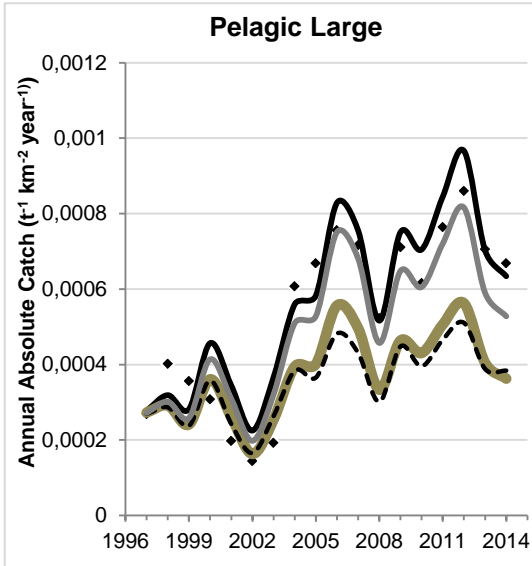
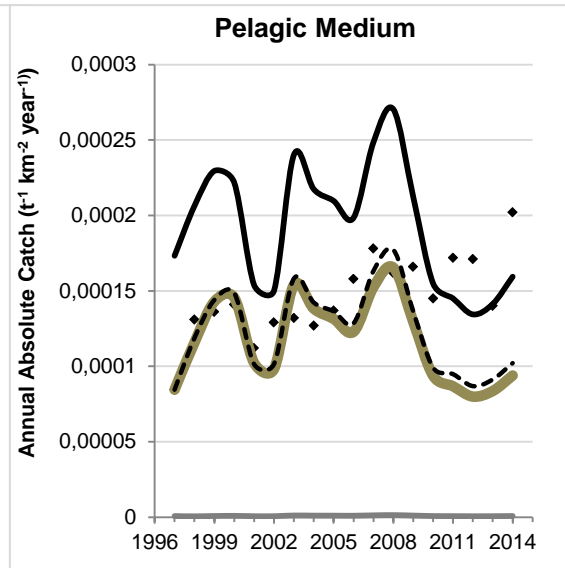
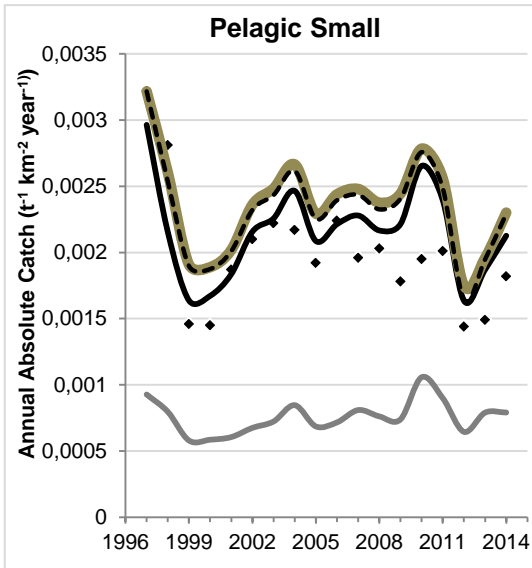
The transition from Ecosim to Ecospace (both Model 1 and Azores model) improved the catch fit of Pelagic Large, Bathypelagic, Bathydemersal Small, *Helicolenus d. dactylopterus*, *Conger conger*, *Beryx decadactylus* and *Pagellus boragaveo* (Figure 13). For the Pelagic Large group, both models followed the catch trends along the model period. For the Bathypelagic group, Model 1 was closer to represent the trends, although smoothly underestimated. On the other hand, the Azores Ecospace model overestimated the catch. The catch of *Helicolenus d. dactylopterus* was identically predicted by the two models, being the most difference observed during the first two years. The Ecospace model 1 overestimated the catch of *Conger conger* until 2008. The catch dropped from this year to the end of the model, reaching an underestimated minimum in 2012. The Azores model followed the same tendencies, but with more realistic annual values. For *Beryx decadactylus*, the predictions of the two models were very close, although the global trend of Model 1 was overestimated. Finally, for *Pagellus boragaveo* the Azores Ecospace and Model 1 were able to

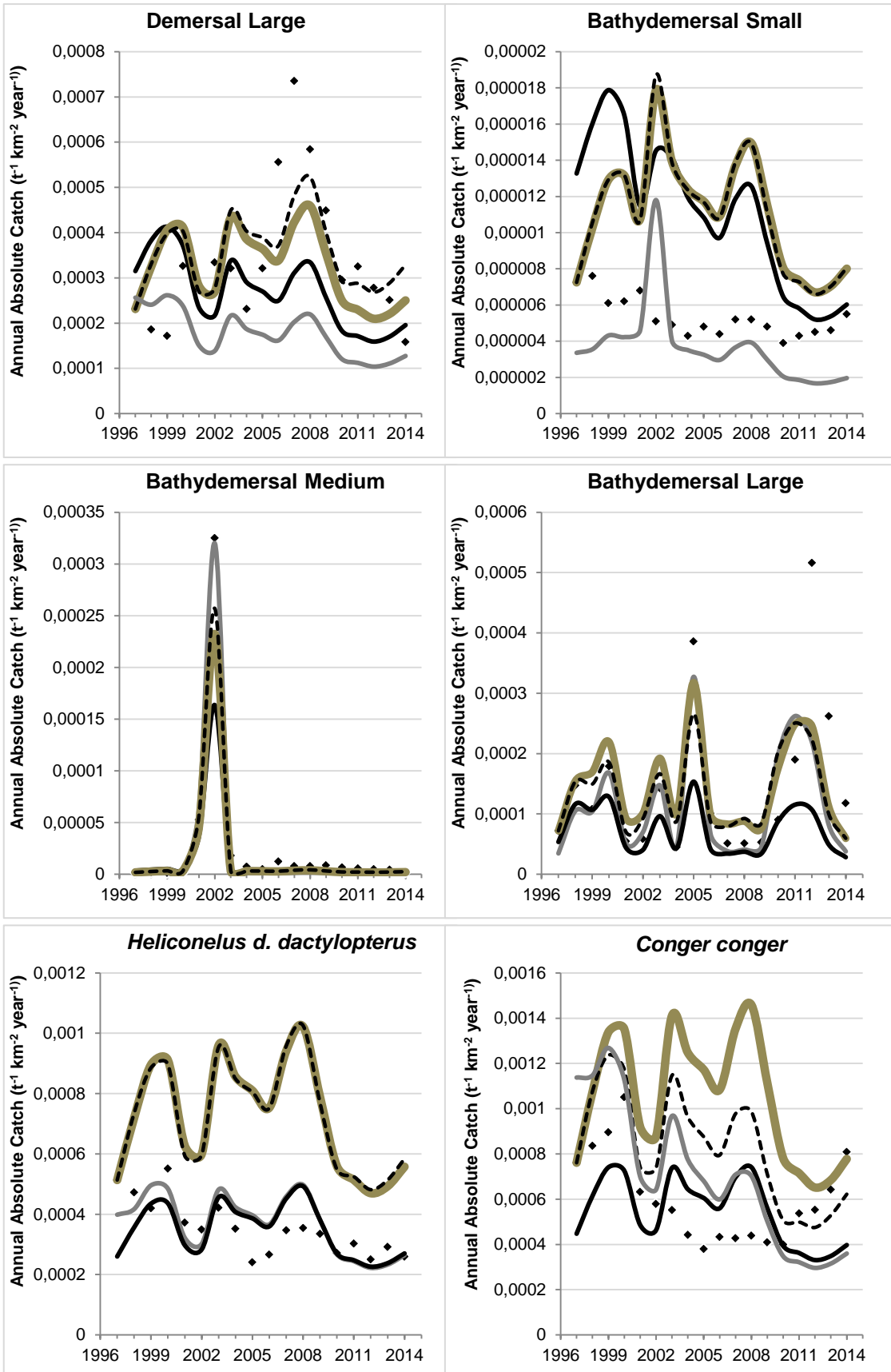
satisfactorily predict the catch trends observed in the last six years. Until this point the Azores model was the closest model to reality.

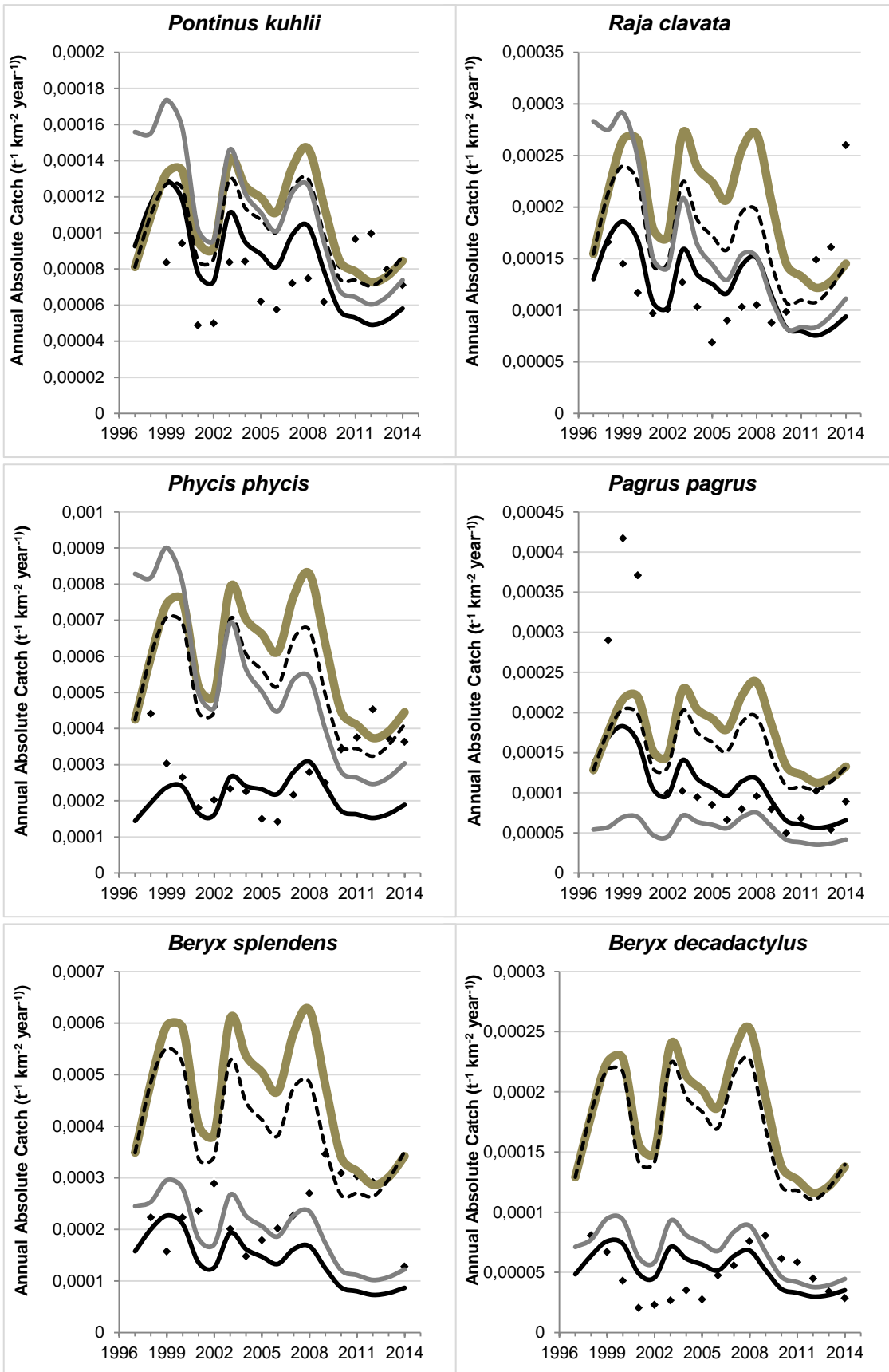
In opposition, the fit of Shrimps, Cephalopods, Crabs, Other benthos, Shallow Water Small and Large, Pelagic Medium, Demersal Medium, Demersal Large, Bathydemersal Medium and Large, *Mora moro*, Pelagic Sharks, Tunas and Turtles decreased with the transition to Ecospace (Figure 13). None of the models was able to replicate the catch tendencies of shrimps. Both models overestimated the catch of Cephalopods, Pelagic Medium, Pelagic sharks, Tunas and Other benthos during the majority of the model period. Nonetheless, for this last group, in the end of the simulation the predictions tended to meet the reference catch. The opposite was observed for Crabs, Demersal Medium and Large, Bathydemersal Large catch and *Mora moro*. The catch prediction of Tunas was considerably good by Model 1, but the Azores model overestimated the values. For turtles, both models exhibited a good fit during the overall period, but during the period 2005-2008, both models underestimated the catch.

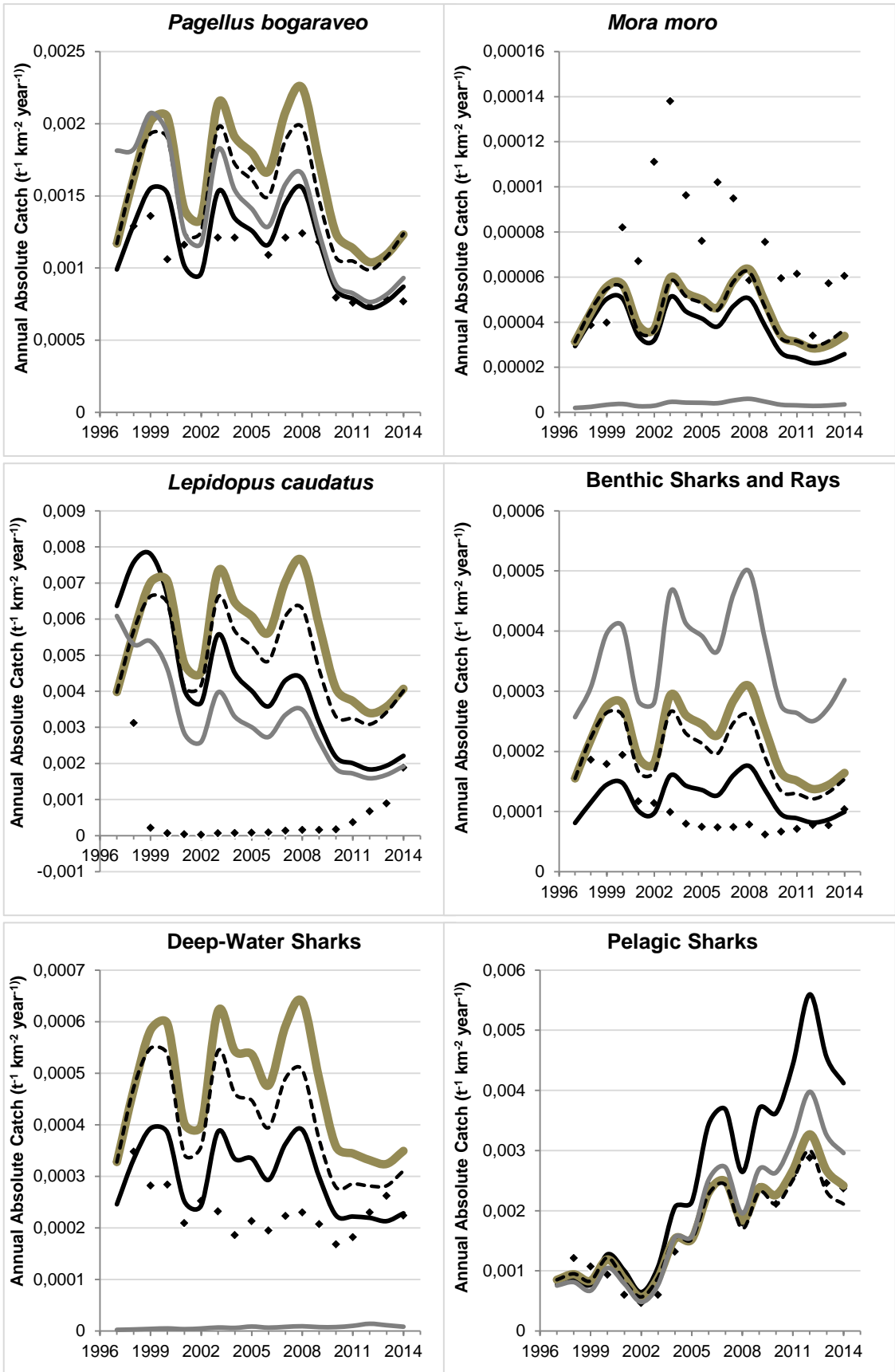












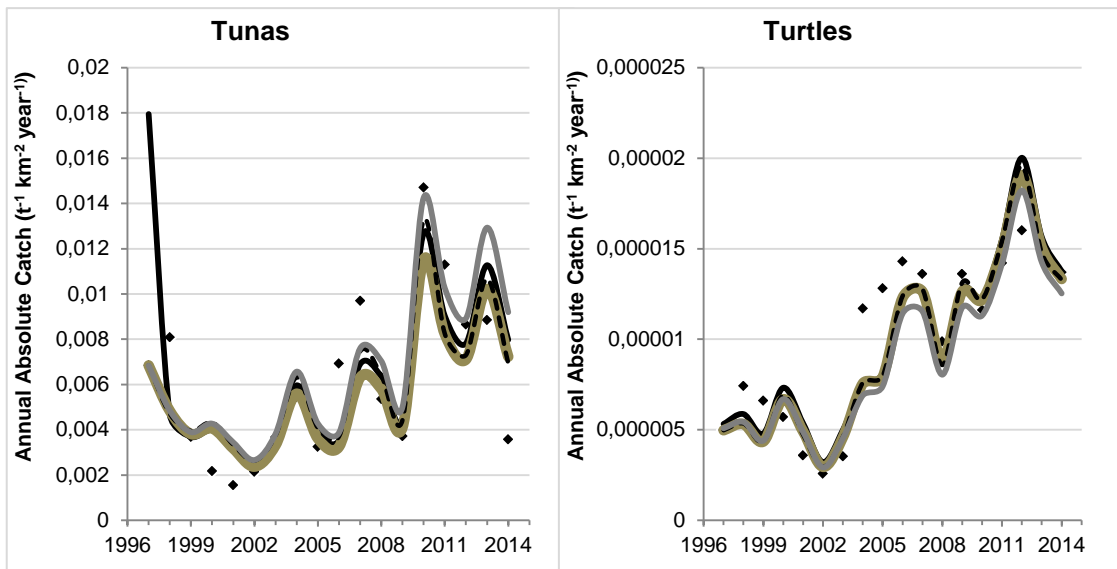


Figure 17 – Annual absolute catch predicted by the Azores Ecospace model (black line), Ecospace model 1 (grey line), Ecospace baseline (beige line) and the underlying Ecosim (black dashed line) per each functional group with reference time-series during the model period. The black dots show the reference time series.

3.4 Comparison between spatio-temporal predictions of Ecospace model 1 and Azores Ecospace model

Comparing the predictions of Model 1 and the Azores Ecospace, the adjustments made in the initial habitat foraging usage criteria of functional groups, improved the biomass fit of all groups, except the Shallow Water Medium, *Helicolenus d. dactylopterus*, *Beryx splendens* and *Pagrus pagrus* (Figure 12). The commercial species *Conger conger* was the group of which fit improved the most, while *Helicolenus d. dactylopterus* was the most negatively affected.

The spatial distribution of relative biomass map of the Shallow Water Medium Group illustrated that in the Azores model, the relative biomass in areas beyond the habitat buffer around the islands dropped, mainly around the central group of islands, promoting the decrement of biomass fit, comparatively to Model 1 (Figure 15 and 18). A similar pattern was observed in the distribution of *Pagrus pagrus*, which biomass suffered a considerable reduction in the areas beyond the buffer habitat, from the beginning to the end of the Azores spatial model (Figure 19). For the *Helicolenus d. dactylopterus*, both models predicted an increment of biomass in the end of the run (Figure 20). The adjustments, allocated the biomass fractions to more cells in the

Azores Model, which improved the conditions of this group to thrive. Consequently, in Azores model the relative biomass remained constant along the model period, while Model 1 predicted a drop that approximated this model to reality (Figure 15). An opposite pattern was observed for *Beryx splendens*. According to both models, the biomass of this group dropped from the beginning to the end of the simulation (Figure 21). The adjustments in the foraging arena of this group increased the number of cells available for this group, so the biomass drop in Azores Ecospace was more pronounced than in Model 1, which justifies the goodness of fit. The relative biomass of *Conger conger* predicted by the Azores Ecospace model remained stable from the beginning to the end of the modulation, while Model 1 predicted a considerable reduction of biomass in areas wherein 1997 the relative abundance was intermediate (Figure 22).

