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Ecology of the short-beaked common dolphin (*Delphinus delphis*) along the North-West coast of Spain

Oriol Giralt Paradell, MSc

Thesis submitted to the National University of Ireland (Cork)
in fulfilment of the requirements for the degree of
Doctor of Philosophy

School of Biological Earth and Environmental Sciences
Head of School: *Prof. Andrew Wheeler*

Academic Supervisor
Prof. *Emer Rogan*

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Dr. *Bruno Díaz López*



BDRI Marine Research Centre

2020

UCC University College Cork, Ireland Coláiste na hOllscoile Corcaigh

Ollscoil na hÉireann, Corcaigh

National University of Ireland, Cork





Ecology of the short-beaked common dolphin (*Delphinus delphis*) along the North-West coast of Spain

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for the degree of

Doctor of Philosophy

University College Cork

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2020

To Júlia, Pol and Biel
El futur és a les vostres mans

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Declaration

This is to certify that the work I am submitting is my own and has not been submitted for another degree, either at University College Cork or elsewhere. All external references and sources are clearly acknowledged and identified within the contents. I have read and understood the regulations of University College Cork concerning plagiarism.

This thesis has been conducted in collaboration with the Bottlenose Dolphin Research Institute BDRI (represented by Bruno Díaz López) that has officially authorized me to use the data to elaborate this thesis. The author and the BDRI give the permission to use this thesis for consultation and to copy parts of it for personal use. Every other use is subject to the copyright laws; more specifically the source must be extensively specified when using results from this thesis.

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Data collection complies with the current laws of the country in which it was performed, Spain.



Oriol Giralt Paradell

Barcelona 2nd January 2021

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Abstract

Studying the ecology of a species requires a comprehensive approach encompassing several techniques aimed at understanding different aspects of their ecology such as distribution and habitat, their role in the ecosystem and interactions with the other species. In a constantly changing world, in which (coastal) marine ecosystems are consistently being impacted by human activities, the improved knowledge on marine top predators ecology is of key importance in order to develop effective conservation measures and management plans. In this regard, this thesis uses different approaches to better understand the ecology of a marine top predator, the short-beaked common dolphin (*Delphinus delphis*, Linnaeus 1758) in Galician waters, North-West Spain, and explores its conservation needs. To do so, the study combines data collected during 273 days at sea, covering a total distance of 9,417 km between March 2014 and October 2017, with information gathered by several studies conducted in the area in previous years. The data collected over four years contributed to improving our understanding of the environmental, topographic and anthropogenic factors influencing the dolphins distribution, and highlighted the areas entailing the most and least suitable habitats for the species and the areas with a higher degree of overlap with fishing activities. This information was combined with regional fisheries information to build an Ecopath with Ecosim framework to study the role of common dolphins in the ecosystem and its relationships with the other species. Furthermore, the approach provided information about the ecological impacts of fisheries on common dolphins and other cetacean species in the area. Results point out the importance of the continental shelf waters for the species and highlight the species vulnerability to direct and especially indirect impacts caused by fisheries, principally trawling activities. In this regard, the study predicts an important population decrease for common dolphins if fishing effort is increased. An interdisciplinary approach combining distribution and habitat use studies with the analysis of trophic food webs was used to explore the overlap between common dolphins and fisheries and the direct and indirect impacts caused on this cetacean species, providing new information on the indirect effects of fisheries on common dolphins, which will be of great value in the development of effective conservation measures and fishing management plans.

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Abbreviations and acronyms

ACF: Auto-Correlation Functions

AIC: Akaike Information Criteria

BDRI: Bottlenose Dolphin Research Institute

CFP: Common Fisheries Policy

CHL-a: Chlorophyll a

EC: European Commission

EE: Ecotrophic Efficiency

EEC: European Economic Community

EGV: Ecogeographical Variable

ENM: Environmental Niche Models

ENFA: Environmental Niche Factor Analysis

EwE: Ecopath with Ecosim

EU: European Union

GAM: Generalised Additive Model

GCV: General Cross Validation

GES: Good Environmental Status

GIS: Geographical Information Systems

GLM: Generalised Linear Model

GPS: Global Positioning System

HP: Horse Power

HSI: Habitat Suitability Index

ICCAT: International Commission for the Conservation of Atlantic Tunas

ICES: International Council for the Exploration of the Sea

IDW: Inverse Distance Weighted

IUCN: International Union for Conservation of Nature

IUU: Illegal Unreported and Unregulated (fishing)

kn: knots

MSFD: Marine Strategy Framework Directive

MSY: Maximum Sustainable Yield

nm: nautical miles

PCI: Predatory Cycling Index

PREBAL: Pre-Balance (diagnostics)

RVI: Relative Variable Importance

SAGA: System for Automated Geoscientific Analyses

SCI: Sites of Community Interest

SDM: Species Distribution Model

SE: Standard Error

SF: Specialisation Factor

SPA: Special Protection Area

SS: Sum of Squares

SSS: Sea Surface Salinity

SST: Sea Surface Temperature

TD: Top-Down effects

TL: Trophic Level

UBRE: Un-Biased Risk Estimator

UI: Upwelling Index

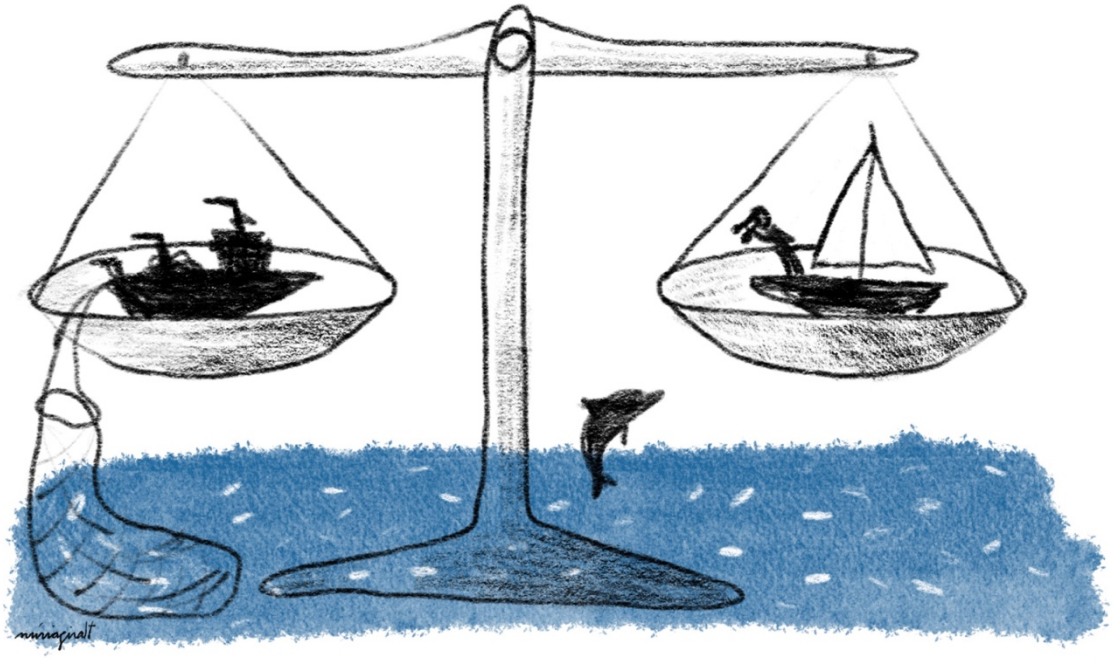
UNCLOS: United Nations Convention on the Law of the Sea

UTC: Coordinated Universal Time

VMS: Vessel Monitoring System

WRF: Weather Research and Forecasting

WSSD: World Summit on Sustainable Development



Drawing by Núria Giralt

Chapter 1

General Introduction

This chapter serves as a literature review that introduces the concept of general ecology and stresses the importance of ecological studies to understand top predator, and more specifically, cetacean populations and their relationship with the surrounding environment, focussing on distribution, habitat use, and trophic interactions. The chapter also describes the different kinds of interactions between fisheries and cetaceans and the consequences for species conservation and management. It then presents the short-beaked common dolphin, as the main species studied in this work, by describing its general status in the North-East Atlantic. The last part of the chapter frames the study in a geographical context by describing the geographical and oceanographic characteristics of the study area, some of the species of cetaceans that occur there and the fisheries operating in Galicia.

The concept "Ecology" was first introduced by Ernst Haeckel in his book Generelle Morphologie der Organismen in 1866. He defined it as "*the whole science of the relations of the organism to the environment including, in the broad sense, all the 'conditions of existence'. These are partly organic, partly inorganic in nature; both, as we have shown, are of the greatest significance for the form of organisms, for they force them to become adapted. Among the inorganic conditions of existence to which every organism must adapt itself belong, first of all, the physical and chemical properties of its habitat, the climate (light, warmth, atmospheric conditions of humidity and electricity), the inorganic nutrients, nature of the water and of the soil, etc.*" (Egerton, 2013). This definition has been slightly modified over the years but its essence has remained intact and nowadays the British Ecological Society defines it as "*the study of interactions among living things and their environment*", keeping in mind that humans play an important role in it (Odum, 1975).

Further to these definitions, ecology classifies the biosphere in a set of integrative, hierarchically organised levels. The components of each level interact to form larger functional systems with new properties, and ecology studies the interactions among the different components of ecosystems (Margalef, 1978). Ecology focuses mostly on the study of populations, communities and ecosystems rather than individual species (Margalef, 1978). However, studies focused on understanding a certain level (i.e. a species) can provide relevant information on several aspects such as trophic interactions with other species, its relationship with the surrounding environment and the influence of human activities. Thus, the integration of studies at different levels can provide information about the ecology of the species and its surrounding environment (Odum, 1975), becoming crucial tools to assess the conservation needs of both species and ecosystems.

1.1. *Studying cetacean ecology*

Cetaceans have adapted to a wide variety of habitats, including coastal and oceanic waters, habitats above the continental shelves and freshwater habitats (Ballance, 2009). Some species, such as the killer whale (*Orcinus orca*, Linnaeus 1758), the common bottlenose dolphin (*Tursiops truncatus*, Montagu 1821, hereafter referred to as bottlenose dolphin) or common dolphins (*Delphinus* spp.) have wide distribution ranges

(Connor et al. 2000; Forney and Wade, 2007; Jefferson et al. 2015), whereas other species such as the four species of the genus *Cephalorhynchus* are restricted to relatively small specific areas (Pichler et al. 2001). By developing unique physical and physiological adaptations, cetaceans have been able to reach and forage at different depths in the water column, from shallow areas to deep waters (Ballance, 2009; Hooker et al. 2012). These adaptations have allowed them to play major roles in ecosystems, influencing their structure and dynamics (Bowen, 1997). Studying cetacean ecology can provide valuable information about the ecosystem they inhabit, their interactions with it and with other species. This information can be used to improve conservation and management strategies.

Given cetacean diversity, their capacity to adapt to a wide range of habitats, their importance in marine ecosystems and the fact that they live in a challenging environment, makes studies to understand their ecology both crucial and complex. Additionally, ecology covers numerous aspects such as distribution, abundance, habitat use, foraging ecology, energetics and behavioural ecology. It aims to interpret the role of a species in its surrounding ecosystem and interactions with other species (Ballance, 2009). To study all these aspects, several techniques have been developed (Boyd et al. 2010) and have been applied to the study of the ecology of different cetacean species (Barlow et al. 2008; Watanabe et al. 2012; Pirotta et al. 2013; Weber et al. 2014; Thompson et al. 2015; Baumgartner et al. 2017; Díaz López and Methion, 2018; Methion and Díaz López, 2019a). The combination of different methods can result in interdisciplinary approaches that can provide a much deeper understanding of the ecology of the studied species. These studies should account for the fact that human activities have altered and are affecting most marine ecosystems (Odum, 1975; Ballance, 2009). In doing so, ecological studies provide an excellent opportunity to evaluate the consequences of human activities and to suggest and improve conservation strategies.

1.1.1.Distribution and habitat use

Cetacean distribution and the processes that influence their habitat choice are major aspects that determine their ecology (Redfern et al. 2006). Hence, studies that aim to identify the factors driving cetacean distribution and habitat use provide valuable information allowing us to make predictions about their distribution, and are crucial to

improve cetacean conservation (Hamazaki, 2002; Rushton et al. 2004; Guisan et al. 2013). Although the influence of environmental variables on species distribution has been known for a relatively long time (Grinnell, 1917), it was not until the last decades of the 20th century that methods to identify and predict cetacean distributions were developed (Hamazaki, 2002).

As with any other top predator, cetacean distribution and habitat selection are heavily affected by the movements of their prey (Redfern et al. 2006). However, since obtaining reliable data on prey distribution and abundance is difficult, most studies use abiotic and biotic factors as a proxy for prey distribution (Elith and Leathwick, 2009; Pirotta et al. 2011; Díaz López and Methion, 2017, 2018). Indeed, the relationship between different abiotic and biotic factors and cetacean distribution has been studied in several areas recently (Hastie et al. 2005; Friedlaender et al. 2006; Praca and Gannier, 2008; Torres et al. 2008; Marubini et al. 2009; Pirotta et al. 2011; Virgili et al. 2017). However, studying cetacean distribution can be a challenging task for several reasons. First, gathering cetacean data in a constantly changing environment often has high logistical and economic requirements (Hammond, 2010). Second, effective research surveys can only be carried out when sea and weather conditions do not negatively affect the probability of spotting these animals. Third, due to the physical and oceanographical dynamics of marine systems, resources are patchily distributed, influencing the movements of small schooling animals, ultimately determining top predator distribution (Croll et al. 2005; Certain et al. 2011). Lastly, most widespread research techniques on cetaceans rely on the visual detection and identification of these animals at the water surface. However, cetaceans are highly mobile marine animals that spent only a fraction of their time at the water surface. All these factors combined hamper the detection of cetaceans at sea, ultimately increasing the difficulty of distribution studies.

Despite these challenges, several methods have been developed. Probably the most widespread methodology to study and assess species distribution is the use of statistical models that link abiotic and biotic factors with the presence of the studied species. These are known as Species Distribution Models (SDMs) (Elith and Leathwick, 2009). Several statistical approaches have been used in this regard, including linear and generalised regressions (GLMs, GAMs), environmental envelopes, Bayesian methods or

neural networks, among others (Guisan and Zimmermann, 2000). The combination of these statistical approaches with Geographical Information Systems (GIS) and the use of remote sensing data drastically increased the use of SDMs, as it allowed ecologists to (1) store and manage increasing quantities of data more easily; and (2) obtain data on abiotic and biotic factors for remote areas (Rushton et al. 2004; Elith and Leathwick, 2009).