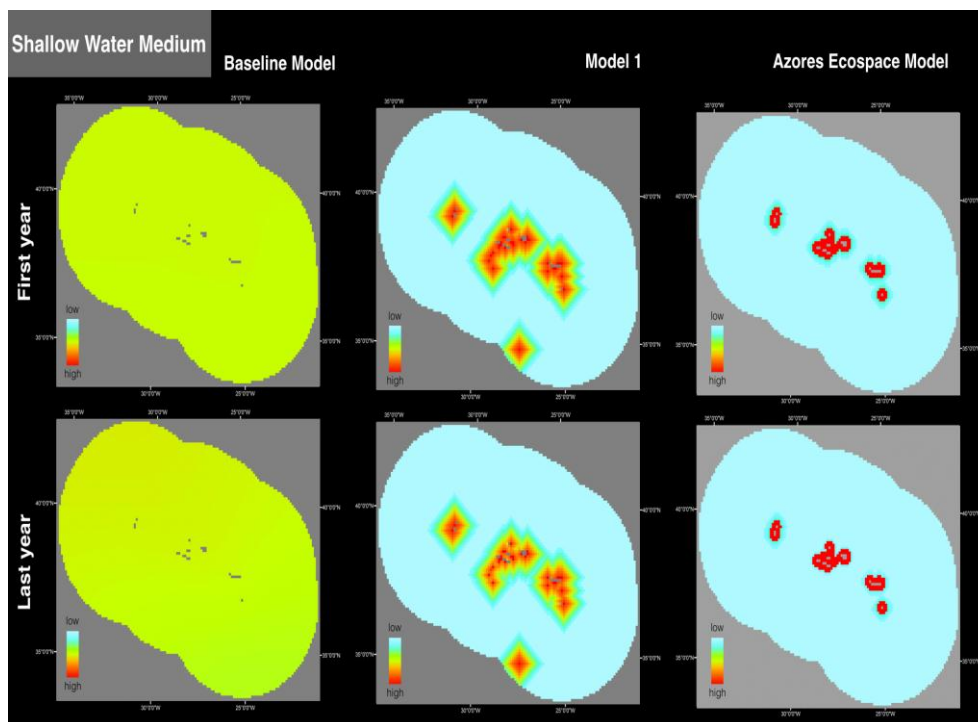


Figure 18 – Spatial distribution of relative biomass of the Shallow Water Medium functional group, predicted by the three Ecospace models, in the end of the first and the last year of the simulation (1997 and 2014).

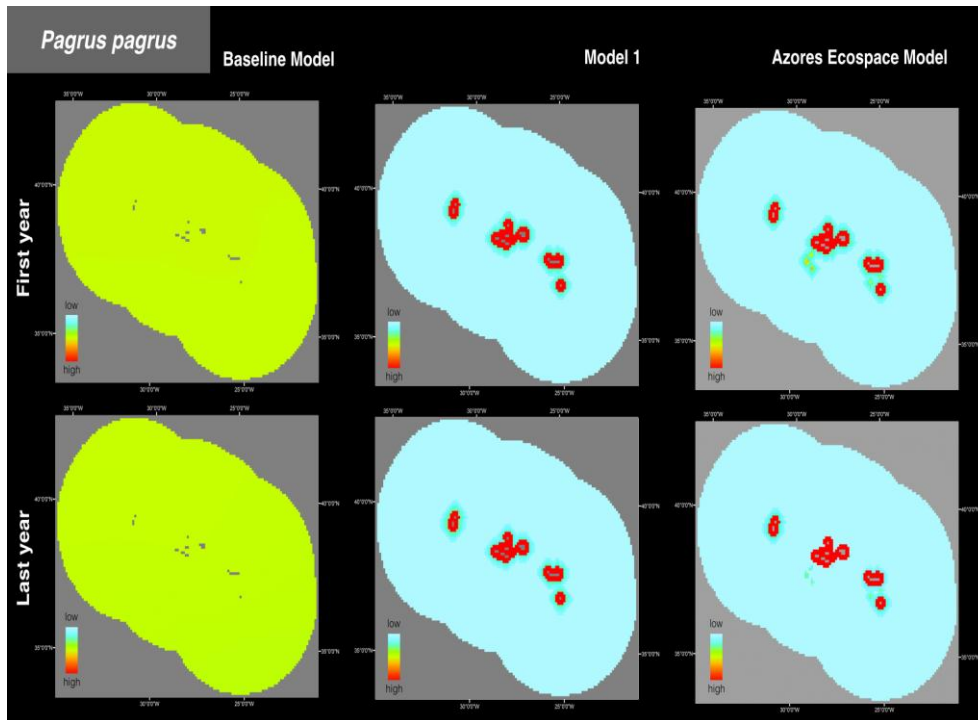


Figure 19 – Spatial distribution of relative biomass of *Pagrus pagrus* predicted by the three Ecospace models in the end of the first and the last year of the simulation (1997 and 2014)

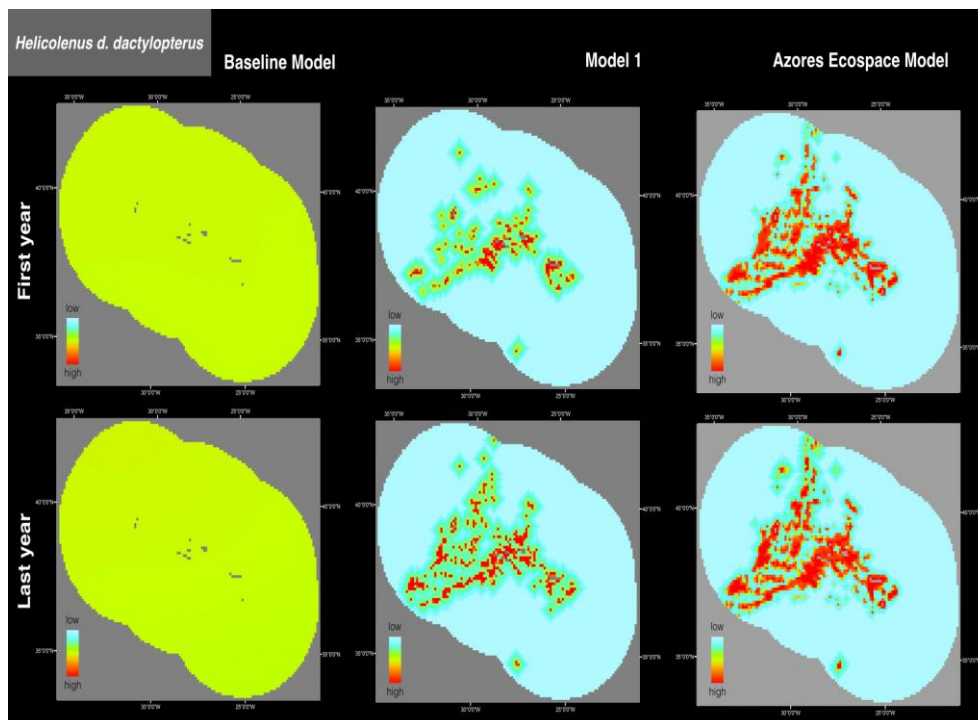


Figure 20 – Spatial distribution of relative biomass of *Helicolenus d. dactylopterus* predicted by the Ecospace Baseline, Ecospace Model 1 and the Azores Ecospace model, in the end of the first and the last year of the simulation (1997 and 2014)

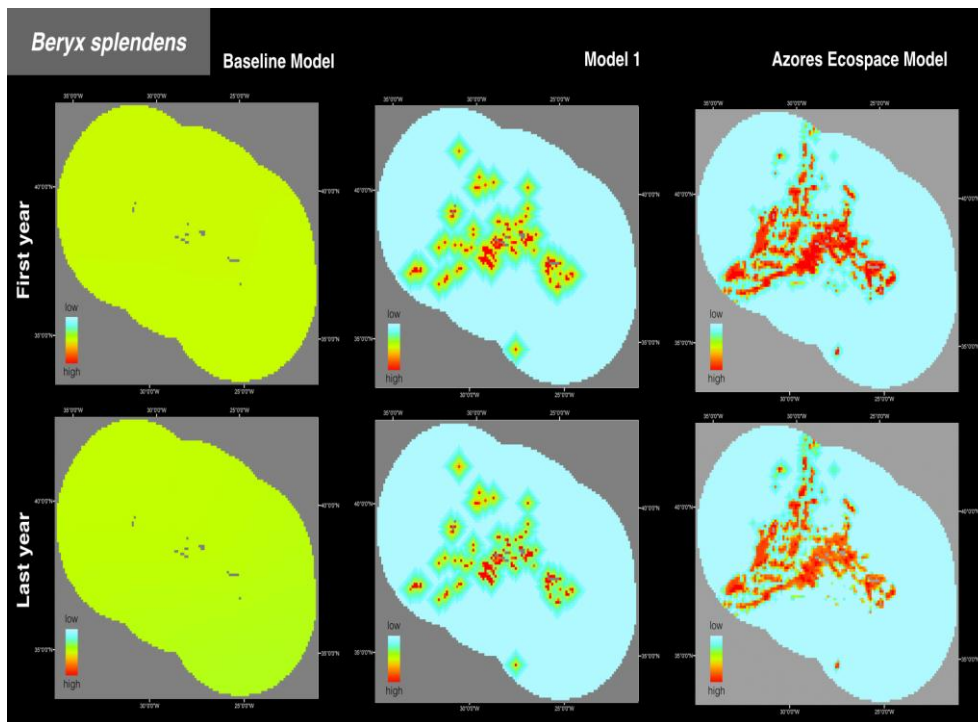


Figure 21 – Spatial distribution of relative biomass of *Beryx splendens* predicted by the Ecospace Baseline, Ecospace Model 1 and the Azores Ecospace model, in the end of the first and the last year of the simulation (1997 and 2014)

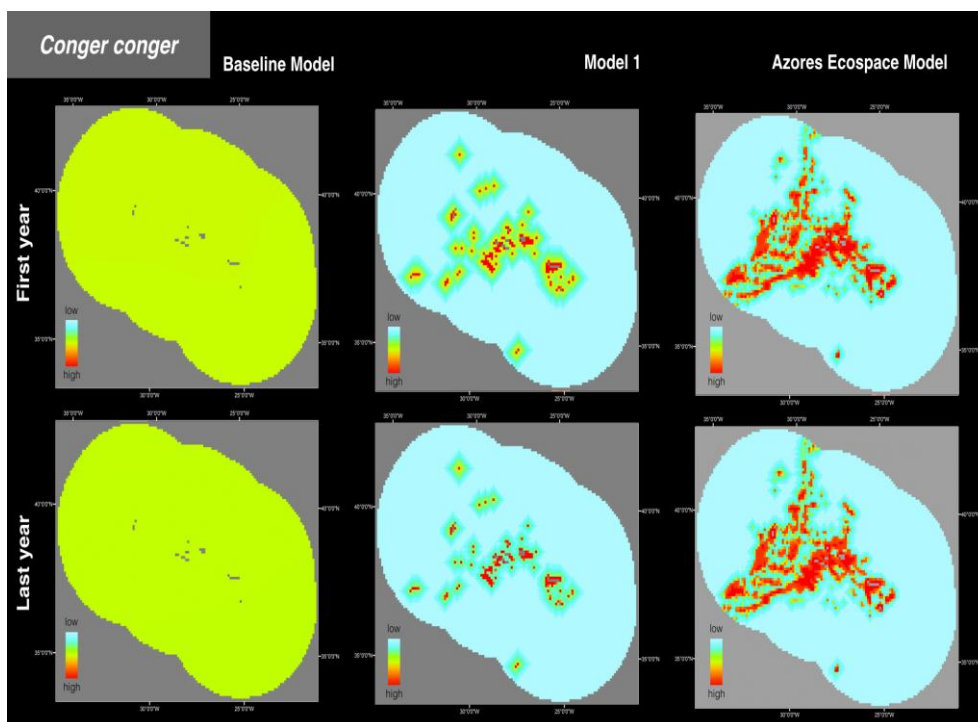


Figure 22 – Spatial distribution of relative biomass of *Conger conger* predicted by the Ecospace Baseline, Ecospace Model 1 and the Azores Ecospace model, in the end of the first and the last year of the simulation (1997 and 2014)

The greatest differences between the two spatial oriented models were though observed in terms of catch predictions of some groups, as the respective goodness of fit reflected. The groups Shallow Water Small, Pelagic Small, Pelagic Medium, *Mora moro* and Deep Water Sharks improved the fit in respectively, 96.9%, 97.5%, 99.4%, 93.9% and 99.1%, in the Azores Ecospace model (Figure 13). Except for the Shallow Water Small group, the catch predicted in Model 1 was very under estimated for these groups, comparing to the observed catch. The reason relied in the excessively big foraging arena of these groups, introduced by the profiles that defined the responses to depth in Model 1. Consequently, Ecospace distributed relatively small fractions of biomass per each grid cell wherein each of the mentioned group is more likely to occur, which diminished the intensity and concentration of predator-prey interactions at the local scale. The gravity model that spatially drives the fishing effort in Ecospace, then allocated very little effort to each cell in proportion to the few biomass available in that cell to fish. This relationship between allocation of fishing effort and available biomass is directly proportional once all exploited groups have the same economic value and fleets the same sailing cost (Villy Christensen et al., 2008, 2014).

The referred patterns were highly sharpened in the spatial distribution of relative biomass predicted by the two models of these organisms. In model 1, from the beginning to the end of the first year, the biomass fractions of Shallow Water Small were spread to a higher amount of cells, which enhanced the “attractiveness” to fish in those areas (Figure 23). By allocating the preferably foraging usage to the buffer around the areas, together with the input of a small fraction in the habitat “<400”, the Azores model intensified the trophic interactions to a smaller amount of cells, which balanced the fishing pressure o this group. For the Pelagic Small and Medium group (Figure 24 and 25), *Mora moro* (Figure 26) and Deep water sharks (Figure 27), the reduction of cells wherein the groups were more likely to occur, permitted the Azores Ecospace to allocate bigger fractions of biomass per each cell, which enhanced the catch of this group to quantities closer to the reference.

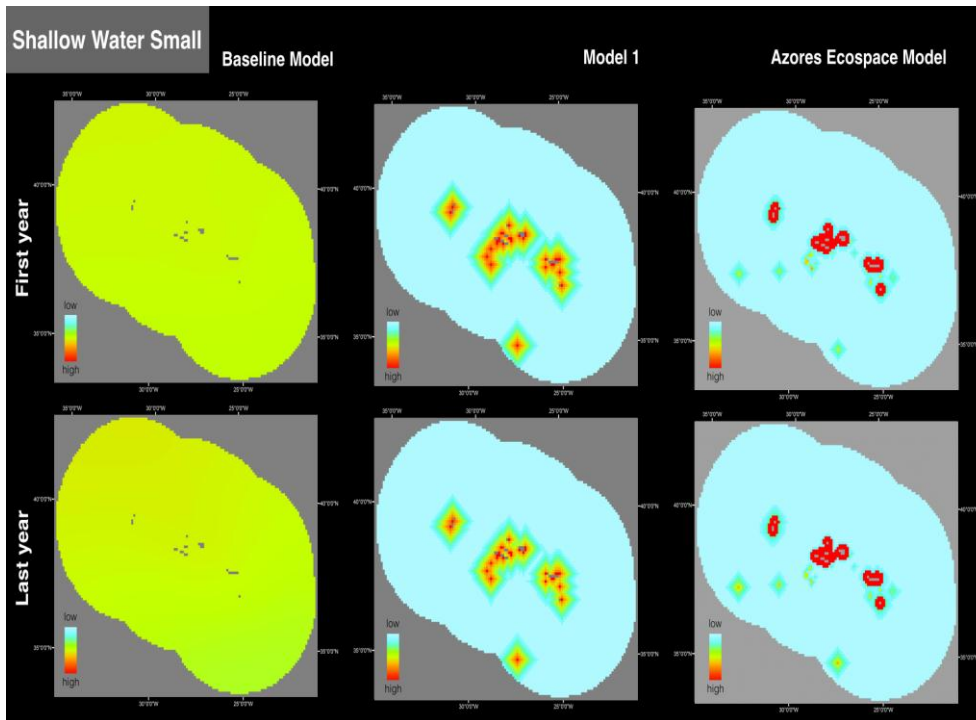


Figure 23 – Spatial distribution of relative biomass of Shallow water Small functional group predicted by the Ecospace Baseline, Ecospace Model 1 and the Azores Ecospace model, in the end of the first and the last year of the simulation (1997 and 2014)

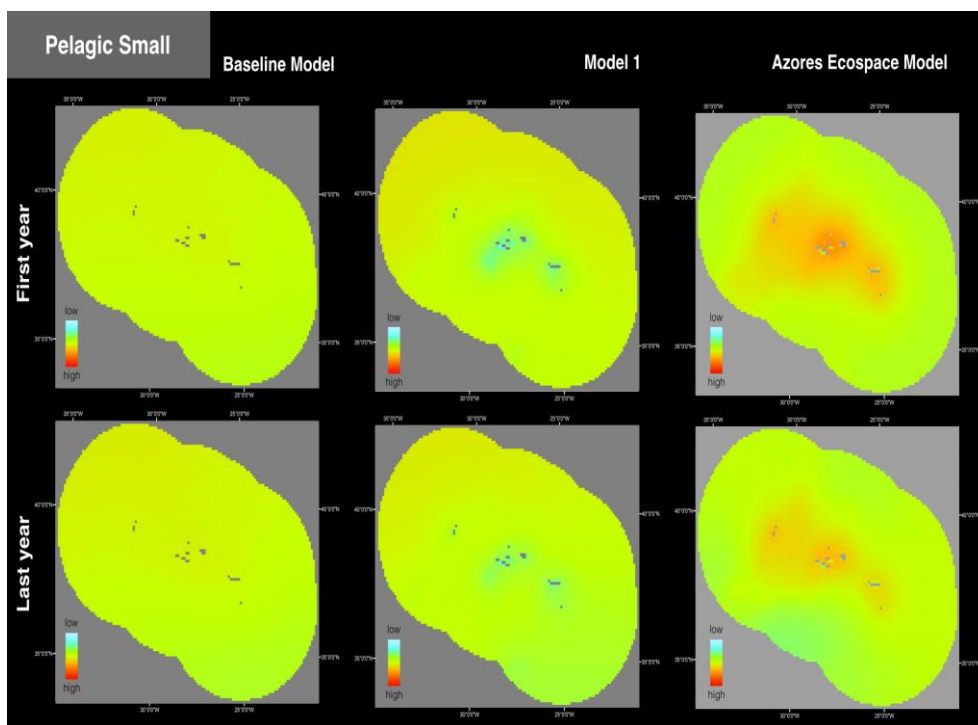


Figure 24 – Spatial distribution of relative biomass of Pelagic Small functional group predicted by the Ecospace Baseline, Ecospace Model 1 and the Azores Ecospace model, in the end of the first and the last year of the simulation (1997 and 2014)

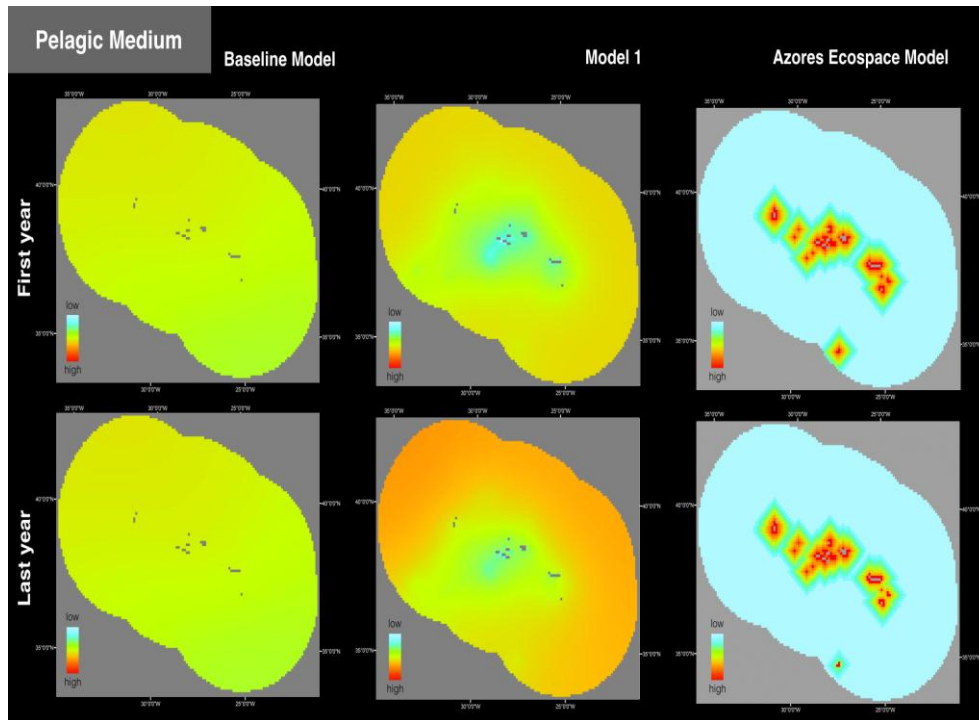


Figure 25 – Spatial distribution of relative biomass of Pelagic Medium functional group predicted by the Ecospace Baseline, Ecospace Model 1 and the Azores Ecospace model, in the end of the first and the last year of the simulation (1997 and 2014)

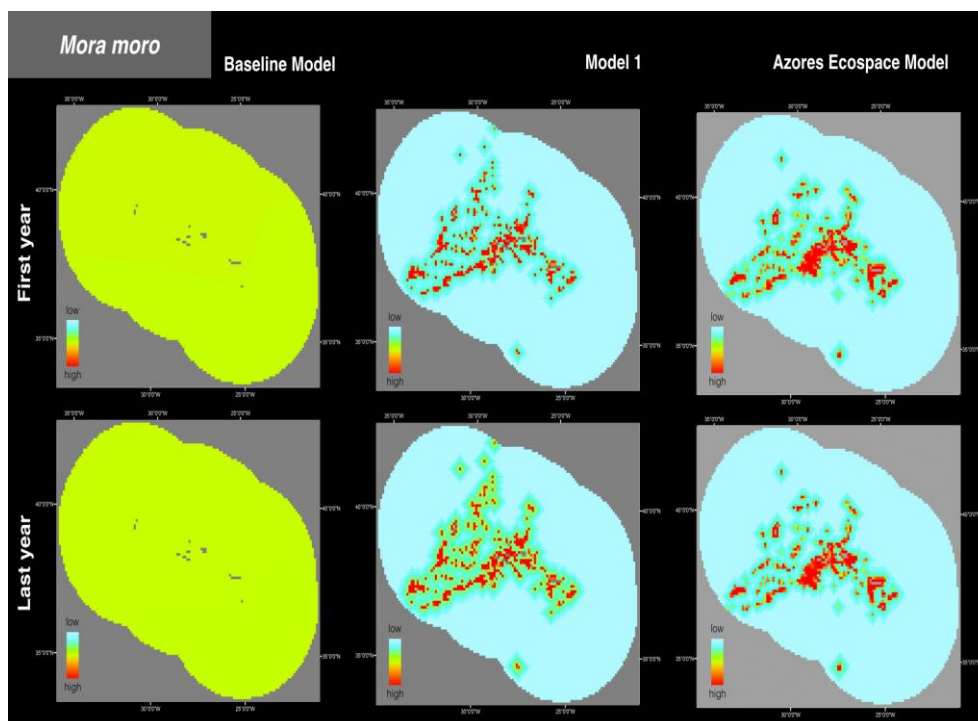


Figure 26 – Spatial distribution of relative biomass of *Mora moro* predicted by the Ecospace Baseline, Ecospace Model 1 and the Azores Ecospace model, in the end of the first and the last year of the simulation (1997 and 2014)

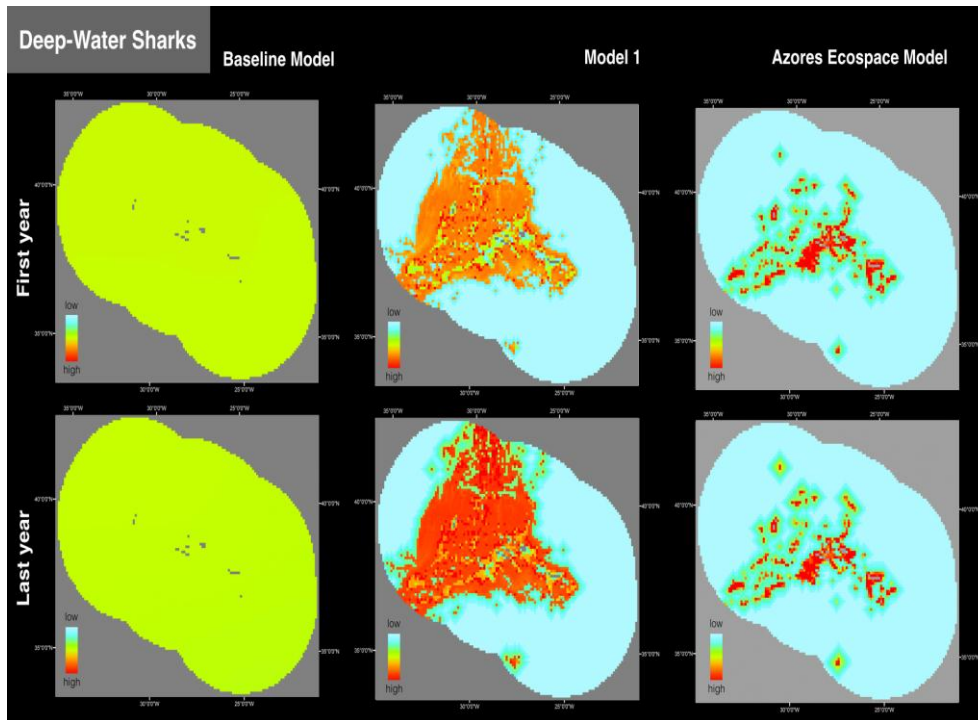


Figure 27 – Spatial distribution of relative biomass of Deep-water Sharks functional group predicted by the Ecospace Baseline, Ecospace Model 1 and the Azores Ecospace model, in the end of the first and the last year of the simulation (1997 and 2014)

4. DISCUSSION

The spatially oriented ecosystem based models developed in the present study were the first of its kind for the Economic Exclusive Zone of the Azores and are pioneer applications of the new habitat capacity model in Ecospace in a deep-sea ecosystem.

The approach remarked the importance to input local detailed spatial information to develop spatial-temporal explicit models that consider environmental drivers, human impacts and food web effects (Navarro, 2015). Additionally, the developed methodology addressed in the study emphasized how indispensable is to evaluate the sensitivity of an ecosystem model and deal with the associated uncertainty, particularly when the goal is to use it as a supporting tool in the decision-making processes of ecosystem-based management (Collie et al., 2014; Essington, 2014; Watters, 2013).

The Azores Ecospace model was able to simulate more realist trends of biomass and fishing catch fluctuations between 1997 and 2014 in the Azores, relatively to the temporal explicit-model. This result highlights that ecosystem models with the capability to include drivers that modify the intensity at which predator-prey interactions occur in spatial explicit contexts, enhances its performance to predict at the local scale, potentially impacts of fisheries in the structure and functioning of an ecosystem (Villy Christensen et al., 2014; Drexler, 2013; Grüss, 2014). Nonetheless, is important to remark that the reference data used to calibrate the fit of the spatial models was time-explicit, due to the lack of local spatial data with sufficient detailed resolution. (Coll, 2016) also faced the same problem regarding the validation of a similar modelling approach. The formal validation of model predictions, based on spatial-oriented data would considerably enhance the realism of the approach (Coll, 2015).

The transition from the temporal to the space-time dynamic model considerably improved the fit of the global model, particularly to high-valued commercial species in the Azores as the blackspot seabream (*Pagellus bogaraveo*), *bluemouth rockfish* (*Helicolenus d. dactylopterus*) and the functional group Pelagic Large that comprises the high exploited species *Xiphias gladius* (swordfish). Given the overall good fit, with special emphasis to the mentioned species, it is believed that the Azores Ecospace model could furthermore be used to perform spatial-oriented management simulations focus on these groups.

The biomass models prediction suggested that fisheries might not be the main driver promoting the biomass shifts observed during the modelled period. A good example to support the fact is the prediction of the most important commercial species

in the Azores, *Pagellus bogaraveo*, of which the goodness of fit was considerably good (both in terms of biomass and catch) but the biomass fluctuations were not replicated. The limitation of the spatial routine in incorporate the forcing functions prevents to inquire whether Northeast Atlantic regime shifts are the main drivers stimulating the oscillation trends. Nonetheless, despite the efforts to clearly understand how regime shift that change community compositions, species abundances and trophic structures of marine ecosystems, it stills unclear which are the main mechanisms responsible for its occurrence (Auber, 2015; Polovina, 2005). This uncertainty naturally delays the development of software routines capable to spatially simulate such environmental drivers. On the other hand, the degree of confidence in the biomass time series is not sufficiently high. None of the methods used to estimate abundances of fish are faultless, and longline surveys are particularly limited in providing absolute abundance estimates given the inherent difficulty to estimate the total area exploited by the gear (Engås and Løkkeborg, 1994). Plus, a considerable biases might be introduced in the method, concerning the processes adopted to attract and defiantly hook the fishes. Concluding, a special precaution must be taken when it comes to evaluate the performance of the model in estimate the observed biomass shifts mainly, due to the uncertainty associated to the reference data and the inherent difficulty to specify which mechanisms influence the most the occurrence of biomass shift in marine ecosystems (DeYoung, 2004).

The most notable improvements of the Azores Ecospace model, were notably for the catch term, for which the model satisfactorily replicated the annual trends of the groups that globally improved the fit relatively to Ecosim. It is likewise important to note that in comparison to the biomass reference data, the time series of catch is highly reliable (Pham et al., 2013), which relatively decreases the global uncertainty associated with the modelling approach. Nonetheless, it is recommended to re assess the foraging usage of the species for which the habitat preferences were based on empirical-knowledge, in order to increase its reliability and consequently goodness of fit (Carl Walters et al., 1999). Desirable would also be the evaluation of model predictions under the input of differential dispersal rates to distinguish the performance of some groups to escape from predation (where fisheries are included) based on the swimming speed (He, 1993; Killen, 2015; Lundvall, 1999).

The goodness of fit analysis submitted that the method used to estimate the goodness of fit, through evaluation of sum of squares deviation, should in the future be complemented with another statistical measure. The logarithmic nature of the

calculation stretches more importance to small deviations rather than great divergences from the reference data. In doing so, it is suggested further analysis of model fit that include for instances, assessments of correlation coefficient between predictions and observations (Romagnoni et al., 2015).

The calibration approach guided by the evaluation of models fit revealed to be a useful tool to highlight particular considerations to have in further model updates. It was expected that the Ecospace Baseline model would have exactly the same fit as Ecosim, which was not observed. This result helped to alert that Ecospace takes several time-step until reach an equilibrium point (Romagnoni et al., 2015) and probably the models of this study would require more time to balance the Ecosim equations in each grid cell. Future version of the model should then include a burn-in period, for instances with the same extension of the time series, with data set equal to the reference year.

The evaluation of Ecospace models fit featured that the method used to build the responses to depth of *Mora moro* and Deep-water Sharks, based on standardized catch per unit effort of depth strata, might not be the most appropriated for this modelling approach. These are the modelled species with deepest habitat preferences, reaching depths considerably above 1000 meters (Menezes et al., 2006). The depth profiles built for these top predators, although capture group's preferences, assumed depth ranges that start in shallow waters (around 150 meters), since occasionally individuals were caught at this depth. If in one hand, the spatial distribution of relative biomass predicted by the model with the responses to depth might be more detailed than model predictions that constrained the groups to specific depth ranges, the catch trends might be considerably under estimated whether the foraging arena is overly large. Such limitation influences the credibility of the model to perform management scenarios evaluation. The introduction of economic-related parameters, such as the market value of *Mora moro* and Deep Water Sharks groups, and sailing costs of fleets, could increase the attractiveness of these species, with a relative big foraging arena, to be fished and consequently improve the fit of the catch.

The most critical future steps in model development should comprise the validation of the spatial distributions of species predicted by the models, to have a formal clue of which method to introduce habitat preferences in Ecospace more closely meets the reality in the ecosystem of the Azores. One approach could be the comparison of the spatial predictions of the Ecospace models with generalised additive models built by Parra et al. 2016 to evaluate the presence-absence and relative abundance to

depth and other environmental variables of commercial important species in the EEZ of the Azores (*Beryx decadactylus*, *Beryx splendens*, *Pagrus pagrus*, *Pontinus kuhlli*, *Pagellus bogaraveo*, *Helicolenus d. dactylopterus* and *Phycis phycis*). Additionally Diogo et al. 2015 reconstructed the historical spatio-temporal patterns of fishing effort and landings in the bottom longline fishery of the Azores for the period 1998-2012. A formal comparison between the results of this study with the spatial distribution of the same fleet predicted by Ecospace could be useful to evaluate the performance of the gravity model to spatially distribute the effort of the most important fleet of the Azores (Villy Christensen et al., 2008).

The present study constitutes the first stage in the process forward the usage of spatially oriented ecosystem based models to assist the implementation of an ecosystem-based fisheries management approach, through marine spatial planning in the archipelago of the Azores. The exercise conducted in this study allowed to improve the empirical knowledge on the modelling approach and to understand the model behaviour under the context of the marine ecosystem of the Azores. Whether the considerations described above, regarding the model fragilities, and the recommended model validations will be taken into account, it is believed that particularly the Azores Ecospace model will be satisfactorily fit to explore the outcomes of different management scenarios in the spatial dynamic of the marine ecosystem of the Azores.

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6. APPENDICES

Appendix I – Functional groups defined for the ecosystem model of open-ocean and deep-sea environments of the Azores

(Description performed by Emile Lemey and adapted by Ambre Soszynski, for the development of the Ecopath with Ecosim model of the Azores in the context of their master thesis)

1.1. Phytoplankton

Santos et al. (2013) evaluated phytoplankton biomass variability and community structure for the Condor seamount in the Azores EEZ. The phytoplankton community is very diverse and show strong seasonal variation, with mainly Diatoms (*Pseudo-nitzschia* spp. and *Chaetoceros* spp.), Dinoflagellates (e.g. *Ceratium* spp.) and Coccolithophores (e.g. *Ophiaster* spp.) present. Highest abundances occurred in March (winter/spring), while lower abundances were noted in November (autumn). A complete list of the identified phytoplankton taxa for the condor seamount is presented in Santos et al. (2013). Due to lack of other data, a phytoplankton biomass estimate of 2.9 t WW/km² was taken from the Ecopath model of the condor seamount (Bon de Sousa, 2012), assuming the condor seamount to be representative for the Azores EEZ zone. The author made a depth integration of Chlorophyll a concentrations of different depths as presented in Lambardi et al. (2011), and used conversion factors of 1 g Chla for 32 g of carbon (Fasham et al., 1985) and 10 g wet weight (WW) for each gram of carbon (Pauly and Christensen, 1995) to calculate the final estimated phytoplankton biomass.

Daily net primary production standard product data was provided by Ocean Productivity and was processed to annual mean values (g.C.m⁻².yr⁻¹) by Patrícia Amorim. These annual mean values were then converted into wet weight through the same conversion factor used for the biomass estimation (Pauly and Christensen, 1995). An average of 1671.2 t WW/km²/yr was obtained for the years 2003-2007, and using the biomass estimate of 2.9 t WW/km² used previously, the P/B ratio equals 576.3 year⁻¹. The phytoplankton communities are present within the whole model area, so the habitat fraction area is set at 1.

1.2. Macro-algae

The Azorean algal flora mainly inhabit the shallow rocky subtidal zone (0–50 m) around the islands. Neto (2001) studied the benthic algal communities of two subtidal sites on opposite coasts of the São Miguel Island in the Azores archipelago. *Corallina* spp. and other red algae such as *Pterocladia capillacea* were the most abundant species at the 5m subtidal zone, while brown algae such as *Zonaria* and *Stypocaulon* dominated at 15m. A full list of macro-algal species is provided by the author (Neto 2001). The same author investigated algal density and reported an average density of 500-600 g dry weight/m² for the shore of São Vicente (Neto, 1997). Using a ratio of 0.21 g dry weight for each gram of wet weight (Mackinson, 1996), this resulted in a

biomass estimate for the inhabitable area of 2619 t/km². Due to lack of data, the P/B of 4.34 for benthic plants, presented in the Strait of Georgia model (Canada) was used (Mackinson, 1996). Half of the 0-50m depth range is assumed to be inhabitable for algal species, amounting to a total of 331 km² of potential algae beds, and thus a habitat fraction area of 0.00035 is used.

1.3. Small zooplankton

Small zooplankton communities over and around the Condor seamount, collected in the first 100m of the water column, were recently characterized (Lambardi et al., 2011). The author reported that the communities showed significant variation in diversity and abundance among and between seasons. Maximum abundance (2.41 individuals.L-1) and biomass (57.47 mg.m-3) together with lowest taxonomical diversity (95% of copepods) was registered in March, while lower levels of abundance and biomass were registered in August and November. Copepoda Calanoida and Copepoda Poecilostomatoida were most abundant year-round, and form together with Chaetognata, Appendicularia and Cladocera the most abundant zooplankton groups. Bivalve larvae, Radiolaria, Copepoda Cyclopoida, Ostracoda, Appendicularia and Doliolida were among the lesser abundant taxa identified in the Condor Bank area. The Condor seamount zooplankton community is considered as representative for the zooplankton community in the entire model area. These zooplankton groups are considered to inhabit the whole model area, thus the habitat fraction area is set at 1 for both.

The small zooplankton group was mainly made up of copepods, radiolaria, ostracoda, appendicularia and doliolida. A P/B of 11.2 and a Q/B of 43.3 was taken from Morato et al. (2009). EE was set at 0.9. Diets for the small zooplankton group was taken from Guenette and Morato (2001) and consists of 90% phytoplankton and 10% detritus.

1.4. Zooplankton

This group consists of large and gelatinous zooplankton. Gelatinous zooplankton consists mainly of thaliacea, hydrozoa and scyphozoa, while the large zooplankton consists amongst others of mysids, euphausiids, chaetognaths and decapods' larvae (Morato and Pitcher, 2002). P/B and Q/B for the large and gelatinous functional zooplankton groups, as presented in Morato et al. (2009), were averaged to respectively 4.8 and 15.5 year-1. Diet for the zooplankton group was also averaged from the large and gelatinous zooplankton groups in Morato et al. (2009). Consequently the resulting zooplankton group is assumed to feed 50% on detritus, 10% on phytoplankton, 20% on small zooplankton, 15% large and gelatinous zooplankton (cannibalism), and 5% on shrimps. This diet was modified to 30% feeding on phytoplankton, 50% on small zooplankton, 15% on detritus, and 5% of cannibalism, based on empirical knowledge.

1.5. Shrimps

The groups of shrimps includes pelagic and benthic shrimps such as *Acantheephyra purpurea*, *Systellapsis debilis*, *Oplophorus spinosus*, *Ligur ensiferus*, *Plesionika narval*, *Plesionika edwardsii*, *Plesionika williamsi*, *Plesionika martia*, *Plesionika gigliolii*, *Plesionika ensis*, *Heterocarpus laevigatus*, *Heterocarpus ensifer*, *Heterocarpus grimaldii*, *Parapasiphae sucatifrons* and *Funchalia villosa* (Martins and Hargreaves,

1991; D'Udekem D'Acoz et al., 2001 and De Girolamo et al., 2011). Some Palaemonid shrimps are commercially harvested (Pham et al., 2013). P/B and Q/B values were taken from Morato et al. (2009) and were equal to 1.5 year⁻¹ and 9.7 year⁻¹. The shrimp species are expected to inhabit the total EEZ area, and the habitat fraction area is thus set at 1. Diet for the shrimp group was taken from Guenette and Morato (2001) and averaged for the benthic and pelagic shrimps. The resulting diet is 38% small zooplankton, 25% large zooplankton, 25% phytoplankton and 13% detritus.

1.6. Cephalopods

This group consists of the highly exploited cephalopod species *Loligo forbesii* and *Octopus vulgaris*, together with the commercially less important species *Ommastrephes bartramii*, *Pteroctopus tetracirrhus* and *Scaevargus unicirrhus*, and a number of small and large non-commercial cephalopods among which Chiroteuthidae, Enoploteuthidae, Ommastrephidae, Octopoteuthidae and Histioteuthidae spp. (Clarke, 1993 and Pham et al., 2013). The values of P/B and Q/B were calculated from Morato and Pitcher (2009) by averaging the groups of resident, drifting small, and drifting large cephalopods, used in the model. The estimated values for P/B and Q/B amounted to 3.28 year⁻¹ and 12.29 year⁻¹. Different cephalopod species can inhabit both the shallow and deeper parts of the model area and the habitat fraction area will be set at 1. The diet for the cephalopods was averaged from the same three cephalopod groups (resident, drifting small and drifting large), this time used in Morato et al. (2009). The resulting diet is 8% small zooplankton, 25% large zooplankton, 10% shrimps, 3% crabs, 2% shallow water small fish, 3% pelagic small fish, 22% mesopelagic fish, 7% bathypelagic fish, 10% bathydemersal fish and 10% detritus.

1.7. Crabs and lobsters

This groups includes the commercial lobster species *Palinurus elephas* and *Scyllarides latus*, and the not commercially important *Scyllarus arctus*. The group is further made up by the moderate commercially important crab species *Maja squinado*, *Grapsus grapsus*, *Cancer bellianus*, *Paromola cuvieri*, *Chaceon affinis*, *Scyllarides latus* and *Dardanus callidus* and a few non-commercial shallow and deep-sea crab species (e.g. *Cryptosoma cristata*) (Paula et al., 1992; Pham et al., 2013). The P/B of 1.6 year⁻¹ and Q/B of 10 year⁻¹ for the crabs and lobsters group were obtained from Morato and Pitcher (2002). The crabs and lobsters groups include both shallow and deep-sea species and thus the habitat fraction area will be set at 1. The diet for the crabs and lobsters was taken from Guenette and Morato (2001) and consisted of 3% shrimps, 3% crabs, 5% benthic filter feeders, 7% other benthos, 3% benthic worms and 79% detritus.