Broadly speaking, SDMs can rely on two types of species data, presence-only and presence/absence data (Elith and Leathwick, 2009). The first type consists of records of the locations where the species has been recorded, excluding those areas in which the species was absent (Elith and Leathwick, 2009). The second type includes information of both locations in which the species was present and locations in which it was absent (Elith and Leathwick, 2009). Presence/absence methods can provide precise information on species distribution (Elith and Leathwick, 2009), however true absences (i.e. when the species is not present in the sampled location) might be difficult to record for highly mobile species such as cetaceans (Austin, 2002; Jiménez-Valverde et al. 2008; Praca and Gannier, 2008). Indeed, absence of cetaceans in a sampled location might be explained because (1) the sample location is an unsuitable habitat; (2) the sample location is a suitable habitat, but the species was not present; and (3) the species could not be detected. Therefore, the use of presence-only methods can pose a better option when studying the distribution of highly mobile and cryptic species (Hirzel et al. 2002).

1.1.2.Cetaceans as part of the ecosystem

The relationships between the organisms and their environment was a central aspect in both Haeckel's and the British Ecological Society's definition of ecology. Many cetacean species are considered top predators, and as such, they are fundamental components of marine ecosystems (Bowen, 1997). Their importance lies in the fact that they can impact other species through direct processes, like predation, and indirect processes, such as resource facilitation (making prey available to other predators) and their response to predation risk, determining the composition and functioning of the ecosystem (Wirsing et al. 2008; Morissette and Brodie, 2014; Kiszka et al. 2015; Estes et al. 2016). Similarly, cetaceans are influenced by bottom-up processes, in which available resources can determine the abundance and distribution of top predators (Estes et al.

2016). Additionally, cetaceans are susceptible to ecosystem alterations caused by human activities, which can have direct, indirect and cumulative effects on marine top predators (Harwood, 2001; Díaz López et al. 2008; Davidson et al. 2012; Maxwell et al. 2013; Weir and Pierce, 2013). All these characteristics make cetaceans fundamental components of ecosystems, not only because they influence and regulate processes within them, but also because they can serve as indicators of ecosystem health (Maxwell et al. 2013).

Placing cetaceans within an ecosystem context provides information about their relationships with other species, the surrounding environment and human activities, and the role that they play in it (Katona and Whitehead, 1988; Bowen, 1997). Therefore, studies that incorporate as many of these aspects as possible are key to explore cetaceans ecology (Ballance, 2009). Such studies can be used to evaluate the conservation status of the different species, especially if they address the effects of human activities as well (Reynolds et al. 2009). However, marine ecosystems are complex entities in which processes are not always evident (Coll et al. 2009a), and assessing the role that cetaceans play within them is not straightforward (Bowen, 1997).

Important contributions throughout the 20th century laid the foundations of the current understanding of ecosystem functioning and processes (Layman et al. 2015). Building on these contributions different mathematical models were developed to describe the main processes within ecosystems and even simulate the evolution of a given ecosystem and its components (Christensen and Pauly, 1993a). Among the different approaches, Ecopath with Ecosim (EwE), a mass-balance ecosystem modelling software, has become the most widely used application to study marine ecosystems (Coll et al. 2015). EwE provides a framework to create mass-balance trophic models of (mainly) marine ecosystems, the dynamics that shape them over time and the effects of fishing and the environment on them and all their components (Pauly et al. 2000; Christensen and Walters, 2004). EwE has mostly been used as a tool to describe food web dynamics, to assess fishing impacts on ecosystems and to suggest management strategies (Christensen, 2009; Colléter et al. 2015). Additionally, it provides a comprehensive approach to the ecosystem dynamics that can be used to explore the effect of fisheries on top predators like cetaceans and to suggest potential measures to promote their conservation (Piroddi et al. 2010; Lassalle et al. 2012).

1.2. *Marine Fisheries*

Fish resources are the most important source of protein and micronutrients for many human communities, especially in Africa, Asia and Oceania (Béné et al. 2015; Pauly and Zeller, 2016; Loring et al. 2019). Indeed, marine ecosystems have been fundamental for numerous civilisations and they have been exploited by humans since ancient times (Lackey, 2005). It is however, from the second half of last century that global fishing catches increased significantly, reaching their peak around the early 1990s and showing a slight but steady decline since then (Pauly and Zeller, 2016). In parallel, global fishing capacity and effort have increased steadily since the 1970s (Bell et al. 2017; Rousseau et al. 2019). Despite some controversy about its extent (Pauly, 2008; Daan et al. 2011; Pitcher and Cheung, 2013), there is now widespread agreement that marine fishing activities cause a drastic impact not only on the harvested species, but also on other marine species and ecosystems (Pauly et al. 2002; Worm et al. 2009; Froese et al. 2012). For instance, global numbers of collapsed and overexploited fish stocks have been steadily increasing since the second half of the 20th century (Pauly, 2008; Froese et al. 2012) and the mean trophic level of world fisheries catches has decreased since then (Pauly et al. 1998).

A similar pattern is found in European waters (Gascuel et al. 2016), where recent studies showed that although some progress has been made since 2001 (Cardinale et al. 2013), 64% of the stocks are being overexploited and only 12% of the stocks were well managed, according to current legislation (Froese et al. 2018). In order to achieve a more sustainable exploitation of the fishing resources and reduce the impact of fishing activities on the ecosystems, the European Union adopted the most recent iteration of the Common Fisheries Policy (CFP), which came into effect in January 2014. This policy built on the United Nations Convention on the Law of the Sea (UNCLOS, 1982), which states that coastal countries should manage fisheries aiming to achieve maximum sustainable yield (MSY). European Member States committed to this at the World Summit on Sustainable Development held in Johannesburg in 2002 (WSSD, 2002). Since its approval in 2002, the CFP urged countries to achieve MSY by 2020 (EC, 2013) and to promote the application of an Ecosystem Approach to Fisheries Management (Jennings and Rice, 2011).

1.3. *Cetaceans and Fisheries*

Numerous human activities are causing impacts on the marine environment (Vitousek et al. 1997; Halpern et al. 2008). These are especially important for marine top predators, such as cetaceans, in coastal ecosystems, where the density of human population is often higher, and increases the extinction risk for marine species (Davidson et al. 2012). Among the various human activities that threaten cetaceans globally, interactions with fisheries are an important, widespread and complex issue (Plagányi and Butterworth, 2009). Due to the spatial, temporal and trophic overlap between cetaceans and fisheries, direct and indirect interactions can lead to detrimental effects on both sides (Trites et al. 1997; Kaschner et al. 2001; Bearzi, 2002; Birkun Jr., 2002; Kaschner and Pauly, 2005; Díaz López, 2006; Gilman et al. 2006; Read, 2008; Morissette et al. 2012; Moore, 2013; Brown et al. 2014). This is in fact a sensitive issue, because it brings into conflict two important sectors. On one side, fishermen and the fishing industry are a key source of employment in many communities, and on the other side, cetaceans are very charismatic marine species, the conservation of which is important for a substantial portion of society (Matthiopoulos et al. 2008).

1.3.1.Impacts on fisheries

Traditionally, cetaceans have been considered as competitors by fishermen (Plagányi and Butterworth, 2009). Although different studies suggest that the resource overlap is not as high as originally thought (Trites et al. 1997; Kaschner et al. 2001; Morissette et al. 2012), it occurs in some specific areas, where interactions with cetaceans can be regarded as a serious problem by fishermen (Kaschner and Pauly, 2005). For instance, dolphins have developed a behaviour known as depredation, which is the ability to take catches or bait from gillnets, traps and longlines (Díaz López, 2006; Brotons et al. 2008; Bearzi et al. 2011; Goetz et al. 2014), probably as a way to optimise their foraging activities while decreasing the energy expenditure (Fertl, 2009). This can result in damage to the fishing gear, devaluation of the catch as a consequence of removals or mutilations, and ultimately time and economic loss (Bearzi, 2002; Fertl, 2009). Other important reasons of concern are competition for the same resources, gear damage, catch and economic losses (Figure 1.1) (Bearzi, 2002; Fertl, 2009).

1.3.2.Impacts on cetaceans: Operational vs ecological effects

Interactions between fisheries and cetaceans also impact the latter directly and indirectly (Figure 1.1). Direct impacts are also known as operational effects and are a consequence of the physical contact with the fishing gear or vessels, resulting in the injury, unintentional capture or death of the animal (Read, 2008; Northridge, 2009). These include entanglement in gillnets, pelagic driftnets and purse seines, accidental capture by trawlers, entanglement in ropes, injuries caused by longline hooks and collision with fishing vessels (Bearzi, 2002; Read, 2008; Northridge, 2009). Some of these examples, like the bycatch by trawlers, are a widespread issue affecting several dolphin populations (Read et al. 2006; Fernandez-Contreras et al. 2010; De Boer, 2012; Thompson et al. 2013), and are becoming a reason for concern in certain areas (ICES, 2020; Peltier et al. 2019). Other interactions, such as the entanglement in driftnets have led to fishing restrictions (Tudela et al. 2005; Sala, 2016). Others, like the use of gillnets in the Gulf of California and New Zealand or the use of lobster pots in the North-West Atlantic, are limited to specific areas, seriously threatening cetaceans species or populations with small distribution ranges, such as the Vaquita (*Phocoena sinus*, Norris and McFarland 1958), the Hector's dolphin (*Cephalorhynchus hectori*, Van Bénéden 1881), or the northern right whale (*Eubalaena glacialis*, Müller 1776), respectively (Dawson and Slooten, 2005; Knowlton et al. 2012; Taylor et al. 2017).

On the other hand, indirect impacts of fisheries on cetaceans, also known as biological or ecological effects (hereafter referred to as ecological effects), are related to direct and indirect competition for resources, habitat degradation and loss and behaviour alteration (Bearzi, 2002; Matthiopoulos et al. 2008; Northridge, 2009). While the link between operational effects and their impacts on cetaceans is apparent, it is much more difficult to detect the consequences of the ecological effects (Northridge, 2009; Moore, 2013). This is due to the fact that there are several factors involved in this type of interaction. For instance, the competition for resources can be direct (when both cetaceans and fisheries target the same species) or indirect (when they target different species that are linked through the food web). Direct competition for resources requires spatial and temporal overlap, while indirect competition could be influenced by ecosystem dynamics and environmental factors (Matthiopoulos et al. 2008; Moore, 2013).

Although it is difficult to establish the true nature of the ecological effects, marine fisheries take between 80 and 110 MT of fish yearly (Pauly and Zeller, 2016), operating in areas where cetaceans regularly occur (Kaschner et al. 2001), and targeting, to some extent, similar species (Plagányi and Butterworth, 2009). All of these aspects can lead to potential ecological effects of fisheries on cetaceans, which, in turn, can become more important in the future due to cetaceans and human populations growth, and thus a higher food demand (DeMaster et al. 2001). Indeed, recent studies have highlighted the consequences of ecological effects on different cetacean populations (Bearzi et al. 2006; Piroddi et al. 2010; Gómez-Campos et al. 2011).

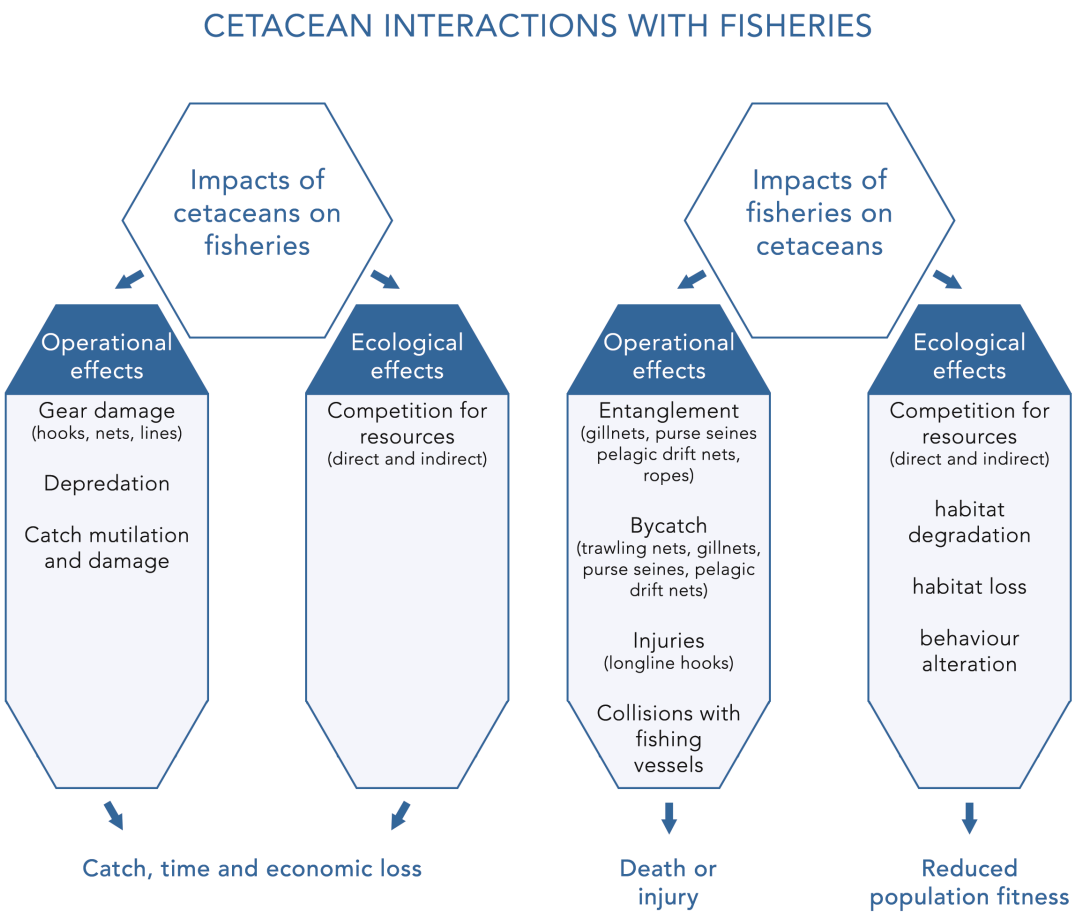


Figure 1.1 Cetacean – Fisheries interactions. *A summary of some of the possible interactions between cetaceans and fisheries and their consequences (Bearzi, 2002; Read, 2008; Northridge, 2009; Plagányi and Butterworth, 2009).*

1.3.3. Consequences for management and conservation

The reduced fishing resources coupled with a steadily growing human population and the consequent higher demand for food, bring fisheries management strategies often into conflict with conservation efforts (DeMaster et al. 2001; Matthiopoulos et al. 2008). On the one side, fisheries are an important economic sector in many countries and a crucial source of employment for many coastal communities (Teh and Sumaila, 2013; Surís-Regueiro and Santiago, 2014; Garza-Gil et al. 2017). On the other side, they cause detrimental effects on marine species and ecosystems (Jennings and Kaiser, 1998; Pauly et al. 2005). Therefore, fisheries management has evolved from trying to obtain the maximum yield from the different stocks, to the more recent Ecosystem Approach to Fisheries Management strategies, which acknowledge the multispecific nature of ecosystems and aim to understand the relationship among their components (Larkin, 1996; Mace, 2001; Jennings and Rice, 2011; Link et al. 2011). In parallel, several countries have created legal frameworks, such as the Directive on the Conservation of Natural Habitats (hereafter referred to as Habitats Directive; Council Directive 92/43/EEC) in Europe and the Marine Mammal Protection Act in the United States of America (EC, 2008; Reynolds et al. 2009; EC, 2013; Rodriguez, 2017), that intend to preserve threatened marine habitats and species, among them cetaceans. In short, fishing management strategies and conservation measures often move in an unstable balance where they have to try to include all involved parties in the decision-making process in order to achieve successful outcomes that promote both the conservation of marine species and habitats and the sustainable exploitation of fishing resources.