1.8. Benthic filter feeders

Benthic filter feeders are regular bycatch of the bottom longline fishery of the Azores (Pham et al., in press). The group is made up of species belonging to four phyla (Porifera, Bryozoa, Cnidaria and Foraminifera) and includes cold-water-corals such as Anthozoans and Hydrozoans (e.g. *Lytocarpia myriophyllum*). The P/B and Q/B were taken from Morato and Pitcher (2002), from estimates based on sponges and corals, and equal to 0.8 year⁻¹ and 9 year⁻¹. Benthic filter feeders are assumed to be able to inhabit the complete model area, thus the habitat fraction area is set at 1. The diet for benthic filter feeders was also taken from Morato and Pitcher (2002), and consisted of 25%

phytoplankton and 75% detritus. This diet composition was modified to 10% phytoplankton, 5% small zooplankton and 85% detritus, because this group is mainly made up of deepwater corals occurring below the photic zone.

1.9. Benthic worms

The benthic worms functional group consists of Polychaetes and Annelida species. P/B and Q/B for this group were taken from the EwE model of the deep-water fisheries (400-2000m) in ICES Division VIa (Howell et al., 2009), and equal respectively 2.3 and 14.4 year⁻¹. The habitat fraction area fraction is set at 1, as it is assumed that the Polychaetes and Annelida species occur in the whole model area. Diet for this group was taken from Guenette and Morato (2001) and consists of 20% small zooplankton and 80% detritus.

1.10. Other benthos

This group includes crustaceans (e.g. the commercially important *Megabalanus azoricus*), echinoderms (e.g. *Hippasteria* spp.), bivalves (e.g. *Neopycnodonte zibrowii*) and gastropods (e.g. the commercial *Patella* spp., *Haliotis tuberculata* and *Murex trunculus*) (Morato et al., 2001; Pham et al., 2013). In absence of local data, the P/B and Q/B of resp. 3 year⁻¹ and 10 year⁻¹ were taken from the P/B and Q/B for benthic invertebrates used in the EwE model of the deep-water fisheries (400-2000m) in ICES Division VIa (Howell et al., 2009). The other benthos group includes both shallow as deep-water species, and the habitat fraction area is thus set to 100% of the model area. The diet of other benthos was obtained from Guenette and Morato (2001) and consisted of 1% other benthos, 1% benthic worms, 0.2% macroalgae, 1.8 % phytoplankton, 15% small zooplankton and 81% detritus.

1.11. Small shallow water fish

This group consists of the shallow water species with an asymptotic length smaller than 25 cm. The shallow water small fish group includes amongst others: *Chelon labrosus*, *Scorpaena scrofa*, *Boops boops*, *Scorpaena maderensis*, *Parablennius ruber*, *Coris julis* and *Echiichthys vipera*. The shallow water small fish are mainly targeted by bottom longline/handline fishery with *Chelon labrosus*, *Scorpaena scrofa*, *Boops boops* and *Scorpaena maderensis*, the main commercial species in this group. A Q/B of 8.3 year⁻¹ was calculated for this group, and a P/Q value of 0.3 was taken from Darwall et al. (2010). The shallow water small fish group is assumed to only occupy the 0-100m depth layer of the model area, amounting to a habitat fraction area of 0.0014. The diet for this group was taken from Guenette and Morato (2001), and is made up of 2% phytoplankton, 20% algae, 15% small zooplankton, 5% large and gelatinous zooplankton, 3% shrimps, 8% crabs, 19% benthic worms, 33% other benthos, 7% shallow water small fish (cannibalism) and 1% detritus.

1.12. Medium shallow water fish

This group consists of shallow water fish species with an asymptotic length larger than 25 cm and smaller than 44 cm. *Diplodus sargus sargus*, *Balistes caprisicus*, *Xyrichtys novacula*, *Mullus surmuletus*, *Pagellus acarne* and *Bodianus scrofa* are the most abundant species in this group. *Diplodus sargus sargus* and *Balistes caprisicus* are the

two most commercially important fish in this group, and are caught by both the recreational and bottom longline/handline fisheries. A Q/B of 6.3 year-1 was calculated for this group, and a P/Q value of 0.2 was taken from Darwall et al. (2010). The shallow water medium fish group is assumed to only occupy the 0-100m depth layer of the model area, amounting to a habitat fraction area of 0.0014. The initial diet for this group was adopted from Guenette and Morato (2001) and consists of 8% phytoplankton, 1% large and gelatinous zooplankton, 3% shrimps, 12% crabs, 1% benthic filter feeders, 7% benthic worms, 25% other benthos, 10% shallow water small fish, 7% shallow water medium fish, 2% mesopelagic fish, 15% demersal small fish and 9% detritus.

1.13. Large shallow water fish

This groups includes amongst others moray eel species like *Muraena helena* and *Gymnothorax unicolor*, and other shallow water fish species with an asymptotic length larger than 44cm, including *Sparisoma cretense*, *Serranus atricauda*, *Pseudocaranx dentex*, *Epinephelus marginatus*, *Labrus bergylta* and *Sarpa salpa*. *Sparisoma cretense*, *Serranus atricauda*, *Pseudocaranx dentex* and *Muraena helena* are the four most commercial species in this group, and they are targeted by the recreational and bottom longline/handline fisheries. A Q/B of 4.4 year-1 was calculated for this group, and a P/Q value of 0.1 was taken from Darwall et al. (2010). The shallow water large fish group is assumed to only occupy the 0-100m depth layer of the model area, amounting to a habitat fraction area of 0.0014. The diet for this group was calculated based on Guenette and Morato (2001), and consists of 11% macroalgae, 3% large and gelatinous zooplankton, 7% shrimps, 8% cephalopods, 13% crab, 3% benthic worms, 15% other benthos, 16% shallow water small fish, 6% shallow water medium fish, 0.2% shallow water large fish (cannibalism), 10% demersal small fish, 7% demersal medium fish and 1% detritus. However, based on empirical knowledge, and 1% was assigned to *Phycis phycis*. To account for this, the total added diet percentages was deducted from the original diet constituents.

1.14. Small pelagic fish

This groups consists of the epipelagic species with an asymptotic length smaller than 53 cm. The species of this group are: *Trachurus picturatus*, *Sardina pilchardus*, *Scomber colias*, *Scomberesox saurus saurus*, *Atherina presbyter*, *Engraulis encrasicolus* and *Cubiceps gracilis*. *Trachurus picturatus*, and *Sardina pilchardus* are the only commercial species in this group, and are caught by the recreational, pole and line livebait, small pelagics and bottom longline/handline fisheries. A Q/B of 9.5 year-1 was calculated for this group, and a P/Q value of 0.3 was taken from Darwall et al. (2010). The small pelagic fish group is assumed to occupy the entire model area, so the habitat fraction area is set at 1. The small pelagic fish group's diet was obtained from Guenette and Morato (2001) and consists of 24% phytoplankton, 33% small zooplankton, 21% large and gelatinous zooplankton, 6% shrimps, 1% cephalopods, 6% crabs, 8% other benthos and 2% small pelagic fish (cannibalism).

1.15. Medium pelagic fish

The medium pelagic fish group consists of the epipelagic species larger than 53 and smaller than 100 cm. The species belonging to this group are: *Sphyraena viridensis*, *Pomatomus saltatrix*, *Pterycombus brama*, *Sarda sarda*, *Seriola dumerili*, *Seriola*

rivoliانا and *Trachinotus ovatus*. *Sphyraena viridensis*, *Pomatomus saltatrix* and *Sarda sarda* are the most important commercial species of this group. They are mainly targeted by the recreational and bottom longline/handline fleets. A Q/B of 4.3 year-1 was calculated for this group, and a P/Q value of 0.2 was taken from Darwall et al. (2010). The medium pelagic fish group is assumed to occupy the entire model area, so the habitat fraction area is set at 1. The diet for this group was taken from Guenette and Morato (2001) and is composed of 3% phytoplankton, 1% small zooplankton, 2% large zooplankton, 3% shrimps, 2% cephalopods, 1% benthic worms, 5% other benthos, 2% small shallow water fish, 1% medium shallow water fish and 80% small pelagic fish.

1.16. Large pelagic fish

The large pelagic fish group consists of epipelagics larger than 100 cm and this group contains the species *Coryphaena hippurus*, *Makaira nigricans*, *Mola mola*, *Tetrapturus albidus* and *Xiphias gladius*. *Xiphias gladius* is a very important commercial species in the Azores EEZ, being one of the main target species of the pelagic longline fishing fleet. *Coryphaena hippurus* is the only other commercially important large pelagic fish species and is caught by the recreational and bottom longline/handline fleets. P/B and Q/B for this group were calculated, and equal 0.7 year-1 and 2.5 year-1. The large pelagic fish group is assumed to occupy the entire model area, so the habitat fraction area is set at 1. Guenette and Morato (2001) estimated that the diet of the large pelagic fish species included in this group consists of 22% cephalopods, 2% small shallow water fish, 1% shallow water medium fish, 40% small pelagic fish, 7% medium pelagic fish, 2% mesopelagics, 7% small demersal fish, 3% medium demersal fish, 2% *Beryx splendens*, 1% *Beryx decadactylus* and 9% *Lepidopus caudatus*.

1.17. Mesopelagic fish

Eustomias obscurus, *Idiacanthus fasciola*, *Lestidiops jayakari*, *Maurolicus amethystinopunctatus*, *Serrivomer beani*, *Vinciguerrria nimbaria*, *Cyclothone microdon*, *Diaphus rafinesquii*, *Cyclothone braueri*, *Benthosema glaciale*, *Vinciguerrria poweriae*, *Notoscopelus bolini* and *Argyropelecus hemigymnus* are the most abundant mesopelagic fish species that make up this group. Mesopelagic species are not targeted by any fishery in the Azores EEZ and are not often caught as bycatch (Pham et al., 2013). A Q/B of 8.6 year-1 was calculated for this group, and a P/Q value of 0.3 was taken from Darwall et al. (2010). The mesopelagic fish group is assumed to occupy the entire model area, so the habitat fraction area is set at 1. The diet for the mesopelagic species was based on Guenette and Morato (2001) and is made up of 2% phytoplankton, 33% small zooplankton, 42% large and gelatinous zooplankton, 10% shrimps, 1% cephalopods, 3% crabs, 3% pelagic s, 3% mesopelagics (cannibalism), and 4% detritus.

1.18. Bathypelagic fish

This group contains, amongst others, the species: *Micromesistius poutassou*, *Chiasmodon niger*, *Centrolophus niger*, *Bathylagus euryops*, *Bathylagichthys greyae* and *Serrivomer beanii*. These species are not targeted any fleet within the Azores EEZ, and are not often caught as bycatch (Pham et al., 2013). P/B and Q/B were calculated for this group, and equal 0.4 year-1 and 4.9 year-1. The bathypelagic fish group is assumed to occupy the entire model area, so the habitat fraction area is set at 1. Diet information was taken from Guenette and Morato (2001) and consists of 25% large and

gelatinous zooplankton, 10% shrimps, 15% cephalopods, 20% benthic filter feeders and 30% mesopelagic fish.

1.19. Small demersal fish

This group contains the demersal species with an asymptotic length larger than 31 cm. The small demersal fish group is made up out of the species *Arnoglossus rueppelii*, *Aspitrigla cuculus*, *Centracanthus cirrus*, *Capros aper*, *Serranus cabrilla*, *Macroramphosus scolopax* and *Anthias anthias*. The different species in this small demersal fish group are of little commercial interest. A Q/B of 7.4 year⁻¹ was calculated for this group, and a P/Q value of 0.3 was taken from Darwall et al. (2010). The small demersal fish group is assumed to only occupy the 100-500m depth layer of the model area, amounting to a habitat fraction area of 0.005. Guenette and Morato (2001) provided the diet information for this group: 15% large and gelatinous zooplankton, 15% shrimps, 1% cephalopods, 28% crabs, 2% benthic worms, 4% other benthos, 19% small shallow water fish, 2% medium shallow water fish, 5% small pelagic fish and 10% small demersal fish.

1.20. Medium demersal fish

The demersal fish species larger than 31 and smaller than 71 cm are assigned to this group. The group is composed of *Antigonia capros*, *Aulopus filamentosus*, *Brama brama*, *Polymixia nobilis*, *Schedophilus ovalis*, *Sphoeroides pachygaster*, *Taractes rubescens*, *Labrus mixtus*, *Lepidorhombus whiffiagonis*, *Coelorinchus caelorhincus* and *Zeus faber*. *Zeus faber*, *Coelorinchus caelorhincus* and *Schedophilus ovalis* are three species caught the by the bottom longline/handline fishery. A Q/B of 4.7 year⁻¹ was calculated for this group, and a P/Q value of 0.2 was taken from Darwall et al. (2010). The medium demersal fish group is assumed to only occupy the 100-500m depth layer of the model area, amounting to a habitat fraction area of 0.005. Diet composition was taken from Guenette and Morato (2001): 13% shrimps, 4% crabs, 16% benthic worms, 17% other benthos, 4% small shallow water fish, 12% medium pelagic fish and 34% small demersal fish.

1.21. Large demersal fish

The demersal fish species with an asymptotic length larger than 71 cm are: *Acantholabrus palloni*, *Molva macrophthalma*, *Polyprion americanus*, *Promethichthys prometheus*, *Ruvettus pretiosus* and *Zenopsis conchifera*. *Polyprion americanus* and *Molva macrophthalma* are two commercially important species in the Azores EEZ targeted by the bottom longline/handline fishery and recreational fishing. P/B and Q/B were calculated for the large demersal fish group and equal 3.5 year⁻¹ and 0.8 year⁻¹. The large demersal fish group is assumed to only occupy the 100-500m depth layer of the model area, amounting to a habitat fraction area of 0.005. Diet information was obtained from Guenette and Morato (2001): 13% cephalopods, 13% other benthos, 3% small shallow water species, 14% medium shallow water species, 11% small pelagic

species, 2% medium pelagic species, 5% mesopelagic species, 19% small demersal species, 15% medium demersal species, 2% large demersal species.

1.22. Small bathydemersal fish

This group consists of the bathydemersal species smaller than 43 cm: *Alepocephalus rostratus*, *Borostomias antarcticus*, *Chlorophthalmus agassizi*, *Hoplostethus mediterraneus mediterraneus*, *Lepidion eques*, *Lepidion guentheri*, *Nezumia aequalis* and *Physiculus dalwigki*. The small bathydemersal fish are of no commercial interest. A Q/B of 5.0 year⁻¹ was calculated for this group, and a P/Q value of 0.1 was taken from Darwall et al. (2010). The small bathydemersal fish group is assumed to only occupy the depth strata lower than 500m within the model area, amounting to a habitat fraction area of 0.994. Diet information was taken from Guenette and Morato (2001) and consists of 9% shrimps, 29% crabs, 33% benthic worms, 18% other benthos, 10% small demersal fish and 1% small bathydemersal fish (cannibalism).

1.23. Medium bathydemersal fish

The bathydemersal fish larger than 43 cm and smaller than 62 cm make up this group. The group consists of the species *Epigonus telescopus*, *Hoplostethus atlanticus*, *Bathygadus melanobranchus*, *Lyconus brachycolus*, *Magnisudis atlantica* and *Trachyscorpia cristulata echinata*. Of these medium bathydemersal fish species, only *Epigonus telescopus* is commercially caught, in low amounts by the bottom longline/handline fishery. A Q/B of 3.3 year⁻¹ was calculated for this group, and a P/Q value of 0.1 was taken from Darwall et al. (2010). The medium bathydemersal fish group is assumed to only occupy the depth strata lower than 500m within the model area, amounting to a habitat fraction area of 0.994. A diet of 11% small zooplankton, 18% large and gelatinous zooplankton, 29% shrimps, 3% cephalopods, 6% other benthos, 19% mesopelagic fish and 13% small demersal fish for this group was obtained from Guenette and Morato (2001).

1.24. Large bathydemersal fish

Bathydemersal fish species larger than 62 cm are grouped here. The species that make up this group are: *Aphanopus carbo*, *Aphanopus intermedius*, *Coryphaenoides guentheri*, *Coryphaenoides rupestris* and *Synaphobranchus affinis* and *Synaphobranchus kaupii*. *Aphanopus carbo* is a commercially important fish species in the Azores, being mainly targeted by the recently started drifting deepwater longline fishery. A Q/B of 3.5 year⁻¹ was calculated for this group, and a P/Q value of 0.1 was taken from Darwall et al. (2010). The large bathydemersal fish group is assumed to only occupy the depth strata lower than 500m within the model area, amounting to a habitat fraction area of 0.994. Diet for *Aphanopus carbo* in the Azores was adopted from Ribeiro Santos et al. (2013) and the rest of the species from Guenette and Morato (2001): 4% large and gelatinous zooplankton, 31% shrimps, 10% cephalopods, 5% crabs, 2% other benthos, 15% medium pelagic fish, 3% mesopelagic fish, 25% small demersal fish, 13% small bathydemersal fish and 13% medium bathydemersal fish.

1.25. *Helicolenus dactylopterus*

The blackbelly rosefish (*Helicolenus dactylopterus*) is a demersal fish species inhabiting the 250-600 depth layer in the Azores archipelago (Menezes et al., 2006), and the habitat fraction area was calculated at 0.0056. The species is an important target for the recreational and bottom longline/handline fisheries. A Q/B of 4.6 year⁻¹ was calculated for this group, and a P/Q value of 0.1 was taken from Darwall et al. (2010). The diet of the blackbelly rosefish was taken from Neves et al. (2012) and consists of 2% large and gelatinous zooplankton, 46% shrimps, 2% cephalopods, 5% crabs, 6% other benthos, 1% small shallow water species, 1% medium shallow water fish, 11% small pelagic fish, 2.6 % mesopelagic fish, 9% medium demersal fish, 2% small bathydemersal fish, 1% medium bathydemersal fish and 4% *Helicolenus dactylopterus* (cannibalism).

1.26. *Conger conger*

The European conger (*Conger conger*) is a demersal fish species inhabiting the 150-550 depth layer in the Azores archipelago (Menezes et al., 2006) and the habitat fraction area was calculated at 0.0052. The species is an important commercial species for the Azores region and is targeted by the recreational and bottom longline/handline fisheries. A P/B and a Q/B of 0.134 year⁻¹ and 2.985 year⁻¹ were calculated for this species. Diet information for the European conger was taken from Morato et al. (1999): 1% shrimps, 7% cephalopods, 6% other benthos, 6% medium shallow water species, 48% small pelagic species, 1% small demersal species, 2% medium demersal species, 7% large demersal species, 1% medium bathydemersal species and 14% *Helicolenus dactylopterus*.

1.27. *Pontinus kuhlii*

The offshore rockfish (*Pontinus kuhlii*) is a demersal fish species occurring in the Azores at a depth range of 150-400m (Menezes et al., 2006), and the habitat fraction area was calculated at 0.0025. The species is a commercial target of the recreational and bottom longline/handline fisheries. P/B and Q/B were calculated for this species, and equal 0.250 year⁻¹ and 3.615 year⁻¹. Diet for the offshore rockfish was taken from Guenette and Morato (2001) and consists of 11% shrimps, 11% crabs, 12% other benthos, 28% small pelagic fish and 38% small demersal fish.

1.28. *Raja clavata*

The thornback ray (*Raja clavata*) is a demersal ray species that can be found in the 50-250m depth layer in the Azores region (Menezes et al., 2006), and the habitat fraction area was calculated at 0.0019. The species is caught as bycatch in the recreational and bottom longline/handline fisheries. A P/B and a Q/B of 0.286 year⁻¹ and 4.104 year⁻¹ were estimated for this species. Diet of the thornback ray was adopted from Gomes et al. (1996) to be composed of 11% large and gelatinous zooplankton, 13% shrimps, 15% crabs, 12% other benthos, 2% small shallow water fish, 11% medium shallow water fish, 31% small pelagic fish, 1% small demersal fish and 4% *Pagellus bogaraveo*.

1.29. *Phycis phycis*

The forkbeard (*Phycis phycis*) is a demersal fish species, occurring at 50-300m in the Azores (Menezes et al., 2006), and the habitat fraction area was calculated at 0.0023. The species is an important commercial species in the Azores EEZ, targeted by the bottom longline/handline fishery. P/B and a Q/B were estimated for this species and equal 0.219 year⁻¹ and 4.501 year⁻¹. Diet information for the European conger was taken from Morato et al. (1999) and consists of 3% shrimps, 17% crabs, 33% small shallow water fish, 39% small pelagic fish, 5% mesopelagic fish and 3% *Helicolenus dactylopterus*.

1.30. *Pagrus pagrus*

The red porgy (*Pagrus pagrus*) is a demersal fish species commonly occurring in the Azores between 50 and 150 m depth (Menezes et al., 2006), and the habitat fraction area was calculated at 0.0012. The species is a commercial target of the bottom longline/handline fishery. P/B and a Q/B were estimated for this species and equal 0.316 year⁻¹ and 4.733 year⁻¹. Diet for the red porgy was taken from Guenette and Morato (2001) and consists of 3% macroalgae, 39% crabs, 12% benthic filter feeders, 1% benthic worms, 25% other benthos, 10% small shallow water species and 10% small pelagic species.