1.4. The common dolphin

The short-beaked common dolphin (*Delphinus delphis*, Linnaeus 1758, hereafter referred to as common dolphin), is an easy to recognise cetacean species due to its external appearance (Figure 1.2). The species has a dark grey colouration on the back and a very distinct "hourglass" colouration on the sides, composed by a pale to ochre thoracic patch and a light grey patch along the tailstock (Jefferson et al. 2015). Common dolphins have two dark stripes at each side, one extending from the chin to the flipper and the second extending from the eye towards the marked crease between the beak and the melon. It has a moderately long beak, clearly separated from the melon. The

dorsal fin is located at the middle of the back and it is mostly dark, although some individuals have a light patch of variable size in the centre. Adult individuals can reach between 2.2 and 2.5 m depending on the region (Jefferson et al. 2015).



Figure 1.2 *A common dolphin seen in Galician waters. Photo credit: Bruno Díaz López – BDRI.*

1.4.1.Taxonomy

Common dolphins belong to the family Delphinidae, order Cetacea within the superorder Cetartiodactyla. Until the end of the 20th century, a single species, *Delphinus delphis* was recognised in the genus (Jefferson and Waerebeek, 2002). In 1994, Heyning and Perrin (1994), described the long-beaked common dolphin (*Delphinus capensis*, Gray 1828), the second species of the genus. Within the short-beaked common dolphins, morphological and genetic evidence suggest that the individuals inhabiting the Black sea would belong to a separate subspecies (*D. delphis ponticus*) (Amaha, 1994; Natoli et al. 2003). Microsatellite and mtDNA analyses suggest that common dolphins in the North-West Atlantic Ocean form a differentiated cluster from the populations living in north-eastern Atlantic waters, and that gene flow between the North-East Atlantic populations is high (Natoli et al. 2006).

1.4.2.Species distribution, abundance and habitat use

Common dolphins are widely distributed in tropical and temperate waters of the Pacific and the Atlantic oceans, where they can be found in both coastal and offshore waters (Jefferson et al. 2015). Although no records exist from the Gulf of Mexico and the Caribbean, they inhabit other enclosed seas, such as the Mediterranean Sea and the Black Sea (Bearzi et al. 2003). In the North-East Atlantic, common dolphins show a wide distribution that ranges from the mid-Atlantic ridge, the Azores and Madeira Islands and the Strait of Gibraltar all the way to the south of Norway (at around 70 N°), although they are most commonly found south from 60° N (Figure 1.3) (Murphy et al. 2013; Correia et al. 2019).

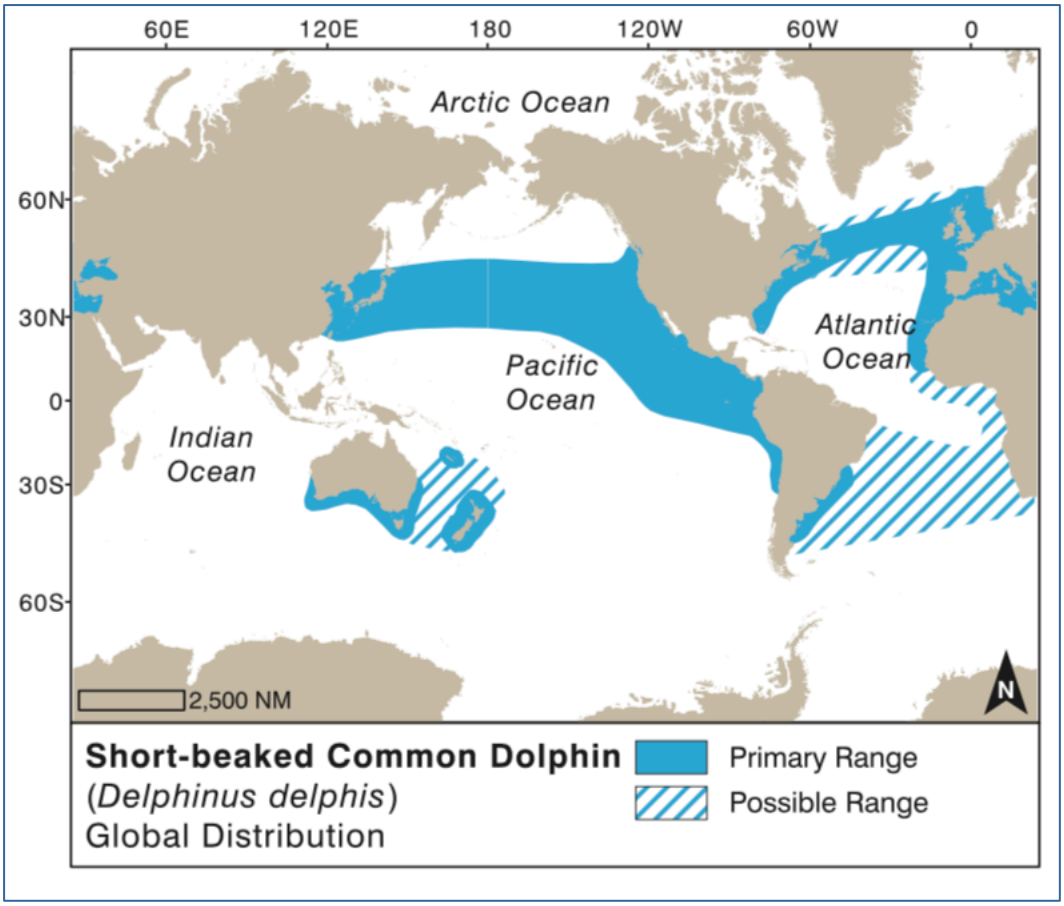


Figure 1.3 *Map showing the global distribution of the common dolphin. Taken from Jefferson et al. 2015.*

Their global abundance has been estimated at just over 3,500,000 million individuals (Jefferson et al. 2015). However, they show differing abundance depending on the region, ranging from 3,000,000 animals in the eastern tropical Pacific to 14,700 in the

Alboran Sea (Jefferson et al. 2015). In the North-East Atlantic, common dolphins are the second most abundant cetacean species with an estimated total abundance of 268,540 individuals (Hammond et al. 2017).

This small cetacean is a pelagic species commonly found above the continental shelf break and beyond, although they can also be seen in shallower waters (Bearzi et al. 2003; Certain et al. 2008; Murphy et al. 2013). Seasonal movements have been reported in numerous regions such as the Alboran Sea, the Bay of Biscay and the English Channel, and they have been linked to different aspects such as topographic and environmental variables or prey distribution (Neumann, 2001; Cañadas and Hammond, 2008; MacLeod et al. 2009).

1.4.3. Diet

As with any other opportunist predator, common dolphins feed on a variety of fish and cephalopod species that differs between regions. Generally, they show a preference for energy rich, small shoaling pelagic fish of the Clupeidae and Engraulidae families (Silva, 1999; Meynier et al. 2008a; Brophy et al. 2009; Spitz et al. 2010; Loizaga de Castro et al. 2016; Marçalo et al. 2018). However, they also feed on demersal fish species of the Merlucciidae and Gadidae families (Santos et al. 2013; Loizaga de Castro et al. 2016), and cephalopods (Meynier et al. 2008b). Despite some regional variability, in the North-East Atlantic they mainly feed on fish species such as blue whiting (*Micromesistius poutassou*, Risso 1827), sardine (*Sardina pilchardus*, Walbaum 1792), European anchovy (*Engraulis encrasicolus*, Linnaeus 1758) and mackerel (*Scomber* spp.) (Silva, 1999; Meynier et al. 2008a; Santos et al. 2013; Marçalo et al. 2018). Common dolphins not only show spatial variation in their diet but they also adjust their diet in relation to prey availability and prey fluctuations (Santos et al. 2013).

1.4.4. Threats and conservation

Due to their widespread distribution and abundance, the International Union for the Conservation of Nature (IUCN) has listed common dolphins as Least Concern (Hammond et al. 2008). However, in some areas, such as the Mediterranean Sea, the species has been listed as Endangered due to fragmentation and a decreasing trend in abundance (Bearzi, 2012). Despite its good conservation status at a global level, common dolphins

have faced and face several threats. Among them, bycatch caused by pelagic purse seine, driftnet and trawl fisheries, is an issue of global concern, since it affects several populations in numerous areas worldwide (Silvani et al. 1999; Tudela et al. 2005; De Boer, 2012; Thompson et al. 2013). This is indeed a matter of special concern in the North-East Atlantic, where bycatch has increased in certain areas recently (Mannocci et al. 2012; Peltier et al. 2019; ICES, 2020), and the European Union has urged some countries to improve their preventive and control measures (European Commission EC, 2020). Another threat to the species is overfishing, which has been suggested as the main cause of the disappearance of common dolphins in specific areas (Birkun, 2002; Bearzi et al. 2008). Further threats are caused by pollutants, climate change, habitat degradation or the ingestion of microplastics (Murphy et al. 2013; Hernandez-Gonzalez et al. 2018).

To minimise these impacts and to ensure common dolphin conservation, the species has been included in several national and international legislations and conventions. The international agreements cover a wide variety of aspects such as international trade (Annex II of the Convention on International Trade in Endangered Species, CITES), conservation of habitats and species (Appendices I and II of the Convention on Migratory Species or Bonn Convention, CMS), development of conservation and management plans (Agreement on the Conservation of Small Cetaceans of the Baltic, North East Atlantic, Irish and North Seas, ASCOBANS; Agreement on the Conservation of Cetaceans in the Black Sea Mediterranean Sea and Contiguous Atlantic Area, ACCOBAMS) and monitoring and reduction of bycatch (EC, 2004). In the European Union, the Habitats Directive covers the different aspects mentioned above, by listing the common dolphin in Annex IV (Council Directive 92/43/EEC). The Habitats Directive specifically prohibits the intentional killing of all species listed in this annex, encourages Member States to monitor the impact caused by incidental captures and killing of these species, and urges governments to promote research and conservation measures to ensure that the impact is kept to a minimum, especially in the areas that include important habitats for the species ecology and reproduction (Council Directive 92/43/EEC).

1.5. *Geographical context*

The ecology of a given marine species, such as the common dolphin, can be influenced by a number of variables such as oceanography, topography and environmental conditions of a particular location. Even the human activities carried out in the marine environment vary from one region to the next and might have differing impacts on marine species. Therefore, it is important to provide contextual information about the area where the study has been carried out, when studying the ecology of a species.

1.5.1. Study area

This work was carried out in Galicia (North-West Spain), a region located at the northern limit of the Canary/Iberian Current Upwelling System (Torres et al. 2003; Arístegui et al. 2009; Kämpf and Chapman, 2016), one of the four major coastal upwelling systems worldwide (Figure 1.4). Its 1,498 km of coastline is shaped by geographical features such as capes and inlets, the latter formed by drowned tectonic valleys called rias (Prego et al. 1999; Dias et al. 2002). These inlets are classified into Rías Altas (marked in green in Figures 1.4 and 1.5), the ones located to the north of Cape Finisterre (marked with a black arrow in Figures 1.4 and 1.5) and Rías Baixas (marked in yellow in Figures 1.4 and 1.5), located to the south of Cape Finisterre (Prego et al. 1999).

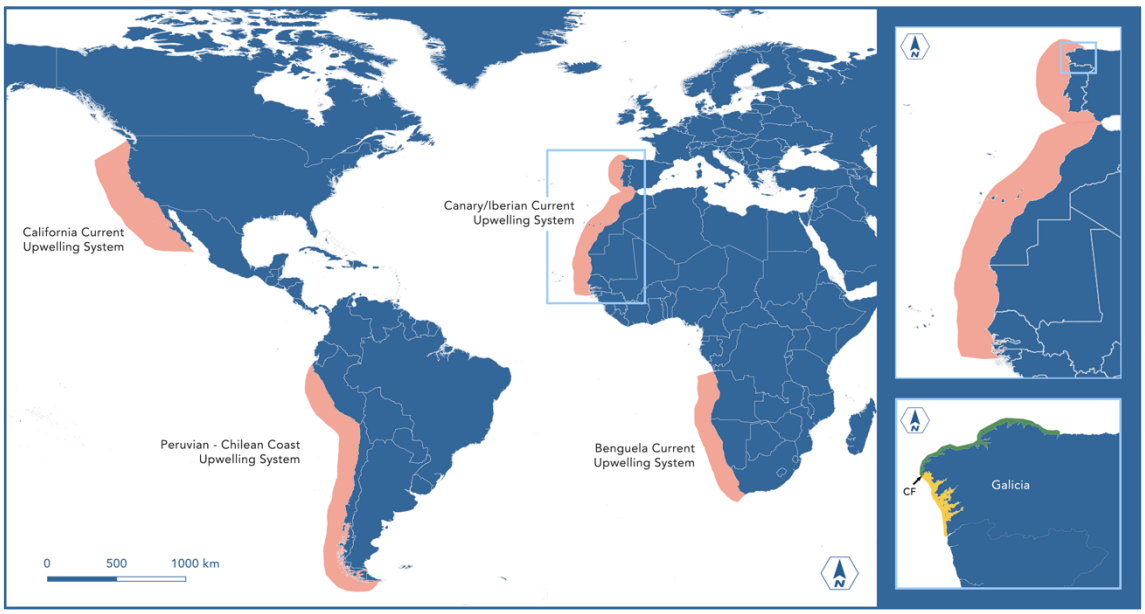


Figure 1.4 *Location of the major coastal upwelling systems of the world (Kämpf and Chapman, 2016). The top right map shows the Canary/Iberian Current Upwelling System in more detail. The bottom right map shows Galicia, and the location of the Rías Altas (green) and the Rías Baixas (yellow) divided by Cape Finisterre (CF).*

The Rías Altas and the Rías Baixas regions are geomorphologically different (Dias et al. 2002; Sanz Alonso, 2005). The latter is characterised by a narrow continental shelf, extending 30 to 50 km west, and the continental break occuring at 180 to 200 m in depth (Dias et al. 2002). The Rías Baixas region is formed by four rias with a NE – SW orientation (Sanz Alonso, 2005) from north to south, Ría de Muros – Noia, Ría de Arousa, Ría de Pontevedra and Ría de Vigo (Figure 1.5).

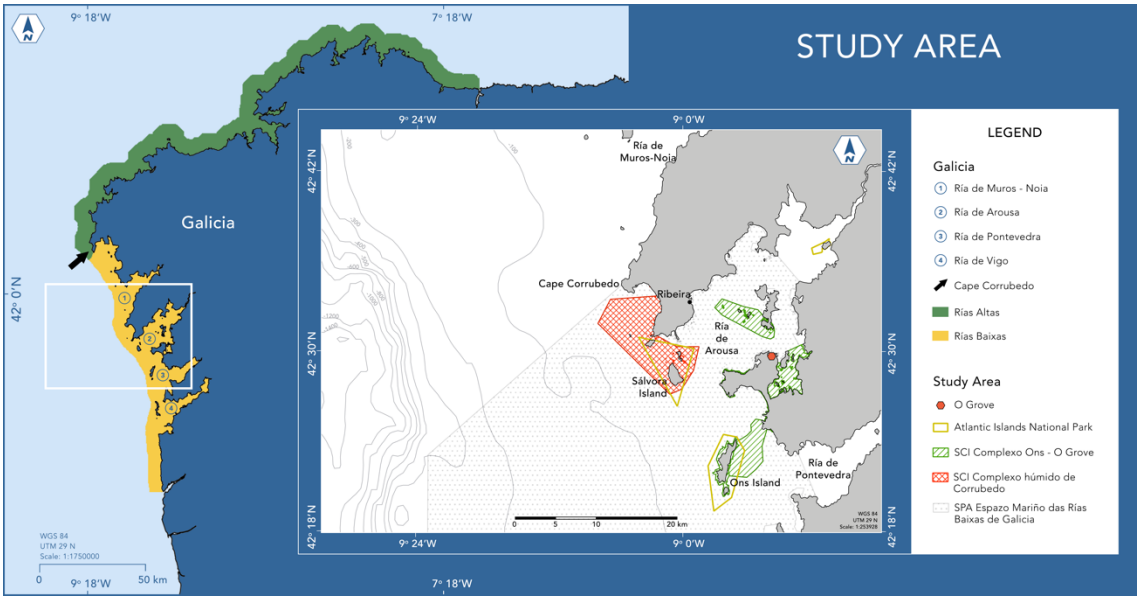


Figure 1.5 *Map of the study area, showing its location in the Rías Baixas and showing the location of the Atlantic Islands National Park and other Natura 2000 sites such as the Sites of Community Importance (SCIs) Complexo Ons – O Grove and Complexo humido de Corrubedo and the Special Protection Area Espazo Mariño das Rías Baixas de Galicia.*

The rias and coastal area adjacent to the Rías Baixas exhibit a high marine primary productivity as a result of the combination of two factors. On one hand, seasonal upwelling events caused by northerly wind regimes carry deep, nutrient-rich waters masses to the photic layer, and on the other hand, terrestrial runoff caused by river discharge, input nutrients into the rias and the coastal areas (Torres et al. 2003; Pitcher et al. 2010; Alvarez et al. 2012). Owing to the enhanced primary productivity, the Rías Baixas and the adjacent continental shelf waters have historically been very important for marine top predators (Pierce et al. 2010; Díaz López and Methion, 2018, 2019), fisheries (Villasante, 2012; Surís-Regueiro and Santiago, 2014) and aquaculture (Figueiras et al. 2002).

The harbour from which the dedicated research boat surveys have been carried out for this study is located in O Grove, Ría de Arousa (Figure 1.5), which is the largest ria in the Rías Baixas region, with a total surface of 230 km^2 (Prego et al. 1999). Research trips included waters of the Ría de Arousa and waters above the continental shelf west from the entrance of three rías (from north to south, Ría de Muros – Noia, Ría de Arousa and Ría de Pontevedra, Figure 1.5).

This is an area of great importance for aquaculture, especially waters inside of the Ría de Arousa (Figure 1.6), and fisheries, which are carried out inside the inlet and in waters above the continental shelf. In parallel, it hosts several protected areas aimed at preserving its biodiversity (Figure 1.5). Among them, the Atlantic Islands National Park, protects 72.85 km^2 of waters around Cortegada, Sálvora, Ons and Cíes Islands (Ley 15/2002). Additionally, several Natura 2000 sites of differing size, protect numerous species of marine birds and some species of cetaceans, such as the bottlenose dolphin and the harbour porpoise (*Phocoena phocoena*, Linnaeus 1758). The biggest of these sites is the Special Protection Area Espazo Mariño das Rías Baixas de Galicia which protects 2,219 km^2 of waters between the border with Portugal and cape Corrubedo (European Environmental Agency; https://www.eea.europa.eu, last accessed August 30th 2020). There are two further Sites of Community Interest (SCIs) that protect 130.64 km^2 of coastal waters inside the Ría de Arousa and between the mainland and the islands of Ons and Sálvora (European Environmental Agency; https://www.eea.europa.eu, last accessed August 30th 2020).



Figure 1.6 *Shows the outer part and the entrance of Ría de Arousa, with Sálvora Island at the back and an area with mussel rafts at the foreground. Photo credit: Oriol Giralt Paradell.*

1.5.2.Fisheries in Galicia

Fisheries have traditionally been a strategic economic sector in Galicia (Villasante, 2012; Surís-Regueiro and Santiago, 2014; Garza-Gil et al. 2017). In 2017, fisheries provided direct employment to nearly 17,000 people (1.53% of the total employment), representing 2.0% of the Galician gross domestic product (IGE, 2020). Together with the aquaculture sector, they are crucial for the economy of the Rías Baixas, especially in areas around Ría de Arousa, where they represent approximately 12.58% of the total employment (Surís-Regueiro and Santiago, 2014). The Galician fishing fleet is the most important fishing fleet in Spain, representing 49% of the Spanish fishing vessels, 42% of the country's GT and 36% of the aggregated power in 2019 (MAPA, 2020). Furthermore, with around 5% of the total number of fishing vessels, it is one of the most important fishing fleets in Europe (MAPA, 2020). Galicia is also an important region in terms of landings at the national and European scales (Vázquez-Rowe et al. 2011; Villasante, 2012).

The fleet can be divided in three categories depending on the area where they operate, (1) the distant-water fleet, that operates in remote waters outside of the European Union jurisdiction; (2) the large-scale fleet, that operates in distant European Union waters; and (3) the small-scale coastal fleet, that operates in Spanish waters (Table 1.1, Figure 1.7). The latter can be further divided into the coastal fleet, that operates in waters above the continental shelf and the artisanal fleet, that mainly operates in waters inside of the rias. The artisanal fleet is the most numerous one and comprises small vessels, with an average length of 6 m, equipped with mixed-gear and targeting different species depending on the season (Surís-Regueiro and Santiago, 2014). The coastal fleet is the second largest category and includes vessels with an average length of 20 metres that use several fishing techniques, such as trawling, purse-seine, gill-net and long-line (Surís-Regueiro and Santiago, 2014). The large-scale and distant water fleets are composed of larger vessels with lengths ranging from 33 to 90 m, that mainly use long-lines, trawls and purse-seines (Surís-Regueiro and Santiago, 2014).

Table 1.1 *Composition of the Galician fishing fleet in 2019 dividing it in different categories according to the fishing grounds where they operate (Surís-Regueiro and Santiago 2014; Xunta de Galicia, Conselleria do Mar, 2020b).*

Fleet Category	Sub category	Area	Number of Vessels	%
Distant-water fleet	Distant water fleet	Remote non-EU waters	99	2
Large-Scale fleet	Large-scale fleet	EU waters	71	2
Small-scale coastal fleet	Coastal fleet	Spanish continental shelf waters	302	7
	Artisanal fleet	Inshore waters	3,852	89



Figure 1.7 *Types of fishing vessels in Galicia. Fishing vessels used in the artisanal (A and D) and coastal (B and C) fisheries in Galicia. Photo credit: Bruno Díaz López (A, B, D) – BDRI.*

1.5.3.Common dolphins in Galicia

Common dolphins are the most abundant cetacean in Galician waters (López et al. 2004; Spyrakos et al. 2011), where they can be seen above the continental shelf and beyond the continental slope, especially in the Rías Baixas region (Fernandez-Contreras et al. 2010; Spyrakos et al. 2011; Saavedra et al. 2018;). Two recent studies have estimated the abundance of the species at 8,137 animals in Galician waters (López et al. 2004), and

12,831 animals in waters along North-West Spain, from the border with France to the border with Portugal (Saavedra et al. 2018). Both studies estimated a similar animal density (0.39 and 0.35 dolphins/km^2 respectively). In Galicia, common dolphins mainly feed on blue whiting, sardine and to a lesser extent on other species of fish such as *Atherina* spp., horse mackerel (*Trachurus* spp.), and squid (Santos et al. 2013). As is the case in other areas, the major threat to the species conservation is bycatch in fishing activities, mainly by trawlers and gillnets (López et al. 2003; Fernandez-Contreras et al. 2010; Goetz et al. 2014). Despite these studies, common dolphins (the Atlantic population) are still listed as data deficient in the Red Book of Spanish Vertebrates, the Spanish List of Wildlife Species under Special Protection Regime and the Spanish Catalogue of Threatened Wildlife (Blanco and González, 1992; Ley 42/2007; Real Decreto 139/2011). Additionally, several national and regional legislations affect the protection of the species in a direct or indirect manner (Ley 15/2002; Real Decreto 1727/2007; Ley 41/2010).

1.5.4.Other cetaceans in Galicia

Up to 19 species have been recorded in Galician waters. These include several odontocetes, such as bottlenose, striped (*Stenella coeruleoalba*, Meyen 1833) and Risso's dolphins (*Grampus griseus*, G. Cuvier 1812), pilot whales (*Globicephala melas*, Traill 1809) and harbour porpoises, as well as various mysticetes, such as minke (*Balaenoptera acutorostrata*, Lacépède 1804), fin (*B. physalus*, Linnaeus 1758) and blue whales (*B. musculus*, Linnaeus 1758) (López et al. 2002, 2004; Pierce et al. 2010; Methion and Díaz López, 2018; Díaz López and Methion, 2018, 2019).

1.5.5.Interactions between cetaceans and fisheries in Galicia

As a result of being a very productive area, the waters above the continental shelf of Galicia are attractive for both cetaceans and fisheries. This shared interest has led and continues to lead to interaction between cetaceans and fisheries. Indeed, interviews with Galician fishermen revealed impacts on both fishing gear and cetaceans (Goetz et al. 2014). For instance, direct impacts on fisheries were mainly caused by common and bottlenose dolphins and included catch damage or depredation, scattering of fish and damage to driftnets, gillnets, trawls and purse seines (Goetz et al. 2014). The same

interviews showed that bycatch was only perceived as a problem by a small percentage of fishermen (Goetz et al. 2014). However, other studies revealed that around 20% of the cetaceans found dead in Galician beaches showed signs of or were reported as bycatch (López et al. 2002), and that around 800 cetaceans were estimated to be incidentally caught in the area every year (López et al. 2003; Fernandez-Contreras et al. 2010; Goetz et al. 2014). The species most frequently caught was the common dolphin, which was mainly incidentally caught in trawling operations and gillnets (López et al. 2003; Fernandez-Contreras et al. 2010; Goetz et al. 2014), bycatch events occurring in around 2% of the trawling trips (Fernandez-Contreras et al. 2010). Bycatch was also reported in other fishing techniques, such as purse seines, trammel nets and bottom-set gillnets, mostly affecting common and bottlenose dolphins and to a lesser extent, harbour porpoises, striped dolphins and pilot whales (López et al. 2003; Goetz et al. 2014). As a result of these interactions, bycatch on common dolphins has been considered to exceed safe removal limits for the species (López et al. 2003; Saavedra et al. 2018). However, the level of knowledge of the indirect interaction between cetaceans and fisheries in Galicia, especially the competition for resources is low, despite the evidence of direct interactions between cetaceans and fisheries (Santos et al. 2014).

1.6. *Aims of the thesis and outline*

1.6.1. Aims of the study

The overarching aim of this study is to add to the existing knowledge of common dolphin ecology in Galicia, furthering management and conservation of this species. Specifically, this works aims to:

1. Determine the distribution and habitat use of the species in the area.
2. Assess the environmental and geographical variables that influence this distribution and habitat use.
3. Define the ecosystem dynamics in the Rías Baixas region and outline the role of the common dolphin in it.
4. Evaluate the impact of fisheries on common dolphins, by:
    a. Assessing the spatial overlap and the degree of vulnerability of the species towards different types of fisheries.
    b. Understanding the ecological effects of fisheries on common dolphins using an ecosystem approach.
5. Examine potential consequences for common dolphin conservation and suggest alternative approaches to ensure the protection of the species.

1.6.2. Thesis outline

This work is structured in six main chapters that cover different aspects of the ecology of the common dolphin in Galician coastal waters. Chapters two to five are written as complete studies in a manuscript format, as they have been submitted to peer reviewed journals. Among them, chapters two, three and four have already been published in three different peer reviewed journals. Chapters two to five discuss different aspects of common dolphin ecology, interaction with fisheries and conservation and highlight the same integrative approach to the species ecology and conservation.

Chapter one serves as a general introduction to the study of cetacean ecology and its application as a tool to improve species conservation. It also introduces the short-beaked common dolphin as the main species studied in this work and the Rías Baixas region (Galicia, North-West Spain), the area where the study has been carried out.

Chapter two uses Species Distribution Models (SMDs) to look into the common dolphin spatial distribution and determine optimal habitats for the species in waters above the continental shelf. It assesses the main environmental and geographical variables that explain this distribution and suggests measures to improve the conservation of the species.

Chapter three delves into the study of the spatial distribution of the species and explores the spatial overlap between common dolphins and different types of fisheries in the area.

Chapter four creates a mass-balance trophic model of the Rías Baixas shelf ecosystem, an ecosystem located in waters above the continental shelf of the Rías Baixas region. The chapter analyses the characteristics and the dynamics of the ecosystem, defines the role of common dolphins, together with other two species of cetaceans like bottlenose dolphins and harbour porpoises.