1.31. *Beryx splendens*

Splendid alfonsino (*Beryx splendens*) is a demersal fish species inhabiting the 300-600m depth layers in the Azores (Menezes et al., 2006). The habitat fraction area was calculated at 0.0052. The species is a commercially important target of the recreational and bottom longline/handline fisheries. A P/B and Q/B of 0.395 year⁻¹ and 3.575 year⁻¹ for the splendid alfonsino were calculated. Diet information was taken from Gomes et al. (1996). Diet consists of 41% large and gelatinous zooplankton, 25% shrimps, 1% cephalopods, 13% other benthos, 2% small shallow water fish, 2% medium shallow water fish, 9% small pelagic fish, 2% mesopelagic fish, 3% bathypelagic fish and 2% small demersal fish.

1.32. *Beryx decadactylus*

The alfonsino (*Beryx decadactylus*) is a demersal fish species inhabiting 350-700m depth layers in the Azores (Menezes et al., 2006). The habitat fraction area was calculated at 0.0070. The species is a commercially important target of the recreational and bottom longline/handline fisheries. A P/B and Q/B of 0.262 year⁻¹ and 2.743 year⁻¹ were calculated. Diet information was taken from Gomes et al. (1996). It consists of 14% large and gelatinous zooplankton, 42% shrimps, 20% crabs, 5% other benthos, 2% small shallow water fish, 2% medium shallow water fish, 13% mesopelagic fish, 1% small demersal fish and 1% small bathydemersal fish.

1.33. *Pagellus bogaraveo*

The blackspot seabream (*Pagellus bogaraveo*) is a demersal fish inhabiting the 100-500m depth layer in the Azores region (Menezes et al., 2006), and the habitat fraction area was calculated at 0.0048. The species is a commercially important target of the

recreational and bottom longline/handline fisheries, and the juvenile is caught as live bait for the tuna fisheries (Pham et al., 2013). A P/B of 0.3 year⁻¹ and Q/B of 4.7 year⁻¹ was calculated for the blackspot seabream. Diet composition for the species was taken from Morato et al. (2001) and consisted of 25% large zooplankton, 1% shrimps, 4% cephalopods, 3% benthic worms, 1% other benthos, 33% small pelagic fish, 33% mesopelagic fish and 4% medium demersal fish.

1.34. *Mora moro*

The common mora (*Mora moro*) is a bathydemersal fish with commercial interest in the Azores, and is targeted by bottom longline/handline fleets (Pham et al., 2013). The habitat fraction area is equal to 0.994, as the species inhabits the depth layer deeper than 500m. A P/B of 0.2 year⁻¹ and Q/B of 2.7 year⁻¹ was calculated for this species. Due to lack of data, the diet composition for the common mora was taken from the large bathydemersal fish group.

1.35. *Lepidopus caudatus*

The silver scabbardfish (*Lepidopus caudatus*) is a demersal fish inhabiting the 100-500m depth strata in the Azores region (Menezes et al., 2006), and the habitat fraction area was calculated to 0.005. The silver scabbardfish species is an important commercial species in the Azores EEZ, and is targeted commercially by the bottom longline/handline fisheries. A P/B of 0.3 year⁻¹ and Q/B of 4.8 year⁻¹ was calculated for this species. Diet composition for the silver scabbardfish was taken from Guenette and Morato (2001): 12% small pelagic fish, 22% mesopelagic fish, 56% small demersal fish and 10% *Lepidopus caudatus*.

1.36. Benthic sharks and rays

The groups of the other sharks and rays is made up of the shark species *Galeorhinus galeus*; and the rays *Dasyatis pastinaca*, *Dipturus batis*, *Dipturus oxyrinchus*, *Leucoraja fullonica*, *Mobula tarapacana*, *Myliobatis aquila*, *Pteroplatytrygon violacea*, *Raja brachyura*, *Raja maderensis*, *Taeniura grabata*, *Manta birostris* and *Torpedo nobiliana*. *Galeorhinus galeus* and *Dipturus batis* are important bycatch species of the bottom longline/handline fisheries (Pham et al., 2013). A Q/B of 3.1 year⁻¹ was calculated for this group, and a P/Q value of 0.1 was taken from Darwall et al. (2010). The group is assumed to only occupy the depth strata shallower than 500m within the model area, amounting to a habitat fraction area of 0.006. Diet contents for this group was assessed based on Guenette and Morato (2001): 10% large and gelatinous zooplankton, 6% shrimps, 1% cephalopods, 7% crabs, 3% benthic worms, 10% other benthos, 3% small shallow water fish, 7% medium shallow water fish, 4% large shallow water fish, 24% small pelagic fish, 17% small demersal fish, 0.01% *Phycis phycis* and 10% *Pagellus bogaraveo*. From this original diet composition, 4% was taken from both the small demersal and small pelagic fish and distributed evenly among the single species groups *Helicolenus dactylopterus*, *Conger conger*, *Pontinus kuhlii*, *Pagrus pagrus*, *Beryx splendens*, *Beryx decadactylus*, *Mora moro* and *Raja clavata*.

1.37. Deepwater sharks

The deepwater shark species in this group are: *Centrophorus granulosus*, *Centrophorus squamosus*, *Centroscymnus coelolepis*, *Centroscymnus crepidater*, *Centroscymnus cryptacanthus*, *Dalatias licha*, *Deania calcea*, *Deania profundorum*, *Etmopterus pusillus*, *Galeus melastomus*, *Galeus murinus*, *Heptranchias perlo*, *Pseudotriakis microdon*, *Scymnodon obscurus*, *Etmopterus spinax*, *Etmopterus princeps* and *Squaliolus laticaudus*. *Centrophorus squamosus* is an important bycatch species for the bottom longline/handline and the recent drifting deepwater longline fisheries (Pham et al., 2013). *Centrophorus granulosus*, *Deania calcea*, *Deania profundorum*, *Dalatias licha* and *Etmopterus spinax* are also regular bycatch of the bottom longline/handline fishery. A Q/B of 3.6 year⁻¹ was calculated for this group, and a P/Q value of 0.1 was taken from Darwall et al. (2010). The group is assumed to occupy the depth strata deeper than 500m within the model area, amounting to a habitat fraction area of 0.994. Diet composition of the deepwater sharks was compiled from Guenette and Morato (2001) and literature review (Mauchline and Gordon, 1983; Cortés, 1999; Jakobsdóttir, 2001; Dunn et al., 2010; Navarro et al., 2014). It consists of 50% of teleost fish (12.5% bathypelagics, 10% demersal and bathydemersal fish groups, 7.5% mesopelagics, 5% of pelagics and other single-species groups), 20% of cephalopods, 20% crustaceans (14% shrimps, 5% crabs, 1% other benthos) and 10% of chondrichthyens (5% benthic sharks and rays, 1.5% pelagic sharks, 0.5% *Raja clavata*, and 3% of cannibalism).

1.38. Pelagic sharks

The pelagic shark groups is made up of the species *Lamna nasus*, *Alopias superciliosus*, *Hexanchus griseus*, *Isurus oxyrinchus*, *Prionace glauca* and *Sphyrna zygaena*. The blue shark (*Prionace glauca*) is the most important commercial species in this group and is caught by the pelagic longline fishery (Pham et al., 2013). The shortfin mako shark (*Isurus oxyrinchus*) and the smooth hammerhead shark (*Sphyrna zygaena*) are important bycatch species of the bottom longline/handline fishery. A Q/B of 2.7 year⁻¹ was calculated for this group, and a P/Q value of 0.1 was taken from Darwall et al. (2010). The group is assumed to occupy the entire model area, the habitat fraction area is thus set at 1. Diet contents were compiled from Guenette and Morato (2001) and consist of 2% cephalopods, 7% small shallow water fish, 10% medium shallow water fish, 44% small pelagic fish, 10% medium pelagic fish, 10% mesopelagic fish, 1% bathypelagic fish and 11% small demersal fish.

1.39. Tunas

The tuna species who make up this group are: *Katsuwonus pelamis*, *Thunnus alalunga*, *Thunnus albacares*, *Thunnus obesus* and *Thunnus thynnus*. *Katsuwonus pelamis* is the most important commercial species caught in the Azores EEZ, and is caught by the pole and line fishery. *Thunnus obesus* is also a very important commercial species of this fishery (Pham et al., 2013). P/B and a Q/B were calculated for this species and equal 0.219 year⁻¹ and 4.501 year⁻¹. The group is assumed to occupy the entire model area, the habitat fraction area is thus set at 1. Diet information was taken from Guenette and Morato (2001) and consists of 7% large and gelatinous zooplankton, 2% cephalopods, 1% other benthos, 69% small pelagic fish, 13% medium pelagic fish, 1% small demersal fish and 8% medium demersal fish.

1.40. Turtles

This group consists of the turtle species *Caretta caretta*, *Dermochelys coriacea* and *Chelonia mydas*. The loggerhead turtle is a regular bycatch species of the pelagic longline fishery (Pham et al., 2013). P/B and Q/B were taken from Morato et al., (2009) and were estimated at 0.15 and 3.5 year⁻¹. The group is assumed to occupy the entire model area, the habitat fraction area is thus set at 1. Diet information for turtles was taken from Guenette and Morato (2001) and consists of 94% large and gelatinous zooplankton (mainly gelatinous species), 1% cephalopods and 5% mesopelagic fish.

1.41. Seabirds

The seabirds group consists of the species: *Bulweria bulwerii*, *Calonectris diomedea*, *Larus michahellis*, *Puffinus assimilis*, *Puffinus puffinus*, *Oceanodroma castro*, *Sterna hirundo* and *Sterna dougallii*. P/B and Q/B for this group were taken from Guenette and Morato (2001) and equal 0.04 and 67.77 year⁻¹. The group is assumed to occupy the entire model area, the habitat fraction area is thus set at 1. Also diet information was taken from Guenette and Morato (2001) and consists of 3% small zooplankton, 1% large and gelatinous zooplankton, 4% shrimps, 4% crabs, 20% cephalopods, 44% small pelagic fish, 18% mesopelagic fish and 6% small demersal fish.

1.42. Dolphins

The dolphin group contains the cetacean species *Globicephala melas*, *Globicephala macrorhynchus*, *Delphinus delphis*, *Stenella coeruleoalba*, *Stenella frontalis*, *Hyperoodon ampullatus*, *Tursiops truncatus*, *Grampus griseus*, *Ziphius cavirostris*, *Mesoplodon bidens* and *Mesoplodon europaeus*. There are no records of marine mammal bycatch in the Azores fisheries (Silva et al., 2010). P/B and Q/B for this group were taken from Guenette and Morato (2001) and equal 0.07 and 11.41 year⁻¹. The group is assumed to occupy the entire model area, the habitat fraction area is thus set at 1. Diet information for the dolphins was compiled from Guenette and Morato (2001) and was assumed to consist of: 6% shrimps, 20% cephalopods, 1% crabs, 2% other benthos, 30% small pelagic fish, 5% medium pelagic fish, 16% mesopelagic fish and 20% small demersal fish.

1.43. Baleen whales

The group of the baleen whales consists of the species *Balaenoptera acutorostrata*, *Balaenoptera borealis*, *Balaenoptera musculus*, *Balaenoptera physalus* and *Megaptera novaeangliae*. A P/B and a Q/B for this species were taken from Guenette and Morato (2001) and equal 0.06 year⁻¹ and 5.56 year⁻¹. The group is assumed to occupy the entire model area, the habitat fraction area is thus set at 1. Diet information was taken from Guenette and Morato (2001) and consists of 25% small zooplankton, 65% large and gelatinous zooplankton, 5% small pelagic fish and 5% mesopelagic fish.

1.44. Toothed whales

The top predator toothed whale group consists of the species *Orcinus orca*, *Pseudorca crassidens*, *Globicephala* spp., *Hyperoodon ampullatus*, *Mesoplodon europaeus*, *Mesoplodon bidens*, and *Physeter macrocephalus*. A P/B of 0.02 and a Q/B of 10.27

was taken from Morato et al. (2009). The group is assumed to occupy the entire model area, the habitat fraction area is thus set at 1. Diet information was taken from Guenette and Morato (2001) and is estimated to contain 2% large and gelatinous zooplankton, 75% cephalopods and 23% mesopelagic fish. This initial diet matrix was changed to include 2% pelagic sharks, 3% tunas, 1% turtles, 1% seabirds and 2% dolphins. The diet percentages were reallocated from mesopelagics (3%) and from cephalopods (6%).

1.45. Detritus

Biomass for the detritus group, which comprises of both dissolved and particulate organic matters, was guesstimated by Guenette and Morato (2001) at 1 ton/km². Detritus is assumed to occupy the entire model area, the habitat fraction area is thus set at 1.

Appendix II – Input data in the Ecopath with Ecosim Model of the Azores

Table I - Input parameters for Azores ecosystem model showing those estimated by the model in bold. P/Q is the production rate over biomass, Q/B is consumption rate over biomass, EE is ecotrophic efficiencies, P/Q is production rate over consumption rate and OI is the omnivory index.

Group name	Trophic level	Habitat (%)	Biomass in habitat (t/km ²)	Biomass (t/km ²)	P/B (yr ⁻¹)	Q/B (yr ⁻¹)	EE	P/Q	OI
1 Phytoplankton	1.00	100.00	2.9000	2.9000	576.2858		0.12		0.00
2 Algae	1.00	0.03	2619.0480	0.9072	4.3400		0.02		0.00
3 Small Zooplankton	2.00	100.00	4.3821	4.3821	11.2100	43.29	0.90	0.26	0.00
4 Large Zooplankton	2.58	100.00	3.4011	3.4011	4.7800	15.50	0.90	0.31	0.29
5 Shrimp	2.77	100.00	2.2210	2.2210	1.4500	9.67	0.95	0.15	0.41
6 Cephalopods	3.72	100.00	0.3182	0.3182	3.2800	12.29	0.95	0.27	0.57
7 Crabs	2.26	100.00	1.9641	1.9641	1.6000	10.00	0.95	0.16	0.27
8 Benthic filter feed.	2.05	100.00	2.1419	2.1419	0.8000	9.00	0.95	0.09	0.05
9 Benthic worms	2.20	100.00	1.1491	1.1491	2.2800	11.40	0.95	0.20	0.16
10 Other benthos	2.17	100.00	1.0259	1.0259	3.0000	10.00	0.95	0.30	0.15
11 Shallow-water S	3.16	0.14	10.9503	0.0148	2.4924	8.31	0.95	0.30	0.29
12 Shallow-water M	3.28	0.14	12.6046	0.0170	1.2600	6.30	0.95	0.20	0.56
13 Shallow-water L	3.57	0.14	1.2235	0.0017	0.4423	4.42	0.95	0.10	0.58
14 Pelagic S	2.99	100.00	0.5024	0.5024	2.8422	9.47	0.95	0.30	0.39
15 Pelagic M	3.86	100.00	0.1194	0.1194	0.8660	4.33	0.95	0.20	0.18
16 Pelagic L	4.47	100.00	0.0008	0.0008	0.7270	2.50	0.95	0.29	0.22
17 Mesopelagics	3.35	100.00	0.9519	0.9519	2.5860	8.62	0.95	0.30	0.23
18 Bathypelagic	3.90	100.00	0.6578	0.6578	0.4370	4.90	0.95	0.09	0.33
19 Demersal S	3.56	0.48	12.4709	0.0597	2.2287	7.43	0.95	0.30	0.11
20 Demersal M	3.83	0.48	3.8416	0.0184	0.9326	4.66	0.95	0.20	0.34
21 Demersal L	4.31	0.48	0.8216	0.0039	0.4610	3.82	0.95	0.12	0.32
22 Bathydemersal S	3.29	99.39	0.9692	0.9632	0.4950	4.95	0.95	0.10	0.05
23 Bathydemersal M	3.83	99.39	0.0036	0.0036	0.3310	3.31	0.95	0.10	0.23
24 Bathydemersal L	4.39	99.39	0.0003	0.0003	0.3526	3.53	0.95	0.10	0.24
25 <i>H. dactylopterus</i>	4.09	0.56	3.6246	0.0201	0.4566	4.57	0.95	0.10	0.31
26 <i>Conger conger</i>	4.61	0.52	1.1666	0.0061	0.1340	2.99	0.95	0.04	0.21
27 <i>Pontinus kuhlii</i>	4.00	0.25	0.1671	0.0004	0.2500	3.62	0.95	0.07	0.26
28 <i>Raja clavata</i>	4.25	0.19	0.3096	0.0006	0.2860	4.10	0.95	0.07	0.23
29 <i>Phycis phycis</i>	4.08	0.24	2.1593	0.0051	0.2190	4.50	0.95	0.05	0.36
30 <i>Pagrus pagrus</i>	3.39	0.12	0.7982	0.0010	0.3160	4.73	0.95	0.07	0.29
31 <i>Beryx splendens</i>	3.75	0.51	0.4378	0.0023	0.3950	3.58	0.95	0.11	0.15
32 <i>Beryx decadactylus</i>	3.73	0.70	0.3434	0.0024	0.2620	2.74	0.95	0.10	0.15
33 <i>Pagellus bogaraveo</i>	4.04	0.48	2.5793	0.0124	0.3050	4.68	0.95	0.07	0.22
34 <i>Mora moro</i>	4.27	99.39	0.0016	0.0016	0.1700	2.69	0.95	0.06	0.27
35 <i>Lepidopus caudatus</i>	4.32	100.00	0.0444	0.0444	0.2510	4.79	0.95	0.05	0.13
36 Rays and sharks	4.16	0.61	0.0899	0.0006	0.3126	3.13	0.95	0.10	0.46
37 Deepwater sharks	4.39	99.39	0.0028	0.0028	0.3566	3.57	0.95	0.10	0.27
38 Pelagic sharks	4.30	100.00	0.0486	0.0486	0.2678	2.68	0.95	0.10	0.15
39 Tunas	4.09	100.00	0.0883	0.0883	0.3640	3.03	0.95	0.12	0.13
40 Turtles	3.63	100.00	0.0404	0.0404	0.1500	3.50	0.95	0.04	0.04
41 Seabirds	4.15	100.00	0.0001	0.0001	0.2500	84.39	0.23	0.00	0.18
42 Dolphins	4.31	100.00	0.0019	0.0019	0.1000	11.41	0.38	0.01	0.15
43 Baleen whales	3.49	100.00	0.0208	0.0208	0.0600	5.56	0.46	0.01	0.11
44 Toothed whales	4.64	100.00	0.0560	0.0560	0.0200	10.27	0.13	0.00	0.06
45 Detritus	1.00	100.00	1.0000	1.0000			0.05		0.09

Table II – Diet matrix for the balanced Azores Ecosystem model

GROUPS	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	
1 Phytoplankton	0.900	0.300	0.250			0.100		0.017	0.018	0.092		0.236	0.033		0.015							
2 Algae								0.002	0.081		0.107	0.006										
3 Zooplankton S		0.500	0.375	0.085		0.050	0.200	0.150	0.155		0.003	0.327	0.012		0.333							0.115
4 Zooplankton L		0.050	0.250	0.254					0.049	0.014	0.030	0.216	0.016		0.417	0.250	0.221					0.185
5 Shrimps				0.102	0.030				0.041	0.036	0.066	0.057	0.026		0.100	0.100	0.214	0.134	0.007	0.100		0.289
6 Cephalopods									0.005		0.080	0.006	0.015	0.209	0.005	0.150	0.010	0.002	0.144		0.100	0.033
7 Crabs				0.034	0.030				0.094	0.129	0.168	0.055			0.030		0.409	0.042	0.004	0.321		
8 Benthic Filter feed.					0.050				0.002	0.008						0.200						
9 Benthic worms					0.030			0.010	0.159	0.078	0.030		0.012				0.028	0.158			0.364	
10 Other benthos					0.070			0.010	0.324	0.273	0.200	0.076	0.054					0.172	0.142	0.200	0.059	
11 Shallow-water S			0.001						0.021	0.070	0.154		0.010	0.022			0.010	0.038	0.028			
12 Shallow-water M									0.005	0.021	0.059		0.006	0.052			0.011		0.160			
13 Shallow-water L											0.019											
14 Pelagic S				0.034					0.012	0.108	0.057	0.022	0.817	0.380	0.030		0.077	0.237	0.117			
15 Pelagic M														0.069				0.118	0.026			
16 Pelagic L																						
17 Mesopelagics										0.019				0.075	0.030	0.300			0.054		0.192	
18 Bathypelagics				0.220																		
19 Demersal S				0.068					0.010	0.059	0.020			0.010			0.020	0.100	0.127	0.005	0.027	
20 Demersal M									0.010					0.026					0.165			
21 Demersal L														0.048					0.000			
22 Bathydemersal S																					0.011	0.100
23 Bathydemersal M					0.102																	
24 Bathydemersal L																						
25 <i>H. dactylopterus</i>																						
26 <i>Conger conger</i>																						
27 <i>Pontinus kuhlii</i>																						
28 <i>Raja clavata</i>																						
29 <i>Phycis phycis</i>									0.005		0.008											
30 <i>Pagrus pagrus</i>																						
31 <i>Beryx splendens</i>															0.019							
32 <i>Beryx decadactylus</i>															0.007							
33 <i>Pagellus bogaraveo</i>																						
34 <i>Mora moro</i>																						
35 <i>Lepidopus caudatus</i>															0.083							
36 Rays and sharks																						
37 DW sharks																					0.025	
38 Pelagic sharks																						
39 Tunas																						
40 Turtles																						
41 Seabirds																						
42 Dolphins																						
43 Baleen whales																						
44 Toothed whales																						
45 Detritus	0.100	0.150	0.125	0.102	0.790	0.850	0.800	0.811	0.010	0.094					0.040							

Table II - Diet matrix for the balanced Azores Ecosystem model (cont.)