Chapter five uses dynamic simulations of the Rías Baixas shelf ecosystem to investigate its temporal dynamics between 2005 and 2017 and creates nine different future scenarios to investigate the effects of fishing activities on common dolphins. This study also takes into consideration the effects of fishing on bottlenose dolphins and harbour porpoises.

Chapter six discusses the main findings, limitations and strengths of the present work.



Drawing by Núria Giralt

Chapter 2

Modelling common dolphin (Delphinus delphis) coastal distribution and habitat use: Insights for conservation

Adapted from the article published as:

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Contribution to the article:

OGP conceived and designed the study together with BDL, conducted the data analysis and interpretation with inputs from BDL, designed the figures and tables, developed the modelling framework and wrote the manuscript with inputs from BDL and SM. Additionally, OGP contributed to the last year (2017) of data collection on the field.

2.1. *Abstract*

The world's ecosystems are altered to different extents by anthropogenic activities. Marine habitats, especially coastal areas, are subjected to an increasing pressure derived from human activities on both land and ocean. Information about species distribution is fundamental to develop effective conservation and management measures and counteract negative anthropogenic impacts. The present work explores the use of species distribution models by using the Environmental Niche Factor Analysis (ENFA) to assess the habitat suitability of common dolphins (*Delphinus delphis*) in North-West Spain, and its application to the development of effective conservation and management measures. The relationship between presence-only data and ecogeographical variables (EGV) was used to assess the potential distribution of the species. Data was collected during 273 days at sea, covering a total distance of 9,417 km between March 2014 and October 2017 with a total of 91 common dolphin encounters. This study shows that tide level and sea surface salinity are the main EGVs driving the distribution of the species in coastal areas especially in waters above the continental shelf. Additionally, this study reveals the most suitable habitats for common dolphins and outlines the need to develop conservation measures and management plans to promote the protection of this species. Findings of the study contribute to a more accurate and comprehensive understanding of the common dolphin distribution and emphasize the importance of species distribution models in the development of effective conservation and management strategies.

Keywords: Cetaceans, Species Distribution Models, Environmental Niche Factor Analysis, *Delphinus delphis, Coastal conservation, North-West Spain,*

2.2. *Introduction*

Human activities are causing a global impact on the Earth's ecosystems, affecting habitats, populations and species to different extents (Vitousek et al. 1997; Sutherland et al. 2016;). As a consequence, habitat and biodiversity loss are a widespread issue (Myers et al. 2000; Brooks et al. 2002). The impact of human activities is particularly important in marine coastal ecosystems, which are being degraded by impacts such as pollution, anthropogenic noise and overfishing (Shahidul Islam and Tanaka, 2004; Halpern et al. 2008; Reynolds et al. 2009). As a result, a development of effective conservation measures coupled with an increase in scientific knowledge on the distribution, ecology and habitat use of the threatened species is needed (Brooks et al. 2002). Information on the distribution of a species, for instance, can be a very useful tool to improve its conservation (Guisan et al. 2013; Rodríguez et al. 2007). In this context, models that use environmental information to assess the distribution of a species, such as Species Distribution Models (SDMs) and Environmental Niche Models (ENMs), have been acquiring increasing importance in the different steps of spatial and conservation planning (Guisan et al. 2013; Margules and Pressey, 2000; Rodríguez et al. 2007). ENMs are based on the ecological niche concept (Hutchinson, 1957) that relates the fitness of a species to its niche. Among them, the Ecological Niche Factor Analysis (ENFA) defines the ecological niche as a hypervolume with n dimension corresponding to n ecological variables within which a species can exist and reproduce successfully (Hutchinson, 1957) and combines information about a species' distribution with a set of ecogeographical variables (EGVs) to determine habitat suitability (Hirzel et al. 2002).

EGVs (biological, physical and topographic) have been used to explain species distribution (Guisan and Zimmermann, 2000; Elith and Leathwick, 2009). In the marine environment, topographic features and temporal changes in physical and biological factors are known to determine the spatial distribution of a species (Brodeur and Pearcy, 1992). Resource availability is also a crucial aspect that influences the habitat selection (Torres et al. 2008; Planque et al. 2011) and shapes the distribution of marine top predators such as seabirds, sharks and cetaceans, which are heavily influenced by the spatial movements of their prey (Hamazaki, 2002; Redfern et al. 2006; Kohler and Turner,

2008; Torres et al. 2008; Certain et al. 2011; Díaz López and Methion, 2017, 2018). Since it is difficult to obtain reliable information about prey distribution and abundance, physical and biological factors can be used as proxies to both model and make predictions about the distribution of top predators (Guisan and Zimmerman, 2000; Redfern et al. 2006; Elith and Leathwick, 2009; Pirotta et al. 2011; Díaz López and Methion, 2017, 2018).

Information about the distribution of a species can be recorded in terms of presence/absence data (Weir et al. 2012; Díaz López and Methion, 2017, 2018) or presence-only data (Moura et al. 2012; Fernandez et al. 2018). However, detection of highly mobile marine species, such as the common dolphin (*Delphinus delphis*), may be challenging because they spend short periods of time at the surface (Hamazaki, 2002; Praca and Gannier, 2008). Hence, the distinction between true absences (i.e. when common dolphins are not present in the sampled location) and false absences (i.e. when common dolphins are present but could not be detected) can be challenging (Praca and Gannier, 2008; Elith and Leathwick, 2009). More specifically, it can be difficult to assess whether this small cetacean is absent in a known location because (1) the habitat is unsuitable for common dolphins, (2) the habitat is suitable, but common dolphins are not present, or (3) common dolphins are present but could not be detected. In this case models using presence-only data, such as ENFA, are recommended (Hirzel et al. 2002; MacLeod et al. 2008), and have been proved to be a robust technique to assess the habitat suitability of cetaceans (Praca and Gannier, 2008; Skov et al. 2008; Condet and Dulau-Drouot, 2016). Models based on the ENFA approach can reach high predictive accuracy with small sample sizes (Allouche et al. 2008), and are ideal to assess the habitat suitability of highly mobile and cryptic species (Reutter et al. 2003; Praca and Gannier, 2008). Additionally, they have been used to infer potential threats to marine predator conservation, such as habitat loss or interaction with human activities, (Condet and Dulau-Drouot, 2016).

The common dolphin is a small cetacean widely distributed from tropical to cool temperate waters of both the Atlantic and the Pacific oceans (Jefferson et al. 2015). Its distribution in the North-East Atlantic extends from Norway to the south of Spain (Mirimin et al. 2009; Murphy et al. 2013), and is the most abundant cetacean in waters

above the continental shelf of the north-west Iberian Peninsula (López et al. 2002, 2003; Spyrakos et al. 2011). Despite its abundance, the species faces several threats resulting from human activities in the North-East Atlantic (Murphy et al. 2013), where bycatch by purse-seine, gill nets and trawl fisheries is a major concern (López et al. 2003; Rogan and Mackey, 2007; Fernández-Contreras et al. 2010; De Boer et al. 2012). Although the common dolphin has been listed as Least Concern by the International Union for Conservation of Nature (IUCN), its interaction with fisheries could lead to a decline in common dolphin abundance in specific areas (De Boer et al. 2012; Saavedra et al. 2018).

To minimise these impacts and to ensure common dolphin conservation, the species has been included in several national and international agreements and conventions that cover a wide variety of aspects such as international trade, monitoring and reduction of bycatch, and habitat conservation (Murphy et al. 2013). In the European Union, the Habitats Directive lists the common dolphin in Annex IV and urges governments to promote research and conservation measures to ensure that the impacts on the species are kept to a minimum, especially in the areas that include important habitats for the species ecology and reproduction (Council Directive 92/43/EEC). In Spain, common dolphins are listed as data deficient (the Atlantic population) in the Red Book of Spanish Vertebrates (Blanco and González, 1992) and in the Spanish Catalogue of Threatened Species (Real Decreto 139/2011). Additionally, common dolphins and their habitat are protected in Spain by regional and national legislations (Ley 3/2001; Ley 15/2002; Ley 42/2007; Ley 41/2010 Real Decreto 1727/2007). However, the existing legal framework is unspecific about the restrictions to be applied to reduce the impact of human activities on common dolphins. Furthermore, despite the available information concerning the threats affecting this small delphinid in Galician waters, there is a lack of studies linking the habitat suitability of the species to its conservation. A better understanding of the key habitats for the species will contribute to developing better management and conservation plans to minimise the impact of anthropogenic activities on common dolphins.

Following the above considerations, this study combines the species distribution modelling approach (ENFA) with data collected during dedicated year-round boat surveys to provide new information on the environmental variables that influence

common dolphin distribution and habitat suitability. These findings were used to assess the best measures to promote the conservation of the species and evaluate the areas in which strategies would be more effective.

2.3. *Methods*

2.3.1. Study area

The present study was carried out in waters above the continental shelf of North-West Spain and beyond. The north-western coastline of Spain is characterised by a series of drowned tectonic valleys known as rias that influence the coastal dynamics in the area (Prego et al. 1999; Evans and Prego, 2003). The study area covered approximately 2,479 km^2, and extended from Cíes Islands (42° 15' N) in the South, up to cape Corrubedo in the North (42° 36' N), and from the Ría de Arousa in the East (including the waters inside the inlet) up to the continental break and beyond in the West (Figure 2.1). This region is characterised by a narrow continental shelf, varying from 30 to 50 km in width, with the continental break occurring between 180 and 200 metres in depth (Dias et al. 2002; Sanz Alonso, 2005). The study area includes the Atlantic Islands National Park (Fig. 1), which protects 72.85 km^2 of waters around the Cortegada, Sálvora, Ons and Cíes islands (Ley 15/2002). The park hosts different Special Areas of Conservation, Special Protection Areas for Birds and Sites of Community Importance, and was created to preserve the local marine biodiversity. Among other measures, it requires a permit to navigate in waters protected by the park and it restricts fishing activities to the artisanal fleet (Ley 15/2002).

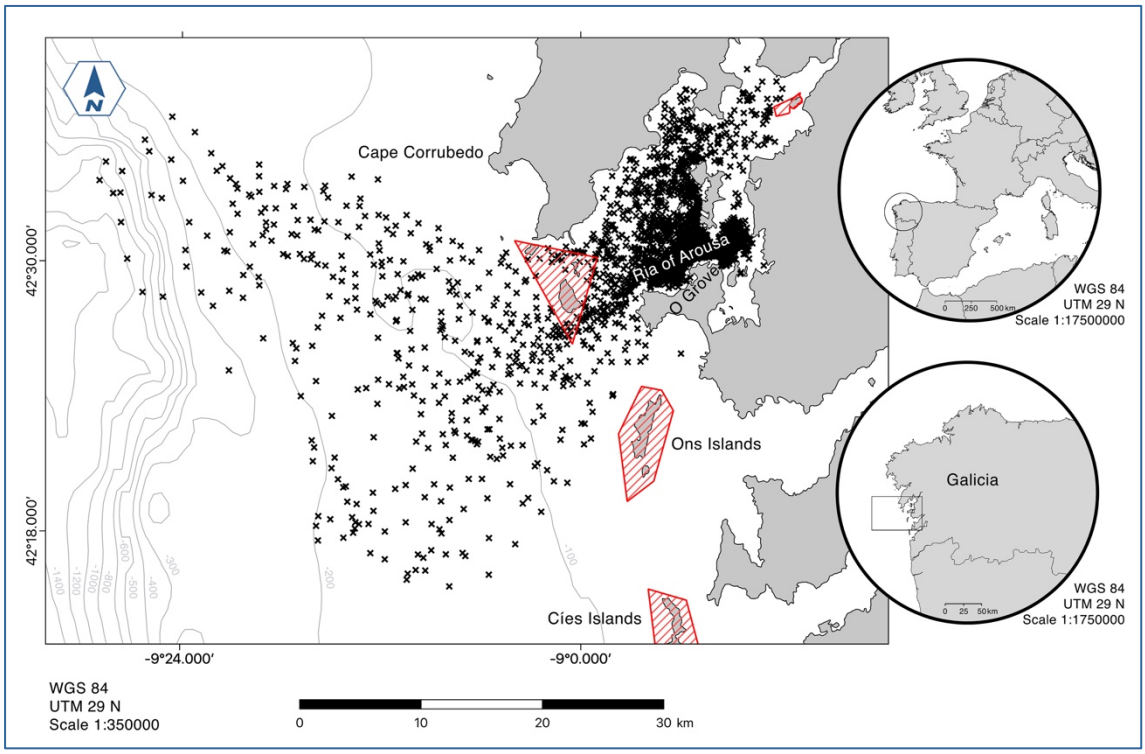


Figure 2.1. *Map showing the study area surveyed in North-West Spain and the 20-minutes samples collected from March 2014 to October 2017. The red boxes with the line pattern show the area of the Atlantic Islands National Park (Cortegada island inside of the Ría de Arousa, Sálvora Island at the entrance of the ria, Ons Islands south from the entrance of the ria and Cíes*

The study area is located on the northern limit of the north-west Africa upwelling system (Gonzalez-Nuevo et al. 2014). Therefore, these coastal waters are dominated by a series of seasonal upwelling events (Torres et al. 2003), which are caused by the action of northerly winds, and are influenced by the orientation and the geographical features of the coastline (Torres et al. 2003; Álvarez et al. 2012). Indeed, upwelling events are especially common in the study area (Lavin et al. 1991; Álvarez et al. 2012) where they are important oceanographic phenomena, as they carry deep, cold and nutrient-rich waters to the photic layer, enhancing the primary productivity (Lavin et al. 1991). Upwelling episodes typically occur during spring and summer months (Torres et al. 2003; Gonzalez-Nuevo, et al. 2014); however, weaker winter upwelling episodes have also been recorded (Álvarez et al. 2012).

2.3.2. Data collection

Data were collected year-round by the research team of the Bottlenose Dolphin Research Institute (http://www.thebdri.com) as part of a long-term study that aims to understand the ecology of cetacean species that inhabit Galician waters (Díaz López et al. 2017; Díaz López and Methion 2017, 2018; Methion and Díaz López, 2018, Chapter 4). Dedicated boat surveys were carried out on board a 12-m single-hulled research vessel, powered by two 180 hp inboard engines on waters above the continental shelf and beyond, between March 2014 and October 2017.

Surveys were conducted during daylight hours at a constant speed of 6 to 8 knots in adequate weather conditions (no fog, no rain and sea conditions <3 on the Douglas sea scale) (Díaz López and Methion, 2017, 2018). Observational effort was carried out by at least three experienced observers located on the flying bridge of the research vessel (4 m above sea level). Observers conducted continuous 360° scans around the research vessel searching for common dolphins at the water surface. Scans were carried out using the naked eye or 10X50 binoculars.

Environmental data were collected every 20 minutes from the beginning until the end of the survey, following Díaz López and Methion, 2017, 2018. These data collection sets (hereafter referred to as 20-minute samples) were used to summarize the environmental conditions during the survey, and to assess the presence of common dolphins. The information collected at each 20-minute sample included the time (UTC), the position of the vessel (WGS 84 latitude and longitude) and the speed (in knots), which were obtained with a hand-held GPS (Garmin eTrex 10). At the same time, the sea surface temperature (SST in degrees Celsius) was measured with a Garmin GPS-Plotter Map Sounder connected to an echo-sounder. Additionally, the sea surface salinity (SSS in parts per thousand) was measured using a portable refractometer.

The presence of common dolphins within a 1 nautical mile radius around the research vessel was recorded at the beginning of each 20-minute sample (Díaz López and Methion, 2018). Depending on its duration, a sighting of common dolphins could include more than one 20-minute sample, however, only the first 20-minute sample within the same sighting was used for the analysis.

QGIS 2.18 (QGIS Development Team, 2018), an open source Geographical Information System (GIS) software package, was used to obtain the topographic variables following Díaz López and Methion (2017). The depth (in metres) was extracted from a 30 arc second bathymetry raster of the General Bathymetric Chart of the Oceans (GEBCO, Weatherall et al. 2015) for each 20-minute sample and each sighting (presented as mean ± standard error). The same bathymetry raster was used to calculate the slope of the seafloor (understood as the rate of change between a given location and its surroundings and expressed as a percentage, hereafter referred to as Slope) and the aspect of the seafloor (compass orientation that a slope faces, hereafter referred to as Aspect) for each 20-minute sample. Additionally, the minimum distance of each 20-minute sample location to the coast (in metres) and to the 200 metres bathymetric line (in metres) was calculated with the NNJoin plugin in QGIS 2.18. The tide level (in metres) was obtained from the tide charts corresponding to the harbour of Vilagarcía de Arousa, located in the Ría de Arousa (Díaz López and Methion, 2018). Chlorophyll a data (in mg/m^3) were extracted from 1 km X 1 km daily rasters from the COPERNICUS Marine Environment Monitoring Services website (http://marine.copernicus.eu, last visited 30/11/2018). The point sampling tool in QGIS 2.18 was used to obtain the chlorophyll a value for each 20-minute sample.

2.3.3.Environmental Niche Factor Analysis

In this study, ENFA was carried out using the software package Biomapper 4.0 (Hirzel et al. 2004), which takes into account the density of observations for any given species in the multidimensional EGVs space to create a habitat suitability map (Hirzel et al. 2002; Hirzel and Arlettaz, 2003). The method requires two types of data: (1) geographical positions where the species has been recorded and (2) a series of EGVs measured in these locations (Hirzel et al. 2002). In this case, depth, Slope, Aspect, distance to the coast, distance to the 200 m bathymetric line, chlorophyll a, SST, SSS and tide level (Table 2.1) were chosen as they have been successfully used to explain cetacean distribution in previous studies (Pirotta et al. 2011; Spyrakos et al. 2011; Fernandez et al. 2017; Díaz and Methion, 2017, 2018). The EGVs were divided into two categories according to their temporal variability: *persistent* and *non-persistent* variables (following Díaz López and Methion, 2017). Depth, Slope, Aspect, distance to the coast and distance

to the 200 m bathymetric line were considered invariable in time and thus named *persistent variables*. On the other hand, chlorophyll a, SST, SSS and tide level were named *non-persistent variables* due to their temporal variability.

Table 2.1 *The nine ecogeographical variables (EGVs) used to create the ENFA model, showing the number of 20-minute samples used to calculate them, the mean, the standard error (SE) and the range. In bold letters the EGVs that were kept for the final model.*

EGV	Type**	Unit	Interpolation method	n	Mean	SE	range
Depth	P	Metres	Points	3,114	35	1	0 – 1,050
Slope	P	%	Points	3,114	0.85	0.02	0.01 – 30.37
Aspect	P	Degrees (compass orientation 0 - 360°)	Points	3,114	205	1.79	4 – 359
Distance to coast	P	Metres	Points	3,114	2614	90	2 – 32,097
Distance to 200 m bathymetry line	P	Metres	Points	3,114	31,402	160	44 – 45,788
Chlorophyll a	NP	Parts per thousand	Centroids	2,029*	3.33	0.07	0 – 17
SST	NP	Degrees Celsius	Centroids	3,017*	16.13	0.04	8.9 – 23.1
SSS	NP	mg/m^3	Centroids	1,389*	34	0.07	13 – 36
Tide level	NP	Metres	Centroids	3,114*	1.88	0.02	0.13 – 4.37

* Maps created from the mean of each surveyed hexagonal cell.
** **P**: Persistent; **NP**: Non-persistent

To compute ENFA in Biomapper, both the EGVs and the species presence data had to be transformed to raster format (Hirzel et al. 2002). To do so, a grid with hexagonal cells was used. This type of grids has been used in various studies (Birch et al. 2000; Chow et al. 2005) and has shown some advantages to the more commonly used square tessellations (Jurasinski and Beierkuhnlein, 2006; Birch et al. 2007). In this study, the hexagonal tessellation was chosen for three reasons: (1) the visual area from the research vessel is circle-shaped, thus hexagonal cells offer a better representation than square or triangular cells; (2) due to its shape, hexagonal cells have a closer perimeter-area ratio to a circle, which could potentially reduce the edge effect (Birch et al. 2007); and (3) neighbour cells are all at the same distance, hence there is the same distance between centroids of adjacent cells (Birch et al. 2007). To generate the raster files, a grid with 294

hexagonal cells (radius = 1 nm) covering the study area was created (Coordinates 42° 14.136′ N – 42° 39.270′ N, 9° 30.000′ W – 8° 46.932′ W). A 1 nautical mile radius was chosen because, given an average speed of 6-8 kn, two consecutive 20-minute samples would be located in adjacent cells. The size and shape of the hexagonal cells were conceived to adapt to both the visual area from the research vessel and the distance covered between each 20-minute sample.

QGIS 2.18 was used to create the raster files. One raster was created to show the presence of common dolphins (hereafter referred to as species map) and nine rasters were created to represent the EGVs (hereafter referred to as biogeographical maps). All rasters had the same size and contained the same number of cells (1,000x1,000 cells). Additionally, the plugin MMQGIS was used to create the grid with hexagonal cells. Finally, the System for Automated Geoscientific Analyses (SAGA), built in QGIS 2.18, was used to create biogeographical maps. Three different methods were used to create the maps:

i. Creation of the species map: A boolean raster (with values 0 or 1) was created to show the areas in which common dolphins were present. Cells with a value equal to 1 were those containing common dolphin sightings and cells with values equal to 0 were those in which the presence of the species could not be proven.

ii. Creation of the biogeographical maps for the non-persistent variables: To take into account the variability of the non-persistent variables, the mean of the values measured at each 20-minute sample in a given cell was calculated. This procedure was repeated in all cells containing at least one 20-minute sample. The final biogeographical maps for the non-persistent variables were created by interpolating the centroids of each cell using the inverse distance weighted (IDW) interpolation. IDW is a spatial interpolation method that assumes that values of nearby points are more similar than values of more distant points (Li and Heap, 2008). Hence, it estimates values at unknown locations by giving a heavier weight to closer sampled points (Li and Heap, 2008; Lu and Wong, 2008). IDW is a computational less-demanding method that has been successfully used to predict environmental variables (Li and Heap, 2008).

iii. Biogeographical maps for the persistent variables: The unchanging nature of the persistent variables enabled the use of the 20-minute samples to create high resolution rasters without the need to use the mean values within a grid. The IDW interpolation was used to generate the biogeographical maps for the persistent variables by directly interpolating all 20-minute sample values.

Since both biogeographical and species maps had a square shape, they included information referring to the oceanic environmental conditions and species presence in areas located on land. The clipping tool in the raster menu in QGIS 2.18 was used to cut and exclude the areas of the species and biogeographical maps that overlapped with the land. Rasters were then transformed to Idrisi format using the *raster*, *sp* and *rgdal* packages in RStudio (R Core Team, 2016) to make them suitable for Biomapper 4.0.

2.3.4.Data analysis

All the biogeographical maps, except for the SSS raster, were normalised using a Box-Cox transformation algorithm (Hirzel et al. 2002). The normalised SSS map contained cells with a small range of values, therefore the original raster was kept for the analysis to avoid complications in the subsequent steps (Hirzel, 2004). A correlation matrix containing all EGVs was then computed using the Pearson correlation coefficient r to check for collinearity. Two variables were considered highly correlated to each other when $|r| > 0.7$ (Dormann et al. 2013). In such case, one of them was removed from the analysis as it was considered to contain redundant information, and the more ecologically relevant EGVs were kept for further analysis (Dormann et al. 2013).

A factor analysis was run to generate a number of uncorrelated factors from the same amount of correlated EGVs (Hirzel et al. 2002). The first factor accounted for the marginality, defined by Basille et al. (2008) as "the difference between the conditions used on average by the species and the conditions available in the study area". Marginality varies between 0 and 1, lower values meaning that the species uses similar conditions that the average available conditions and high values, close to 1, meaning that the species occupies a specific habitat within the study area (Hirzel et al. 2002). The specialisation, which can be considered equivalent to the habitat breadth (Praca and

Gannier, 2008), explains the difference between the species variance and the global variance, and is determined by all factors (Hirzel et al. 2002). Specialisation is difficult to interpret, as it varies from 0 to infinity. However, a value higher than 1 denotes some degree of specialisation (Hirzel et al. 2002).

A broken-stick distribution was used to select the number of factors to be used to create the habitat suitability map (Hirzel et al. 2002). Furthermore, following Hirzel et al. 2006, the geometric mean algorithm was chosen to generate the habitat suitability map, as it does not make any assumption on the species distribution. This method takes into account the proximity of the species points in the environmental space and gives a higher suitability where the species points show a higher density (Hirzel and Arlettaz, 2003). In this context, both marginality and specialisation values were used to calculate a habitat suitability index (HSI), which was later used to create the habitat suitability map (Hirzel and Arlettaz, 2003). The HSI varies from 0 to 100, lower values meaning low suitability and higher values meaning high suitability.

To evaluate the prediction error of the model, a k-fold cross-validation method was used. This method splits the data in several equal-sized sets k and uses k-1 sets as a calibration of the model and the remaining set to validate it (Hastie et al. 2001). This procedure is carried out k times, each of them using a different set to validate the model. In this study a 10-fold cross-validation (k=10) was used (Hirzel et al. 2006). Furthermore, the predictive power of the model was assessed with the Boyce index (Boyce et al. 2002). The index range goes from -1 to 1, positive values showing the consistency of the model with the data set used for its assessment. Likewise, values close to 1 indicate that the calculated distribution differs from a distribution expected by chance (Hirzel et al. 2006).

From the Boyce index, a threshold-based method was developed to evaluate the capacity of the model to predict habitat suitability. To do so, the HSI range was divided into different classes, and for each of them two frequencies were calculated: (1) the *predicted frequency* (P_i), which is the number of evaluation points predicted by the model in each class, divided by the total number of evaluation points; and (2) the *expected frequency* (E_i), which divides the area of a habitat suitability class by the total study area (Hirzel et al. 2006). With this information the *predicted-to-expected ratio* (*P/E*)

was calculated for each class. To evaluate the model, the *P/E* ratio was calculated all along the HSI range generating 10 continuous *P/E* curves, one for each of the sets used in the cross-validation process. Three aspects of the *P/E* curves were used to assess the accuracy of the model: (1) the variance among the curves as an indication of the robustness of the model; (2) the shape as the resolution of the model predictions; and (3) the maximum as the deviation of the model from a random expectation (Hirzel et al. 2006). The *P/E* curves were used to generate thresholds to divide the habitat into 4 different classes according to its suitability: unsuitable, marginal, suitable and optimal habitat (Hirzel et al. 2006). In this context, unsuitable habitats represented those areas in which *P/E* ratio was lower than 1. Marginal habitats were defined by *P/E* ratio close to 1. Suitable habitats were described as those areas in which the *P/E* ratio showed an exponential increase, and the areas with the highest *P/E* ratio were considered to represent an optimal habitat.

2.4. *Results*

2.4.1. Survey effort and presence of common dolphins

Field work was carried out for 38 months between March 2014 and October 2017. During that period, 273 daily dedicated boat surveys were completed, covering a total distance of 9,417 km and a total of 1,015 hours at sea. During that time, 3,114 20-minute samples were recorded, 91 in presence of common dolphins (Figure 2.2).

Depth at which common dolphins were spotted varied between 6 and 935 metres (mean = 137 ±13.54 metres). Of the 91 groups of common dolphins encountered during the study, 79 (87%) were found in waters above the continental shelf (between 50 and 200 metres deep). Another six groups (6.5%) were seen in shallower areas and corresponded to sightings recorded inside the Ría de Arousa, whereas the remaining six groups (6.5%) were spotted in waters above the continental break or beyond (waters deeper than 200 metres). Common dolphin presence was recorded in 55 (18.7%) of the cells of the grid that was created to assess the spatial distribution of the species (Fig. 2.2).