GROUPS	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	
1 Phytoplankton														0.010								
2 Algae							0.030															
3 Zooplankton S																		0.025		0.250		
4 Zooplankton L	0.039	0.017						0.410	0.140	0.393	0.019	0.002	0.104	0.033		0.065	0.940	0.011		0.650	0.020	
5 Shrimps	0.127	0.463	0.013	0.110	0.105	0.054		0.248	0.420	0.009	0.082	0.002	0.056	0.120	0.002				0.040	0.060		
6 Cephalopods	0.093	0.020	0.088					0.010		0.058	0.051		0.007	0.230	0.023	0.015	0.010		0.195	0.200		0.690
7 Crabs	0.050	0.050		0.110	0.129	0.308	0.390		0.200		0.047		0.073	0.010	0.001				0.043	0.010		
8 Benthic Filter feeders							0.120				0.020								0.006			
9 Benthic worms	0.001	0.002			0.004		0.008			0.042	0.000		0.036									
10 Other benthos	0.017	0.054		0.120			0.252	0.133	0.050	0.009	0.056	0.001	0.106	0.010	0.002	0.011				0.020		
11 Shallow-water S					0.004	0.121	0.100				0.013		0.034		0.023							
12 Shallow-water M		0.001	0.080		0.131	0.004		0.000			0.074		0.072		0.031							
13 Shallow-water L													0.041									
14 Pelagic S		0.014	0.236	0.280	0.062	0.009						0.412	0.072	0.150	0.506	0.755		0.443	0.300	0.050		
15 Pelagic M	0.149										0.037	0.176		0.005	0.107	0.130				0.050		
16 Pelagic L																						
17 Mesopelagics	0.025	0.031	0.001		0.000	0.081		0.176	0.163	0.316	0.060	0.326	0.000	0.056	0.116		0.050	0.176	0.160	0.050	0.229	
18 Bathypelagics		0.070							0.006					0.030	0.010				0.001			
19 Demersal S	0.248	0.149	0.194	0.380	0.528	0.362	0.100	0.019	0.011	0.171	0.055	0.059	0.188	0.166	0.104	0.014			0.060	0.200		
20 Demersal M		0.089	0.024										0.000	0.100	0.001	0.010						
21 Demersal L	0.005		0.075										0.010									
22 Bathydemersal S	0.124		0.008						0.001		0.298			0.020								
23 Bathydemersal M	0.124								0.009		0.176			0.020								
24 Bathydemersal L								0.004			0.001											
25 <i>Helicolenus d. dactylopterus</i>		0.038	0.173			0.062							0.010		0.001							
26 <i>Conger conger</i>													0.010									
27 <i>Pontinus kuhlii</i>													0.010									
28 <i>Raja clavata</i>													0.005									
29 <i>Phycis phycis</i>		0.000											0.000									
30 <i>Pagrus pagrus</i>													0.005		0.001							
31 <i>Beryx splendens</i>													0.005		0.003							
32 <i>Beryx decadactylus</i>													0.005		0.003							
33 <i>Pagellus bogaraveo</i>			0.098		0.037								0.134		0.002							
34 <i>Mora moro</i>													0.010	0.020								
35 <i>Lepidopus caudatus</i>		0.002	0.011									0.024	0.000		0.008							
36 Rays and other sharks													0.005									
37 DW sharks										0.012				0.020								
38 Pelagic sharks																						0.020
39 Tunas																0.049						0.030
40 Turtles																						0.010
41 Seabirds																						0.000
42 Dolphins																0.000						0.000
43 Baleen whales																						0.001
44 Toothed whales																0.001						
45 Detritus																						

Table III – Total marine reported and unreported catch in the Azores EEZ for the reference year 1997

Group name	Bottom longline & handline	Pole line - tuna & live bait	Small pelagic fishery	Pelagic longline - regional	Recreational fishing	Coastal invertebrate fishery	Squid fishery	Pelagic longline - mainland	Pelagic longline - foreign	Bottom trawling	Drifting DW longline	Total
Algae						0.4						0.4
Shrimp						0.1						0.1
Cephalopods	1.6				26.4	268.5	303.9					600.4
Crabs	9.8					19.6						29.4
Other benthos	0.4					77.0						77.4
Shallow water S	48.3		25.9		21.3							95.5
Shallow water M	149.8				90.4							240.2
Shallow water L	199.1				267.9							467.0
Pelagic S	68.3	291.4	2631.3		80.2							3071.1
Pelagic M	71.8				8.9							80.7
Pelagic L	2.1			252.3	2.2			0.2				256.8
Bathypelagic	2.4											2.4
Demersal S	2.3											2.3
Demersal M	24.7											24.7
Demersal L	214.8				6.0							220.7
Bathydemersal S	6.9											6.9
Bathydemersal M	1.8											1.8
Bathydemersal L	68.7											68.7
<i>H. dactylopterus</i>	469.7				20.4							490.1
<i>Conger conger</i>	718.0				8.5							726.5
<i>Pontinus kuhlii</i>	64.5				12.9							77.4
<i>Raja clavata</i>	141.1				6.5							147.5
<i>Phycis phycis</i>	396.9				8.7							405.6
<i>Pagrus pagrus</i>	110.1				12.6							122.6
<i>Beryx splendens</i>	333.0											333.0
<i>Beryx decadactylus</i>	123.2											123.2
<i>Pagellus bogaraveo</i>	1051.9	6.2			59.0							1117.0
<i>Mora moro</i>	29.9											29.9
<i>Lepidopus caudatus</i>	3796.8											3796.8
Benthic sharks and rays	148.1											148.1
DW sharks	312.9											312.9
Pelagic sharks	94.7			717.8				0.5				813.0
Tunas	10.3	6522.1										6532.4
Turtles				4.7				0.003				4.7
Total	8673.7	6819.7	2657.2	974.9	631.7	365.6	303.9	0.7	-	-	-	20427.4

Appendix III – Reference time series driving the Azores ecosystem model for the period 1997 - 2014

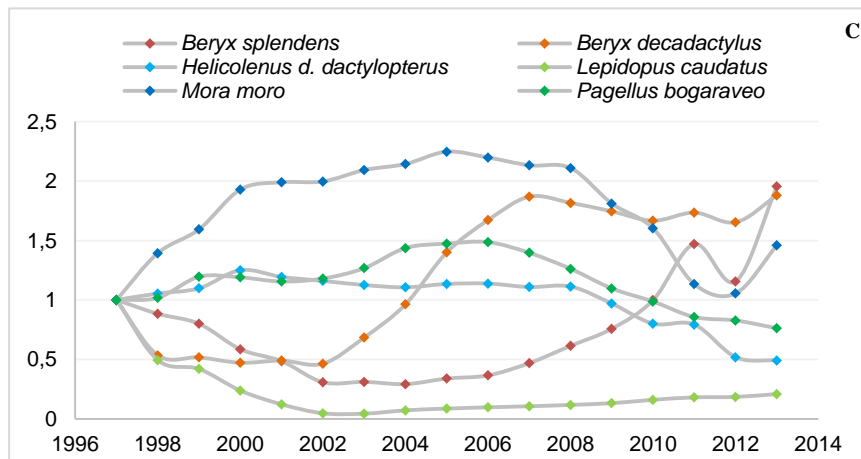
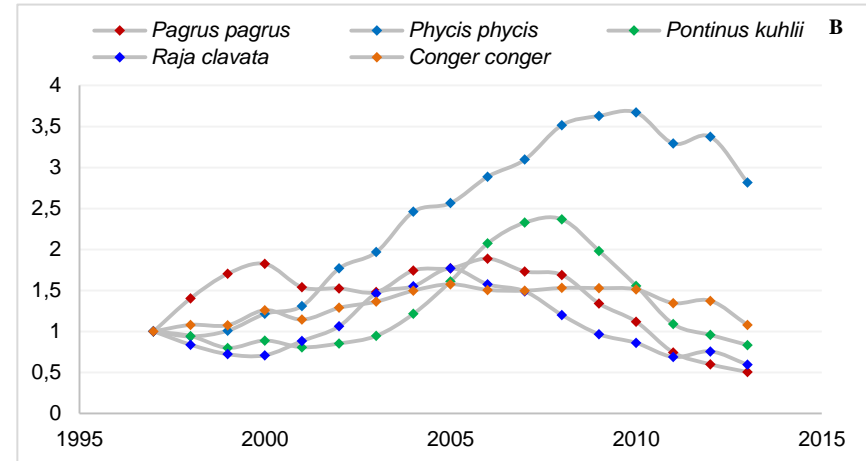
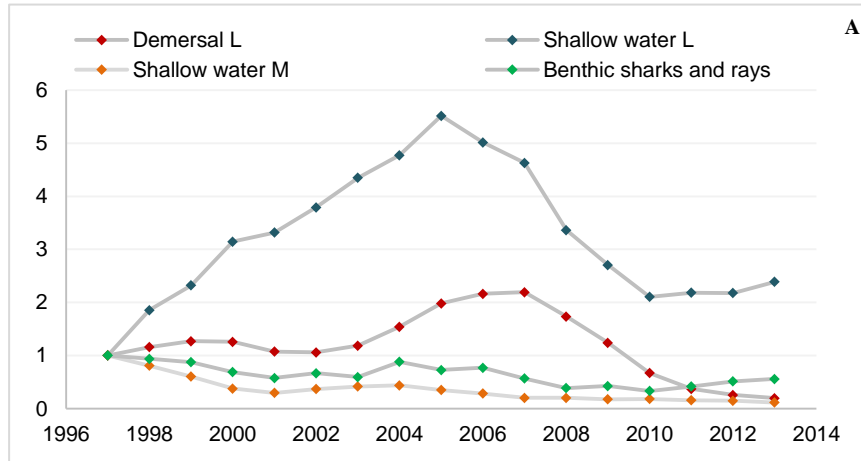
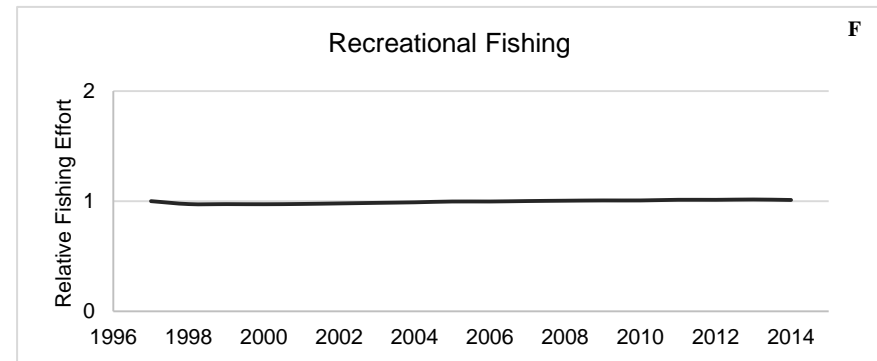
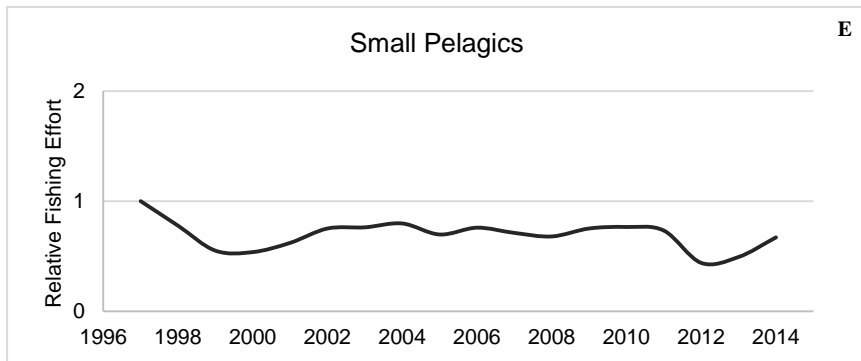
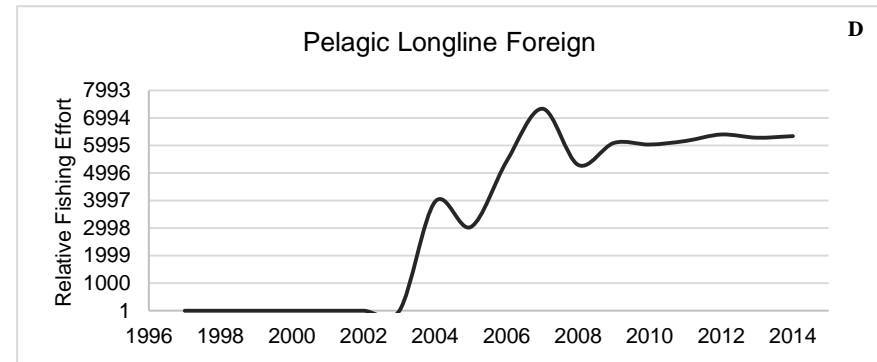
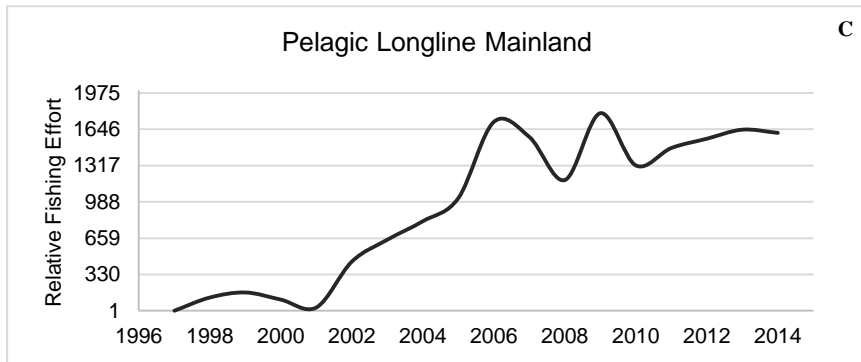
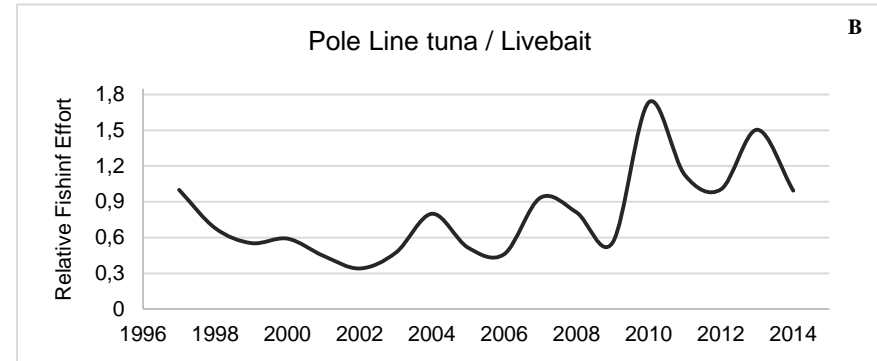
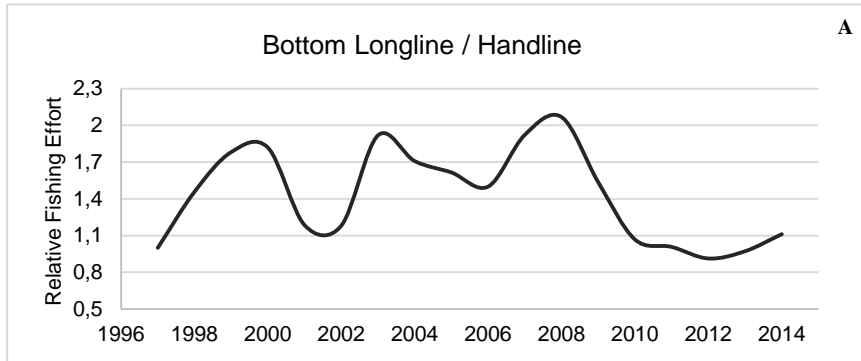


Figure 1 – Relative time series of biomass (A, B and C) for the 15 reference functional groups for the period 1997-2013