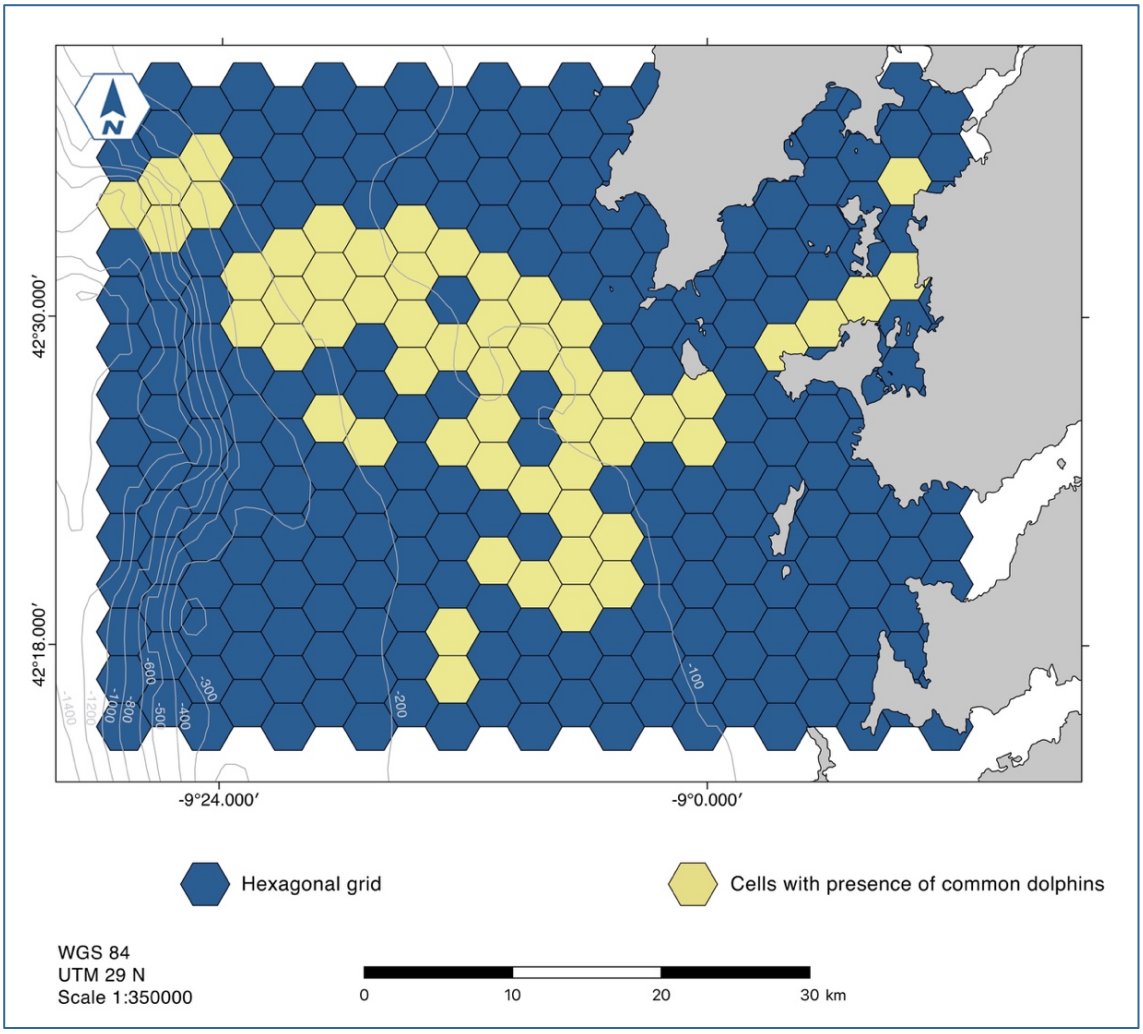


Figure 2.2 *Map showing the hexagonal grid used to create the species map and the biogeographical maps for the non-persistent variables and the cells with presence of common*

2.4.2.ENFA results

In a preliminary analysis, a correlation matrix was generated to assess the collinearity between the EGVs. The matrix showed that five EGVs were highly correlated to each other (Table 2.2). Therefore, depth, distance to the coast, distance to the 200 metres bathymetry line and SST were discarded for the final analysis and chlorophyll a was kept due to its ecological significance (Praca and Gannier, 2008; Moura *et al*. 2012). The EGVs used in ENFA were Slope, Aspect, chlorophyll a, tide level and SSS.

Table 2.2 *Correlation matrix showing the collinearity between the ecogeographical variables EGVs. Two variables were considered highly correlated to each other when |r| > 0.7 (highlighted in bold).*

	Depth	Slope	Aspect	Dist coast	Dist 200 m	Chl a*	SST	Tide level	SSS
Depth	1								
Slope	0.167	1							
Aspect	0.155	0.046	1						
Dist coast	**0.917**	0.096	0.171	1					
Dist 200 m	**-0.83**	-0.132	-0.176	**-0.95**	1				
Chl a*	**-0.825**	-0.151	-0.18	**-0.768**	**0.754**	1			
SST	**0.864**	0.125	0.181	**0.873**	**-0.867**	**-0.814**	1		
Tide level	0.282	-0.115	0.032	0.317	-0.225	-0.233	0.237	1	
SSS	0.659	0.111	0.122	0.65	-0.654	-0.689	0.555	0.183	1

* Chl a stands for chlorophyll a

Of the five factors created by the ENFA model, the first four were kept for the final analysis and they explained 89% of the total specialisation (total sum of eigenvalues). The first factor explained 100% of the marginality and 16% of the specialisation (Table 2.3). The scores of each EGVs for this first factor revealed that marginality was mainly influenced by tide level, chlorophyll a and SSS, showing that common dolphin presence was linked to higher tide level, higher SSS and low chlorophyll a. Aspect and Slope had a smaller effect on the marginality. The remaining factors explained the rest of the specialisation. The first specialisation factor (SF1), which accounted for almost half of the total specialisation (45%), showed that common dolphin's habitat choice was mainly influenced by SSS and Aspect (SSS = 0.741; Aspect = 0.615). The remaining specialisation factors revealed some sensitivity to chlorophyll a and SSS (SF2), and chlorophyll a and Slope (SF3). The EGV with the highest influence on the specialisation, when combining all first four factors, was SSS. Overall, marginality and specialisation calculated by the ENFA model were 0.279 and 1.268 respectively, showing that the conditions of common dolphin habitat were similar to the average conditions in the area and that the species can easily adapt to different environmental conditions.

Table 2.3 *Results of the ENFA model showing the scores of each ecogeographical variable (EGVs) in the marginality and the specialisation factors (SF), and the percentage of information explained by each of the factors. The table only shows the four SF that explained 89% of the variability.*

EGV	Marginality 16%	SF 1 45%	SF2 16%	SF3 12%
Slope	-0.033	-0.12	0.262	0.534
Aspect	-0.223	0.615	0.286	0.162
Chlorophyll a	-0.494	0.201	-0.643	0.685
Tide level	0.713	-0.133	0.063	0.391
SSS	0.443	0.741	-0.657	0.258

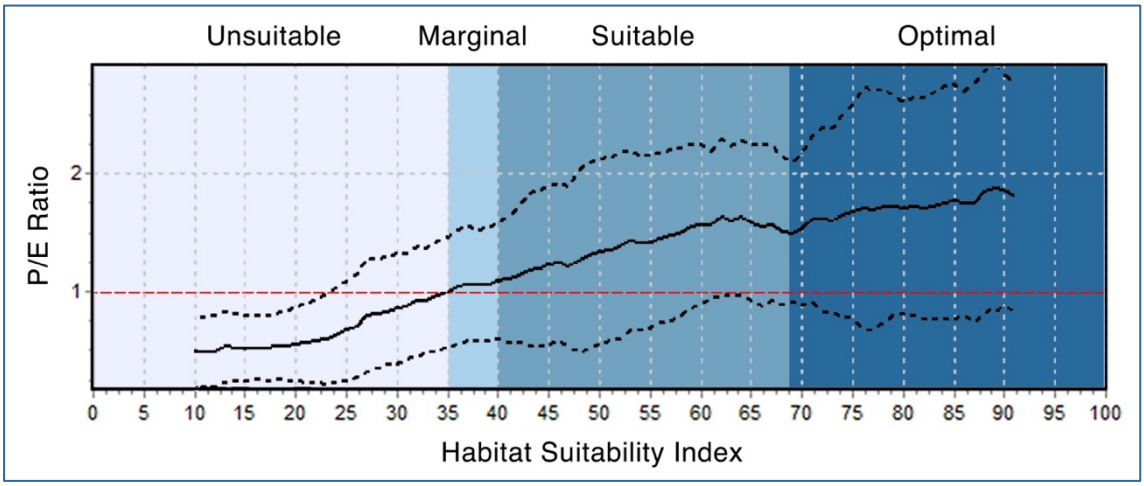


Figure 2.3 *Showing the mean P/E curves for the model and the 4 habitat suitability classes in which the habitat was categorized.*

The cross-validation (Boyce index = 0.552 ±0.2121) and the *P/E* curves showed that the model had a good predictive power. The variance along the *P/E* curves showed a constant increase with the HSI, with a narrower confidence interval for lower HSIs, indicating that the predictive power was more accurate for low suitability areas (HSI < 40) (Figure 2.3). Based on the *P/E* curves, the habitat was categorised into 4 different classes: (1) "unsuitable habitat" for HSI values lower than 35; (2) "marginal habitat" for HSI values between 35 and 40; (3) "suitable habitat" for HSI values between 40 and 69; and (4) "optimal habitat" for HSI values higher than 69. The resulting habitat suitability map for the study area is shown in Figure 2.4. The map reveals that the rias and the shallower coastal waters in the southern part of the study area were not suitable for the species. Marginal habitat was linked to small specific locations around the suitable

habitats. Conversely, the waters above the continental shelf and especially the areas around the 100 metres bathymetry line included the more suitable habitats for common dolphins. Although some areas beyond the continental break included suitable and even optimal habitats for the species, most of the waters deeper than 300 metres were classified as unsuitable.

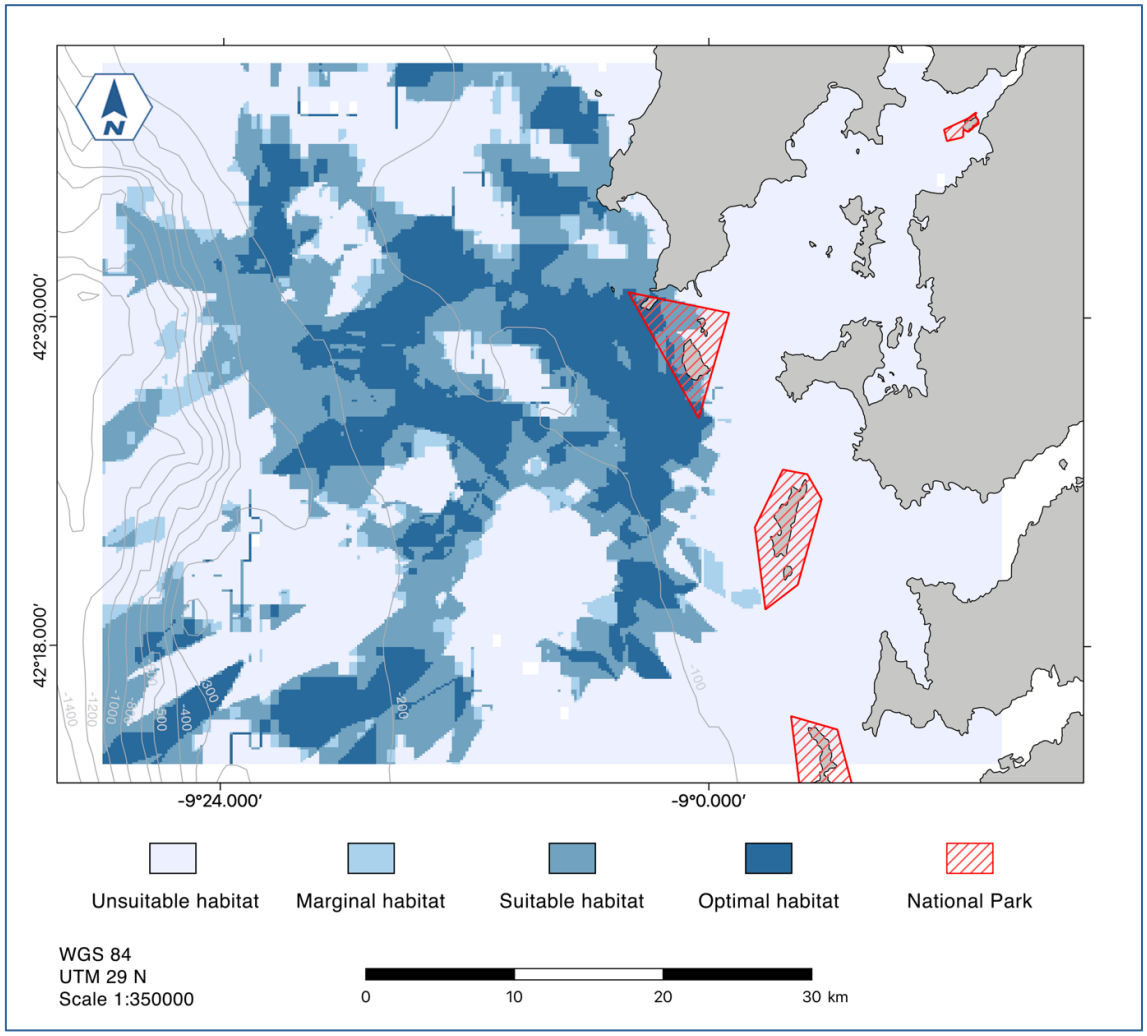


Figure 2.4 *Common dolphin habitat suitability map in the study area based on the habitat suitability index (HSI) calculated with ENFA. The red areas with the line pattern show the Atlantic Islands National Park, pointing out the overlap and close proximity of the northern island of the national park (Sálvora) to the most suitable habitats for common dolphins.*

2.5. *Discussion*

Knowledge on the distribution of a species has become an important tool to develop effective management and conservation plans (Rodríguez et al. 2007; Marshall et al. 2014). Studies that assess the potential distribution of marine top predators are

fundamental in areas such as the north-western coast of Spain, where these species are highly impacted by human activities (Díaz López and Methion, 2018; Methion and Díaz López, 2019b). One of the aims of this study was to explore the development of conservation measures for common dolphins by getting a better understanding of their distribution and their habitat use. To do so, a novel approach was designed by combining the use of hexagonal tessellation and ENFA modelling. The hexagonal tessellation provided an adequate adaptation to the sampling effort which, along with the equal distance between adjacent cells, resulted in the development of high resolution species and biogeographical maps, as has been seen in other studies (Zimmerman et al. 1999; Birch *et al.* 2007). Additionally, the ENFA approach proved to be an adequate tool to assess the habitat suitability and the distribution of a cryptic, highly mobile marine species such as the common dolphin, for which reliable absence data is difficult to obtain. Although some authors have stressed that ecological niche models have a lower predictive accuracy when compared to other models based on presence/absence data (Segurado and Araújo, 2004; Tsoar et al. 2007), the cross-validation and the Boyce Index showed the robustness of the ENFA model and its accuracy to predict habitat suitability and distribution (Macleod et al. 2008; Praca et al. 2009; Costa et al. 2013). Furthermore, this study points out the importance of having a large and reliable presence-only data set to achieve trustworthy results. This was confirmed by the *P/E* curves used to validate the model, which showed a stronger accuracy in predicting areas unsuitable for the species (and in which common dolphins were not regularly seen) such as shallow coastal areas or the rias (Pierce et al. 2010; Saavedra et al. 2018).