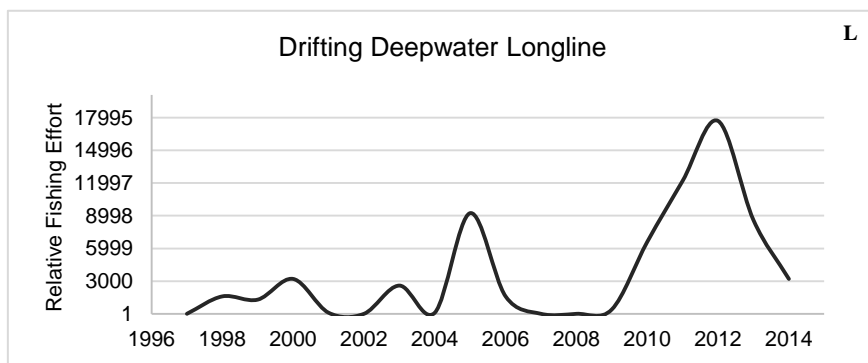
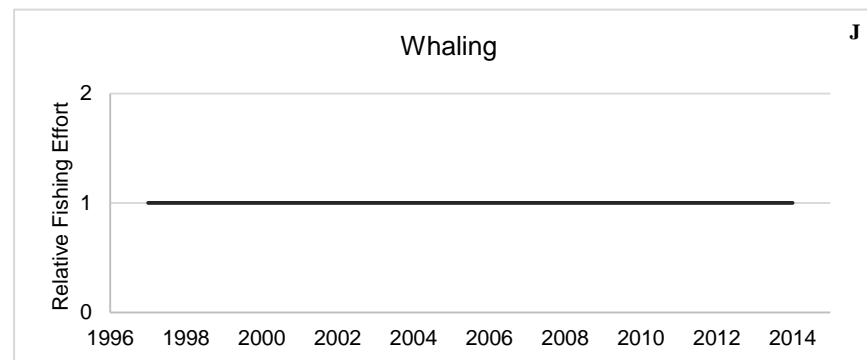
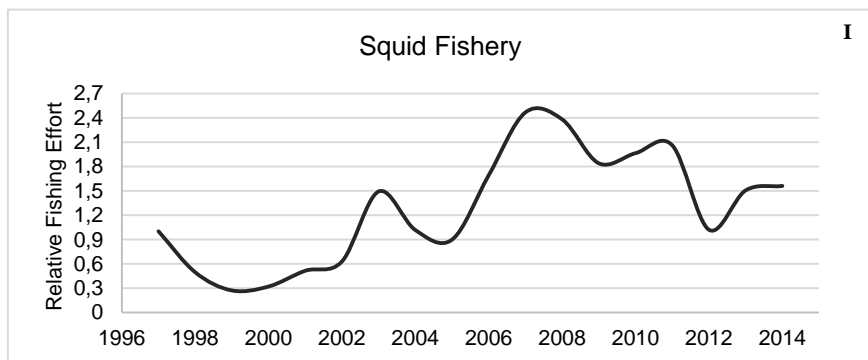
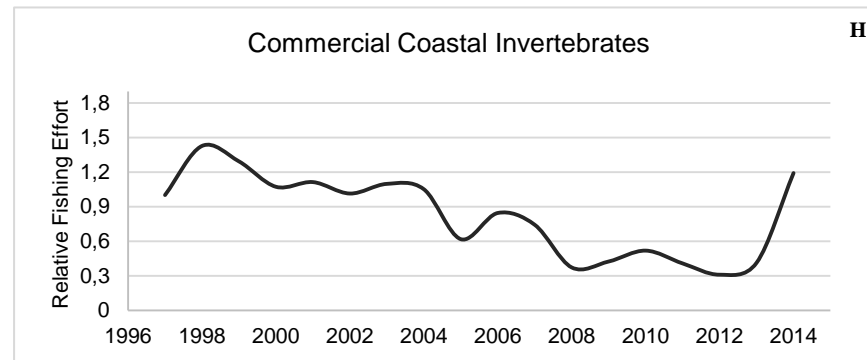
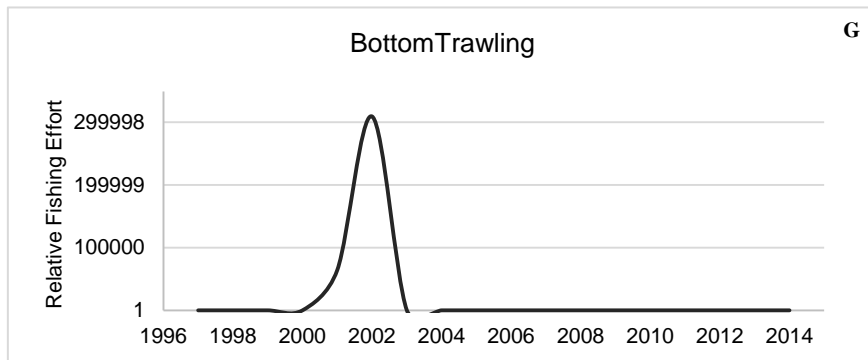
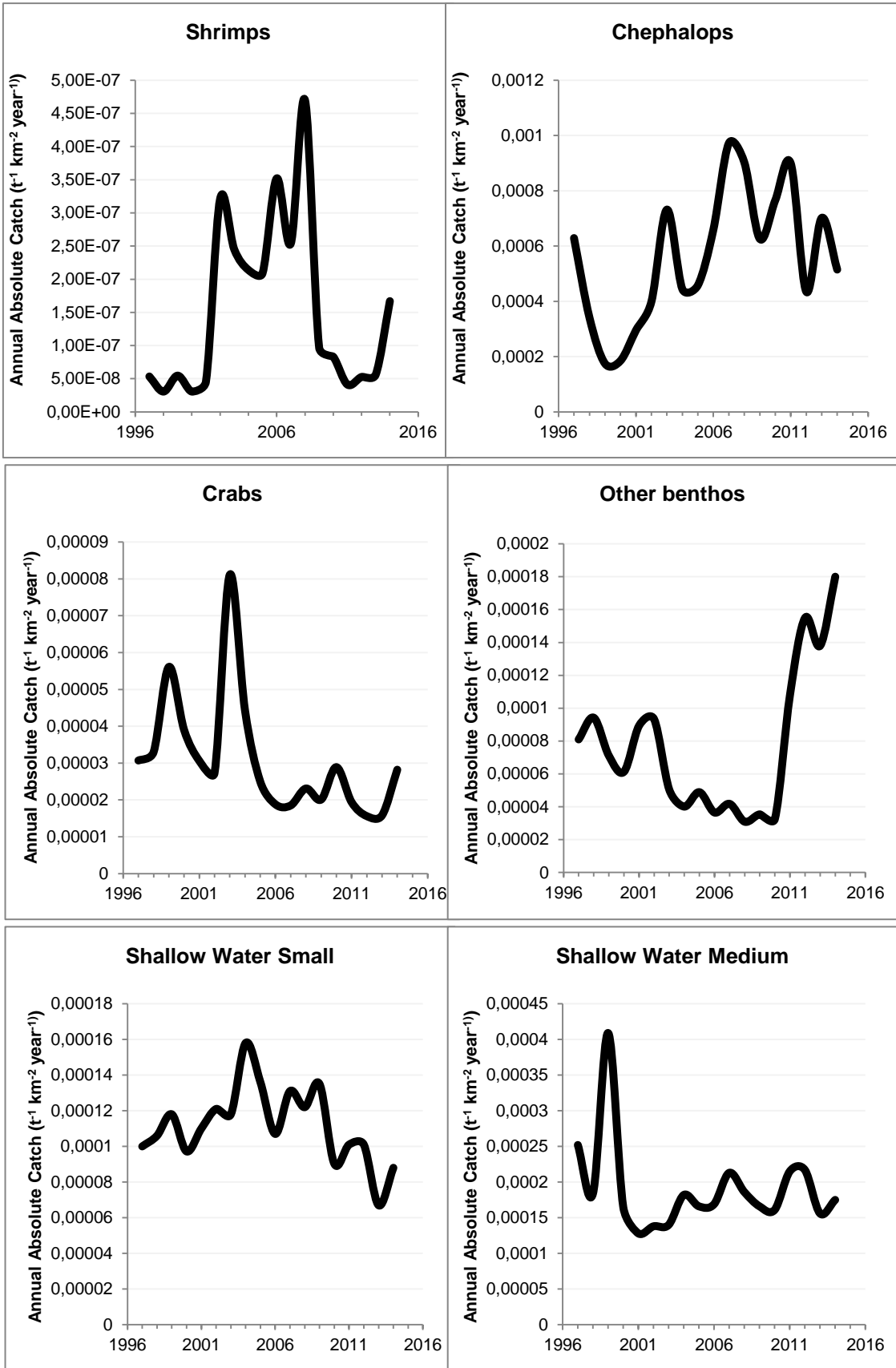
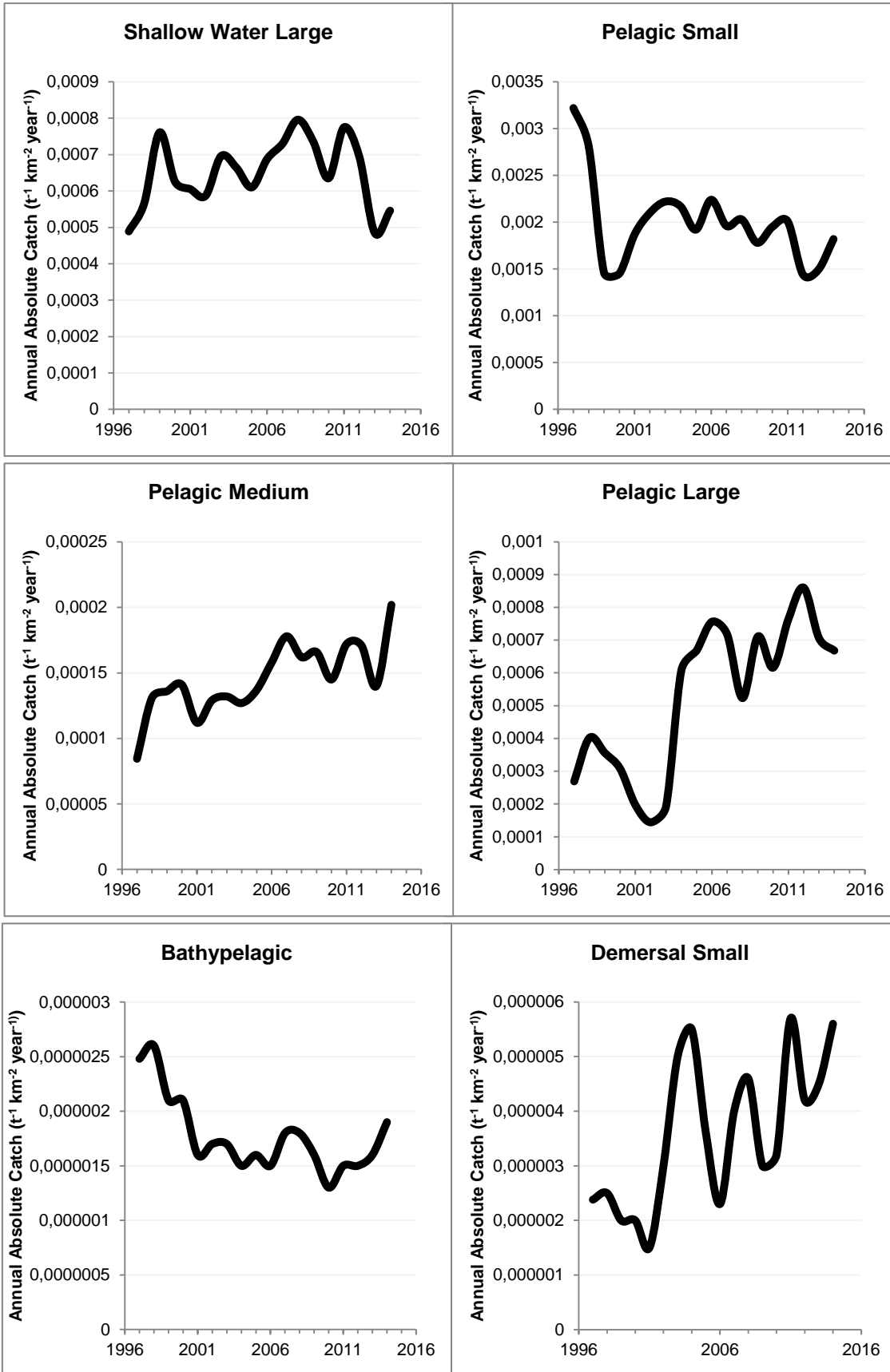
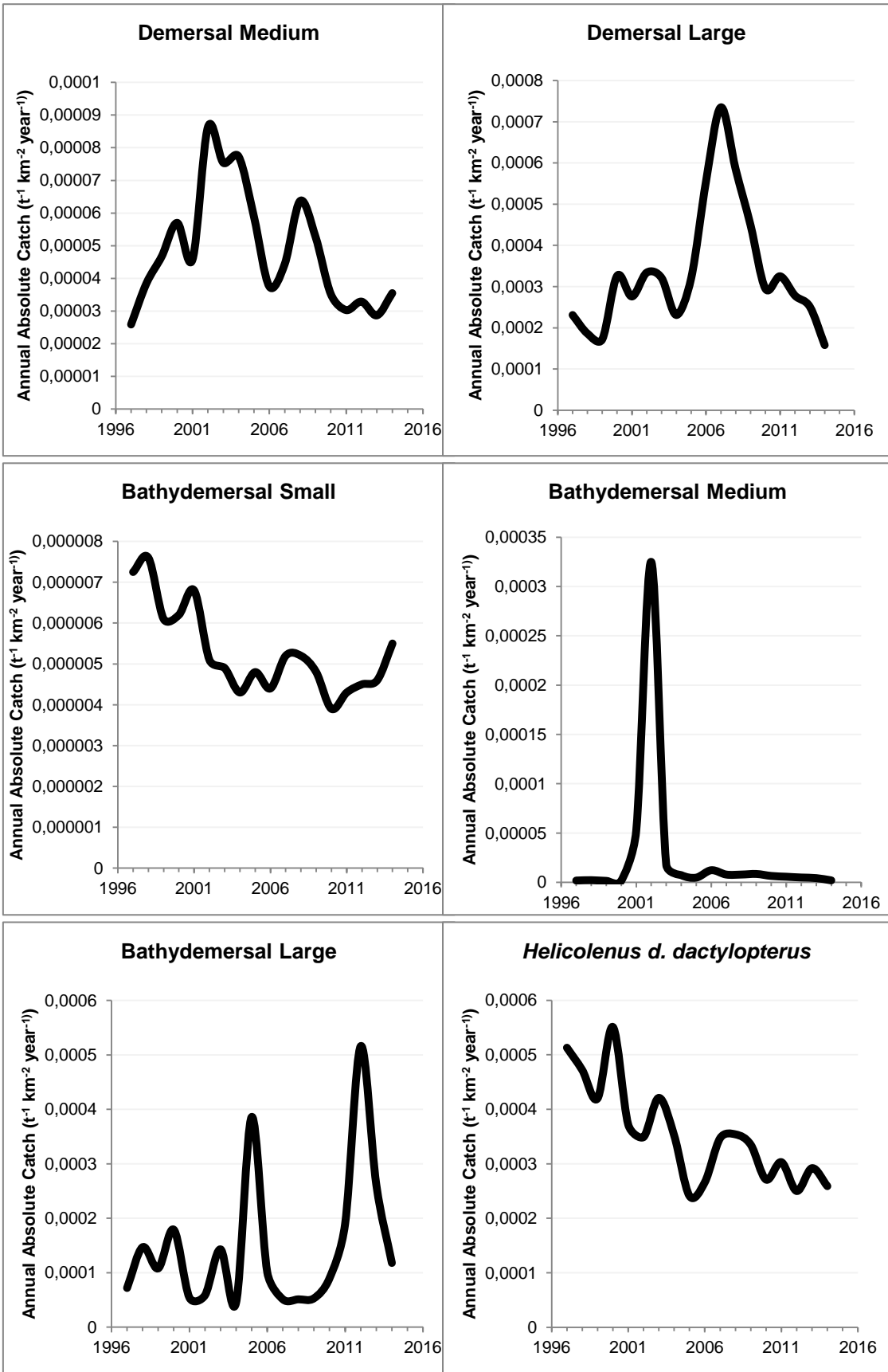
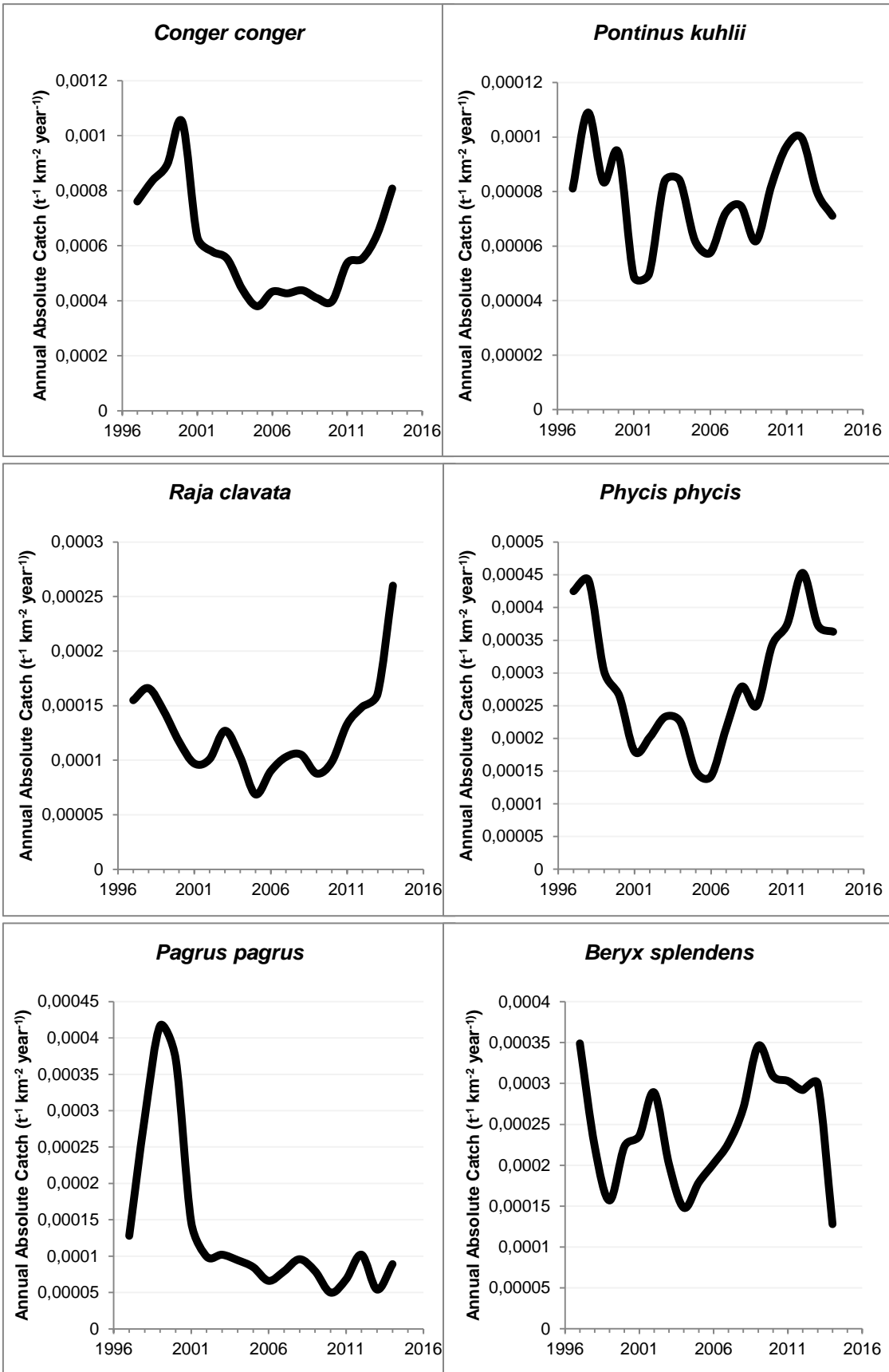


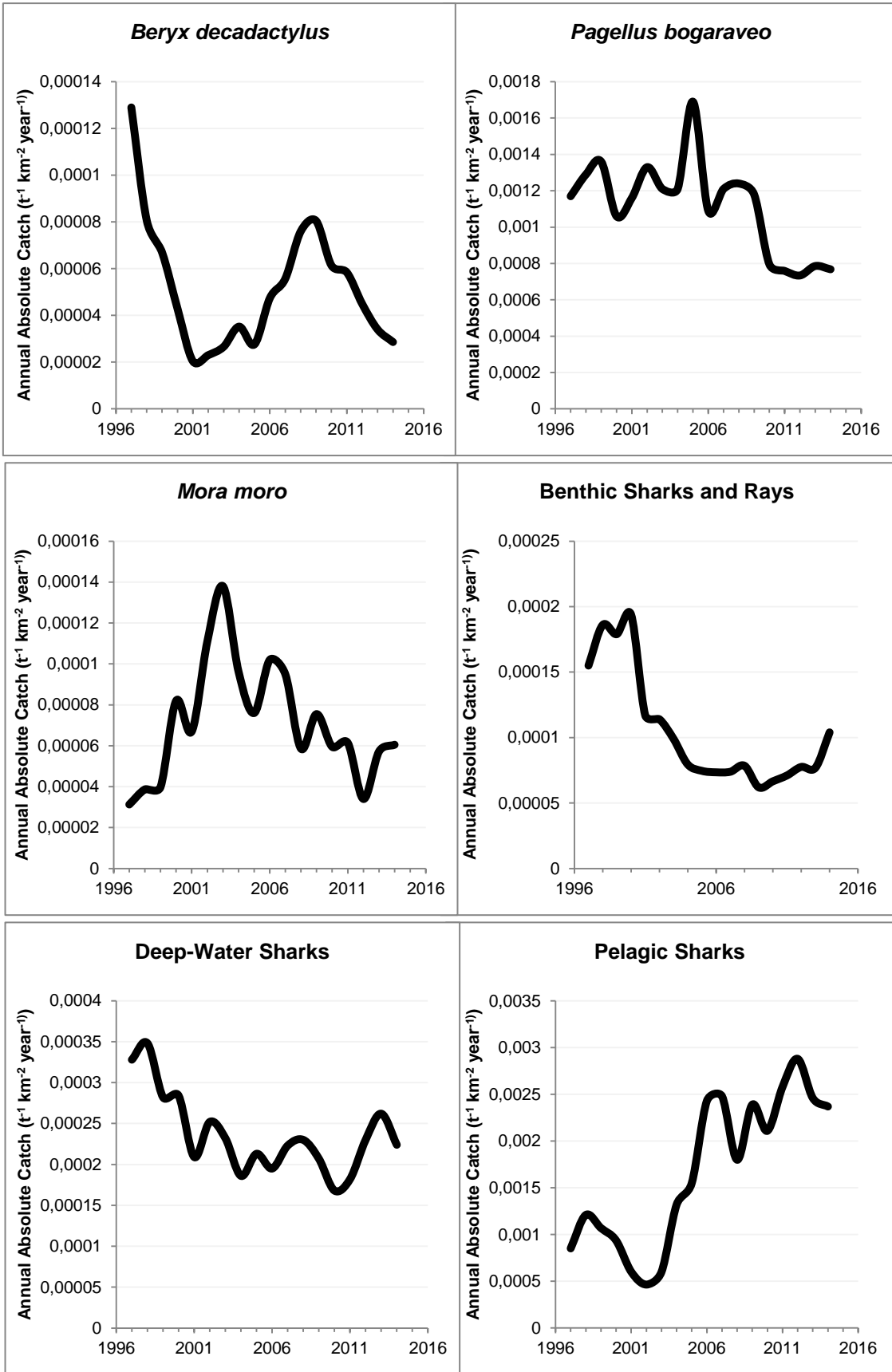
Figure 2 – Relative fishing effort for the fishing fleets of the Azores (A-L) included in the model for the period 1997-2014

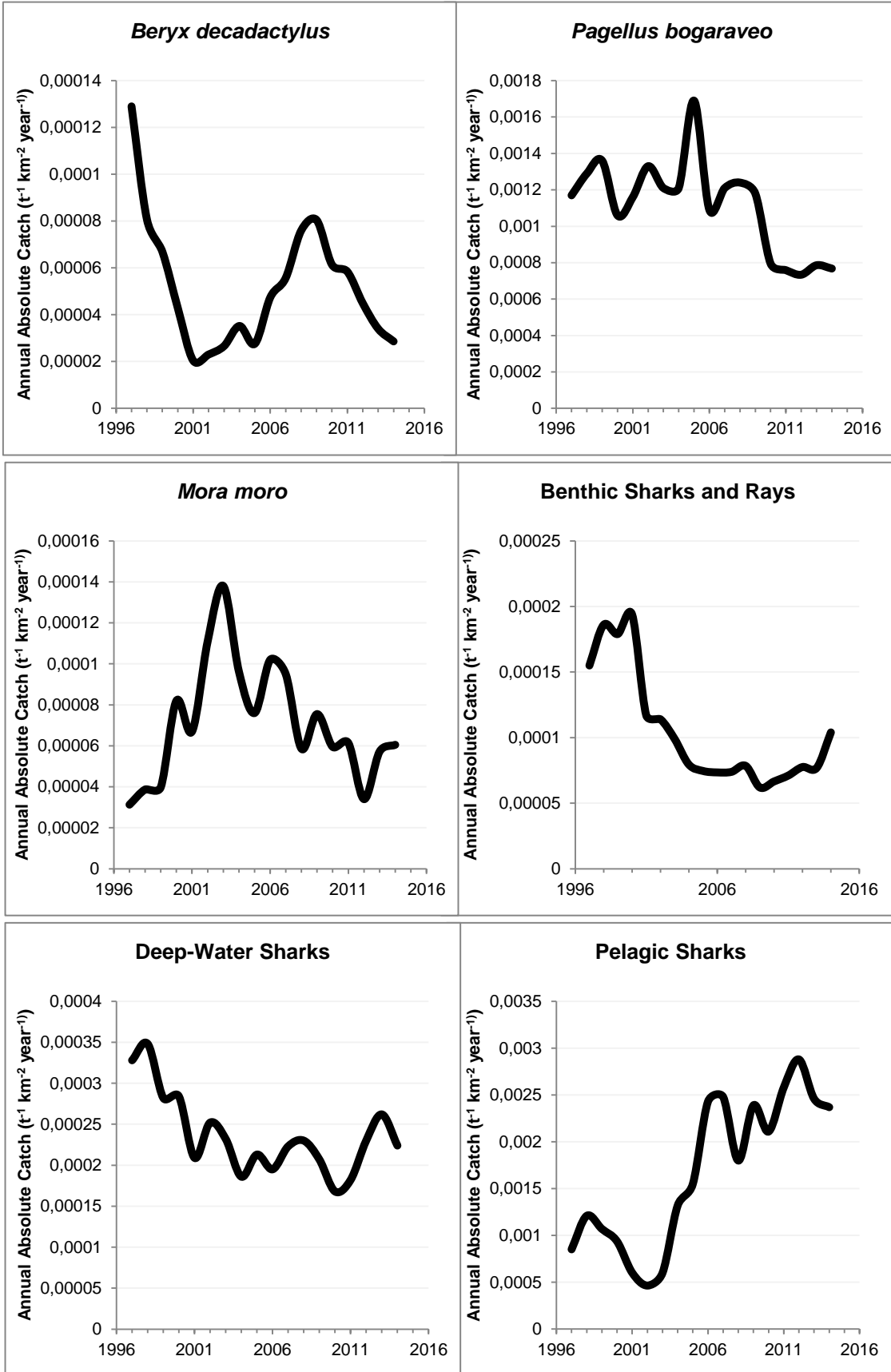












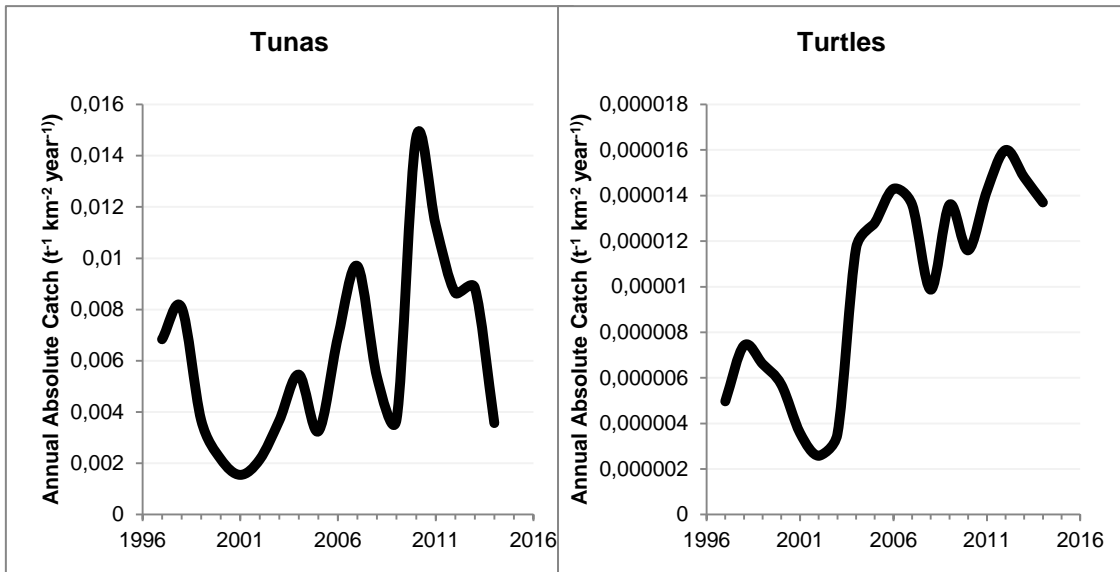


Figure 3 – Reference total catch for the period 1997-2014

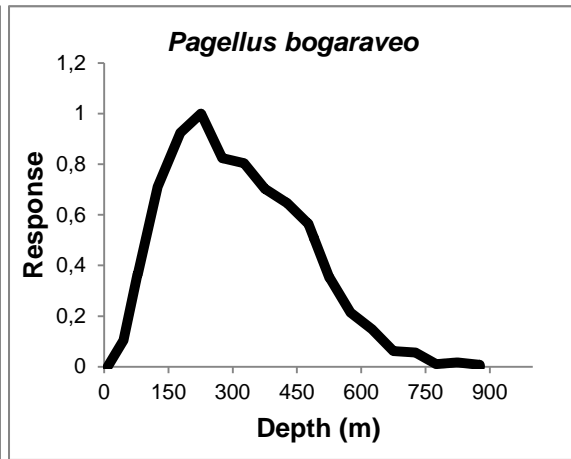
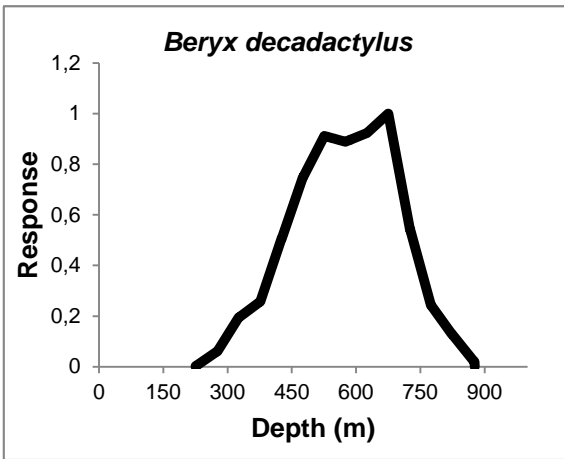
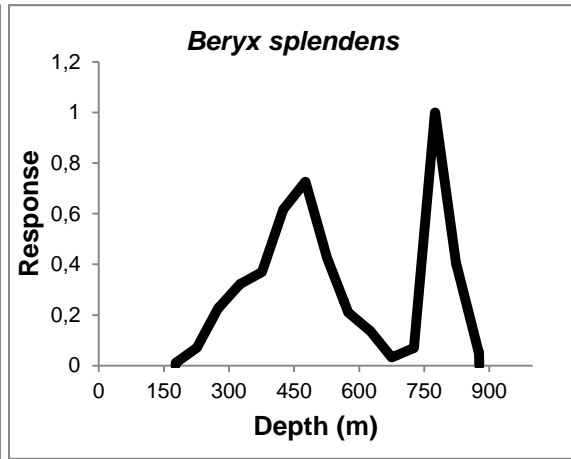
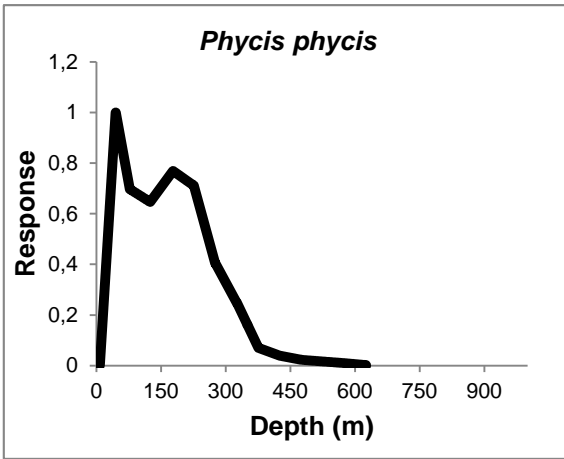
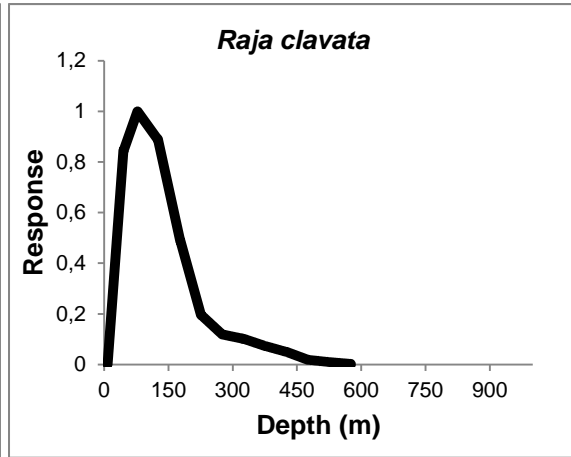
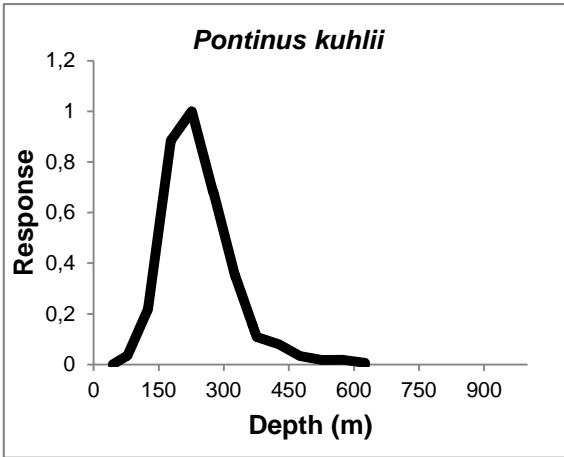
Appendix IV – Habitat foraging usage

Table I – Habitat foraging usage input of Model Baseline

Group\Habitat	All Habitats	<150	< 400	<900	<1500	<5000	20 Km B
Phytoplankton	1						
Algae	1						
Small Zooplankton	1						
Large Zooplankton	1						
Shrimp	1						
Cephalopods	1						
Crabs	1						
Benthic Filter Feeders	1						
Benthic Worms	1						
Other Benthos	1						
Shallow Water S	1						
Shallow Water M	1						
Shallow Water L	1						
Pelagic S	1						
Pelagic M	1						
Pelagic L	1						
Mesopelagic	1						
Bathypelagic	1						
Demersal S	1						
Demersal M	1						
Demersal L	1						
Bathydemersal S	1						
Bathydemersal M	1						
Bathydemersal L	1						
<i>H. dactylopterus</i>	1						
<i>Conger conger</i>	1						
<i>Pontinus kuhlii</i>	1						
<i>Raja clavata</i>	1						
<i>Phycis phycis</i>	1						
<i>Pagrus pagrus</i>	1						
<i>Beryx splendens</i>	1						
<i>Beryx decadactylus</i>	1						
<i>Pagellus bogaraveo</i>	1						
<i>Mora moro</i>	1						
<i>Lepidopus caudatus</i>	1						
Rays and Other Sharks	1						
Deep water Sharks	1						
Pelagic Sharks	1						
Tunas	1						
Turtles	1						
Seabirds	1						
Dolphins	1						
Baleen whales	1						
Toothed whales	1						
Detritus	1						

Table II – Habitat foraging usage input in Model 1

Group\Habitat	All Habitats	<150	< 400	<900	<1500	<5000	20 Km B
Phytoplankton	1						
Algae		1					
Small Zooplankton	1						
Large Zooplankton	1						
Shrimp	1						
Cephalopods	1						
Crabs	1						
Benthic Filter Feeders	1						
Benthic Worms	1						
Other Benthos	1						
Shallow Water S							
Shallow Water M							
Shallow Water L							
Pelagic S		1	1	1	1	1	
Pelagic M		1	1	1	1	1	
Pelagic L		1	1	1	1	1	
Mesopelagic	1						
Bathypelagic				1			
Demersal S							
Demersal M							
Demersal L							
Bathydemersal S				1			
Bathydemersal M				1			
Bathydemersal L				1			
<i>H. dactylopterus</i>							
<i>Conger conger</i>							
<i>Pontinus kuhlii</i>							
<i>Raja clavata</i>							
<i>Phycis phycis</i>							
<i>Pagrus pagrus</i>							1
<i>Beryx splendens</i>							
<i>Beryx decadactylus</i>							
<i>Pagellus bogaraveo</i>							
<i>Mora moro</i>							
<i>Lepidopus caudatus</i>							
Rays and Other Sharks							
Deep water Sharks							
Pelagic Sharks		1	1	1	1	1	
Tunas		1	1	1	1	1	
Turtles		0,85	1	0,9	0,1	0,05	
Seabirds		1	0,1	0,1	0,2	0,1	
Dolphins		1	1	1	0,2	0,1	
Baleen whales	1						
Toothed whales	1						
Detritus	1						



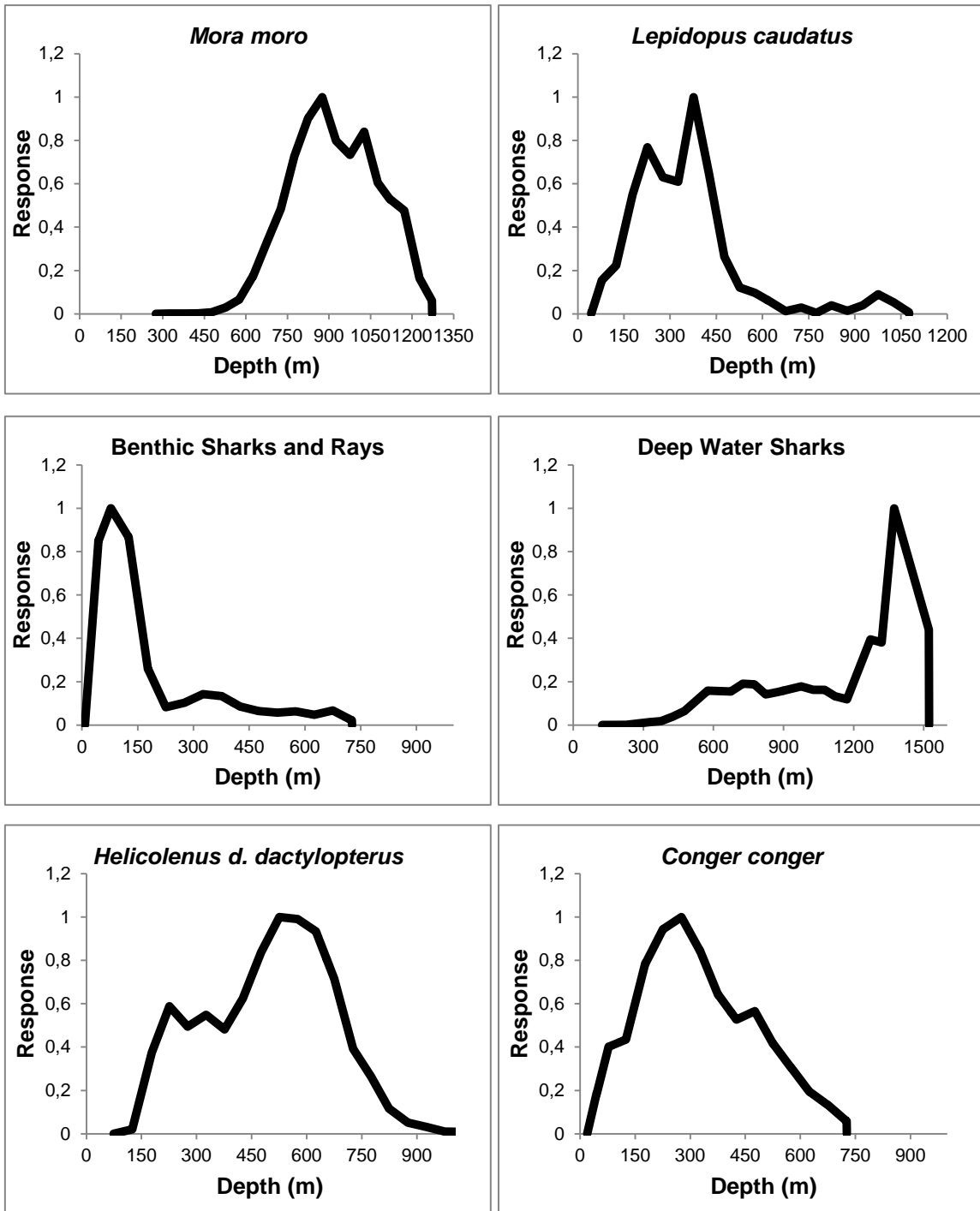


Figure 3 – Environmental responses to depth (depth profiles) of functional groups input in Ecospace Model 1

Table III – Habitat foraging usage input of the initial Azores Ecospace Model

Group\Habitat	All Habitats	<150	< 400	<900	<1500	<5000	20 Km B
Phytoplankton	1						
Algae		1					
Small Zooplankton	1						
Large Zooplankton	1						
Shrimp	1						
Cephalopods	1						
Crabs	1						
Benthic Filter Feeders	1						
Benthic Worms	1						
Other Benthos	1						
Shallow Water S		1	0,27				
Shallow Water M		1	0,063				
Shallow Water L		1	0,093				
Pelagic S		1	1	1	1	1	
Pelagic M		1	1	1	1	1	
Pelagic L		1	1	1	1	1	
Mesopelagic	1						
Bathypelagic				1			
Demersal S		1	0,69	0,02			
Demersal M		0,515	0,323	1			
Demersal L		0,048	1	0,438			
Bathydemersal S				1			
Bathydemersal M				1			
Bathydemersal L				1			
<i>H. dactylopterus</i>		0,036	0,827	1	0,02		
<i>Conger conger</i>		0,378	1	0,304			
<i>Pontinus kuhlii</i>		0,157	1	0,049			
<i>Raja clavata</i>		1	0,314	0,09			
<i>Phycis phycis</i>		1	0,657	0,03			
<i>Pagrus pagrus</i>		0,05					1
<i>Beryx splendens</i>			0,5121	1			
<i>Beryx decadactylus</i>			0,149	1			
<i>Pagellus bogaraveo</i>		0,449	1	0,29			
<i>Mora moro</i>			0,0023	0,657	1		
<i>Lepidopus caudatus</i>		1	0,723	0,063			0,1
Rays and Other Sharks		1	0,212	0,06			
Deep water Sharks				1			
Pelagic Sharks		1	1	1	1	1	
Tunas		1	1	1	1	1	
Turtles		0,85	1	0,9	0,1	0,05	
Seabirds		1	0,1	0,2	0,1	0,1	
Dolphins		1	1	1	0,2	0,1	
Baleen whales	1						
Toothed whales	1						
Detritus	1						

Table IV – Habitat foraging usage input of the final Azores Ecospace Model

Group\Habitat	All Habitats	<150	< 400	<900	<1500	<5000	20 Km B
Phytoplankton	1						
Algae		1					
Small Zooplankton	1						
Large Zooplankton	1						
Shrimp	1						
Cephalopods	1						
Crabs		1	1	1	1	1	1
Benthic Filter Feeders	1						
Benthic Worms	1						
Other Benthos		1	1	1	1	1	1
Shallow Water S		0,1					1
Shallow Water M		0,2					1
Shallow Water L							1
Pelagic S		1	1	1	1		1
Pelagic M		1					
Pelagic L		1	1	1	1	1	
Mesopelagic	1						
Bathypelagic				1			
Demersal S		0,70	1	0,2			
Demersal M			1				
Demersal L							
Bathydemersal S			1				
Bathydemersal M			1				
Bathydemersal L				1			
<i>H. dactylopterus</i>		0,036	0,827	1	0,3		
<i>Conger conger</i>		0,378	1	0,5	0,2		
<i>Pontinus kuhlii</i>		0,157	1	0,25			
<i>Raja clavata</i>		1	0,314	0,29	0,05		
<i>Phycis phycis</i>		1	1	1			
<i>Pagrus pagrus</i>		0,05					1
<i>Beryx splendens</i>			0,5121	1	0,3		
<i>Beryx decadactylus</i>			0,149	1	0,4		
<i>Pagellus bogaraveo</i>			0,5	1			
<i>Mora moro</i>			1	1			
<i>Lepidopus caudatus</i>		1	1				0,1
Rays and Other Sharks		0,3	0,1	1	0,2		
Deep water Sharks				1			
Pelagic Sharks	1						
Tunas		1	1	0,5	0,3		
Turtles		0,85	1	0,9	0,1	0,05	
Seabirds		1	0,1	0,2	0,1	0,1	
Dolphins		1	1	1	0,2	0,1	
Baleen whales	1						
Toothed whales	1						
Detritus	1						

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