In this context, the current study provides new information on common dolphin distribution by showing that waters above the continental shelf are an optimal habitat for common dolphins. Additionally, the strong predictive power of the model for areas of low habitat suitability, and more specifically inside and around the rias, confirms that the species does not show a preference for the inlets. The ENFA also shows that some areas deeper than 300 metres, especially in the south-western part of the study area, include suitable and optimal habitats for the species in concordance with previous studies (Fernández-Contreras et al. 2010). However, this result should be considered

carefully, as offshore waters were not monitored as thoroughly as other parts of the study area, due to logistical and geographical constraints. Coupled with previous studies in the area that show a high abundance of common dolphins in waters above the continental shelf (Pierce et al. 2010; Spyrakos et al. 2011; Goetz et al. 2015; Chapter 3) and waters deeper than 200 metres (López et al. 2003; Fernández-Contreras et al. 2010), these findings contribute to a more accurate and comprehensive understanding of common dolphin distribution, and provide valuable insights for the species' conservation.

To have a better understanding of the causes influencing the distribution and habitat suitability, several EGVs were included in the analysis. However, the link between EGVs and the spatiotemporal movements of the common dolphin is not a straightforward relationship and it might be affected by the interaction among the different EGVs or the temporal lags between physical and biological processes (Redfern et al. 2006; Pirotta et al. 2011). In this context, the ENFA model showed that tide level was the main factor determining the habitat suitability of the species in waters above the continental shelf and that common dolphins showed a preference for higher tide levels. This relationship might be associated to tidal currents, which are especially important around Sálvora Island (at the entrance of the Ría de Arousa), driving oceanic water towards the interior of the inlet and nutrient-rich waters offshore (Otto, 1975; Pinho et al. 2004). These tidal currents have been found to enhance local primary productivity and promote the aggregation of small fish, attracting marine top predators (Johnston et al. 2005; Lambert et al. 2017; Díaz López and Methion, 2018). Hence, the high speeds of the tidal currents and the enhanced primary productivity linked to them, could act as a mechanism to concentrate common dolphin prey in specific areas close to Sálvora Island. These areas include suitable and optimal habitat for the species according to the ENFA model.

Another EGV showing a high influence on common dolphin habitat suitability was SSS. The importance of areas with a higher SSS may be explained by the gradient that exists between the rias and the open ocean, where the innermost waters of the inlets have a lower salinity due to the freshwater inputs (Prego et al. 1999). The model pointed out that the rias were not a suitable habitat for common dolphins, which showed a clear preference for oceanic waters with higher SSS values. Previous studies have shown that

SSS has an influence on cetacean distribution, and can be used as a good predictor for it (Forney, 2000). However, rather than a direct effect, the SSS might be influencing the distribution of common dolphins indirectly, by affecting the distribution of their prey, namely blue whiting (*Micromesistius poutassou*) and, to a lesser extent, Atlantic horse mackerel (*Trachurus trachurus*, Linnaeus 1758) and sardine (*Sardina pilchardus*) (Santos et al. 2013, 2014). Indeed, previous findings show that SSS has an influence on the distribution of the different life stages of these species, which have a preference for areas of higher SSS (Abaunza et al. 2008; Miesner and Payne, 2018).

The findings of this study provide reliable insights on common dolphin distribution and habitat preference in coastal waters which, coupled with information on the threats that common dolphins face in the area, can be used to develop effective conservation measures. The results show that the northern area of the Atlantic Island National Park, especially the waters on the western coast of Sálvora Island, includes and borders optimal habitats for common dolphins. Fishing activities within these waters are restricted to artisanal fisheries to ensure a sustainable exploitation of the resources (Ley 15/2002). However, the waters located in the outer perimeter of the park are used by commercial fisheries, which have been shown to have an impact on this small cetacean (López et al. 2003; Fernández-Contreras et al. 2010; Goetz et al. 2014, 2015; Saavedra et al. 2018; Chapter 3). Indeed, bycatch in pair-trawlers, gill nets and purse-seines has been documented in the study area, where common dolphins are accidentally caught in approximately 5% of pair-trawler tows, and where 23% of the stranded individuals show signs of interaction with fishing gear (López et al. 2003; Fernández-Contreras et al. 2010; Goetz et al. 2014, 2015; Saavedra et al. 2018). The high number of incidental captures might be related to the intense fishing pressure in the area given that Galicia has the biggest fishing fleet in Spain, consisting of 4 466 fishing vessels at the end of 2017, 10% of which operates in coastal waters above the continental shelf (Surís-Regueiro and Santiago, 2014; Ministerio de Agricultura, Pesca y Alimentación, 2017). Furthermore, a recent study highlighted the spatial and temporal overlap between fisheries and common dolphins, especially in areas above the continental shelf between 125 and 200 metres in depth (Chapter 3). This overlap has been confirmed by scientists (Fernández-Contreras et al. 2010; Chapter 3) and by fishermen, which tend to avoid areas with higher

abundance of common dolphins (Goetz et al. 2014). Consequently, the coastal waters above the continental shelf, which include the suitable and optimal habitats for the species, are also impacted by fishing activities.

This work highlights the importance of understanding the spatial distribution of a species for developing management and conservation plans. Indeed, this study suggests that a reassessment of the dimensions and the protection level of the area surrounding Sálvora Island (which currently covers 23.09 km^2), could improve the conservation of this vulnerable species by reducing the spatial overlap with fisheries. This reassessment would include 4 main steps (Table 2.4) and should involve the cooperation between different stakeholders and the development of enforcement methods to ensure compliance with the new regulations and effectiveness of the developed measures (Agardy et al. 2010; Redpath et al. 2013). All these measures could minimise the impact of fisheries on common dolphins by reducing the actual fishing pressure in the most suitable habitats for the species and could lead to a decrease in bycatch, which is one of the major threats to common dolphins in the area (López et al. 2002 and 2003; Silva and Sequeira, 2003; Goetz et al. 2014; Saavedra et al. 2018). Furthermore, these measures could lead to a lower conflict with fisheries than other measures previously proposed such as the regulation of fishing hours or seasonal closures (Fernández-Contreras et al. 2010; Goetz et al. 2014). However, further studies would be needed to understand the potential impacts of the suggested measures in local fisheries and in other marine species (e.g., fisheries displacement to other areas).

This study stresses the applicability of SDMs, and more particularly the use of ENFA, as a comprehensive tool to expand the knowledge on the distribution and habitat use of common dolphins and to develop better management and conservation strategies. However, given the widespread distribution of common dolphins and their seasonal movement patterns in the North-East Atlantic, a joint scientific effort covering the full distribution of the species and the involvement of the different affected stakeholders are needed to ensure that effective management plans and conservation strategies are developed throughout the common dolphin distribution range.

Table 2.4 *Shows the 4 steps that should be considered for the reassessment of the area protected by the Atlantic Islands National Park west of Sálvora Island to improve common dolphins conservation.*

Conservation problem	Measure	Definition	Justification	Parties involved
Overlap between fisheries and common dolphins most suitable habitats	Expansion of the national park	Expansion of the maritime area of the National Park around Sálvora Island to the west, as has already been suggested by other conservation organisations (Aguilar et al. 2009), to include the optimal and suitable habitats for common dolphins.	This expansion would incorporate the areas with the most suitable habitats to the Atlantic Islands National Park, extending the already existing fishing restrictions into the newly created protected area.	The design of the newly created protected area should be the result of a cooperation between marine scientists, fishermen and public administration to reach a satisfactory agreement for the different parties and to develop compensation schemes if needed.
	Designation of a SCI	The designation of the maritime area of the natural park around Sálvora Island (the already existing one and the expansion) as a Site of Community Importance (SCI).	This measure is in agreement with the Habitats Directive, as the area west of Sálvora Islands includes important habitats for common dolphins, which is listed in Annex IV of the directive.	The governments of the different countries are responsible for proposing the designation of SCI to the European Union, according to the Habitats Directive.
	Designation of a SAC	Following the designation as SCI, the designation of this area as a Special Area of Conservation and adding it to the Spanish Network of Marine Protected Areas and Natura 2000 network.	This measure is in agreement with the Habitats Directive which urges governments to promote conservation measures especially in the areas that include important habitats for common dolphin ecology and reproduction.	The governments of the different countries are responsible for proposing the designation of SAC to the European Union, according to the Habitats Directive.
Unspecific legislative framework	Improved legislative framework	The development of a clear legislative framework that unequivocally specifies the fishing pressure that can be exerted in the newly created protected area by establishing the number of fishing vessels allowed to work, the gear that would be allowed, and the fishing quotas.	The fishing restrictions and regulation that currently apply in the maritime area of the Atlantic Islands National Park are scattered in several regional and national Spanish laws and are unspecific about certain aspects. Thus, a new, clear and easy to follow legislative framework should be developed.	The different public administrations (local, regional and national) should be responsible for developing this new framework.



Drawing by Núria Giralt

Chapter 3

Living on the edge: Overlap between a marine predator's habitat use and fisheries in the North-East Atlantic waters (North-West Spain)

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Contribution to the article:

OGP contributed to this study by taking part in the last year (2017) of data collection, analysis of databases on common dolphins, spatial analysis, designing the maps and providing insightful inputs to the final manuscript.

3.1. *Abstract*

The impact of commercial fisheries on marine top predators is currently the focus of considerable international concern. In spite of the recognition of the competition between fisheries and marine predators for the same resources, few comprehensive assessments of the level of overlap between marine predators and fisheries have been conducted. Data from 273 daily boat surveys over a period of 4 years along the north-western coast of Spain were used to assess the environmental, topographic, and anthropogenic correlates of habitat use and relative density of short-beaked common dolphins. Moreover, the degree of vulnerability of this marine top predator to coastal fisheries was assessed by identifying the type of fisheries associated with the presence of common dolphins. Our results reported that common dolphin presents a fine-scale pattern of habitat use, with an unequal use of available habitat and varying relative abundance, which was mostly related to the variation in environmental, topographic, and anthropogenic variables. The high occurrence of common dolphins in zones characterized by a high bottom trawl fishing pressure was indirectly linked to the susceptibility of these marine predators to fishing activities. These findings can be used as a relevant indicator of the degree of vulnerability of common dolphins to human pressure providing comprehensive information on which to base conservation and management strategies.

Keywords: Marine predators, Fisheries, Cetaceans, *Delphinus delphis*, Atlantic Ocean, GAMs

3.2. *Introduction*

Anthropogenic pressure on the marine environment has significantly expanded over the last decades increasing the potential for areas of human and wildlife activity to overlap (Halpern et al. 2008). One of the most detrimental anthropogenic impacts on marine ecosystems is the effect of fishing activities (Pauly et al. 2005) and it is particularly evident on top predators such as sharks, sea birds, and marine mammals (Baum et al. 2003; Lewison et al. 2004; Rogan and Mackey, 2007; Read, 2008; Moore et al. 2009; Anderson et al. 2011). These species are directly affected by operational processes such as direct and incidental captures or collisions with fishing vessels, and by indirect ecological effects (i.e. depletion of prey), which induce changes to the marine food web and competition for food resources (Tasker et al. 2000; Lewison et al. 2004; Northridge, 2009; Anderson et al. 2011; Díaz López, 2018).

Fisheries make certain areas more attractive to marine top predators, by concentrating food resources in particular zones. This indirectly modifies specific habitats that consequently become favourable for feeding (Bearzi et al. 2003; Díaz López 2006, 2018; Guinet et al. 2014). As a result, marine top predators depredate their natural prey species from fishing nets because fish abundance and distribution have been altered by human activities (Bearzi et al. 2003; Guinet et al. 2007; Díaz López, 2018). By doing this, marine predators may come into physical contact with the fishing gear, which ultimately may result in bycatch or injury (Díaz López, 2006). Ecological studies are critical for the better understanding of the impact of human activities on marine top predators (Díaz López, 2018). As information on both distribution and abundance of marine predator food resources is scarce, environmental and anthropogenic variables can be used as substitutes to assess the distribution of these potentially vulnerable species (Pirotta et al. 2011; Breen et al. 2016; Díaz López and Methion, 2017, 2018).

A number of marine mammal species are attracted to fishing vessels and have been observed to feed in association with fisheries (Bearzi et al. 2003, 2008; Díaz López 2006, 2018; Guinet et al. 2007, 2014). One species regularly present in studies about bycatch across different fisheries and regions is the common dolphin (*Delphinus delphis*), a small cetacean widely distributed in temperate and tropical waters worldwide (Jefferson et al.

2009). In the North Atlantic there are two separate populations of common dolphins based on morphological and genetic characteristics: the north-western and the north-eastern Atlantic populations (Natoli et al. 2006; Westgate, 2007). The latter, found in waters off the western coast of Europe from southern Spain up to 60° of latitude in Norway (Mirimin et al. 2009), is one of the most abundant cetacean species in these waters and accounts for most of the fisheries bycatch in the area (López et al. 2003; Fernández-Contreras et al. 2010; De Boer et al. 2012). Although fluctuations in the common dolphin fine-scale use of habitat have been the subject of several studies in different parts of its range (Murphy et al. 2013), there is a lack of information available on interactions between this species and fishing operations (Bearzi et al. 2003). While common dolphin is known to interact with fisheries and to be sensitive to fisheries impact, few studies have included anthropogenic explanatory variables (such as the presence of different types of fisheries) in habitat models (Bearzi et al. 2003; Rogan and Mackey, 2007; Fernández-Contreras et al. 2010; De Boer et al. 2012; Marçalo et al. 2018). Furthermore, very few studies with long-term and year-round monitoring datasets on common dolphin habitat preferences and interaction with inshore fisheries are available. This lack of information is clearly evident along the north-western coast of Spain (Galicia), a region that supports significant pelagic and demersal fisheries associated with coastal upwelling events (Pérez et al. 2010) and where previous studies have reported high rates of common dolphin bycatch (López et al. 2003; Fernández-Contreras et al. 2010; Goetz et al. 2014; Saavedra et al. 2017).

In this paper, a year-round comprehensive investigation of common dolphin habitat use along the coastal and shelf waters of Galicia (North-West Spain) is presented for the first time. This was achieved by examining the relationships between environmental, topographic, and anthropogenic variables and presence and relative density of common dolphins. Additionally, the degree of vulnerability of this marine top predator to coastal fisheries was assessed by identifying the type of fisheries associated with the presence of common dolphins.

3.3. *Methods*

3.3.1. Study area

The present study was performed along the north-western coast of the Iberian Peninsula, more particularly along the southern coast of Galicia (Spain), covering the entire continental shelf from Muros (42° 47.4′ N, 9° 9′ W) to Cíes Islands (42° 21.6′ N, 8° 56.4′ W) (Figure 3.1). The study area encompassed 1,300 km^2, with 92% of the area corresponding to continental shelf and inshore waters (depth < 150 m) and the rest covering the continental slope down to a depth of 1,050 m. These waters are influenced by oceanographic processes associated with wind-driven coastal upwelling events that enhance primary production. This area is heavily affected by human activities, including but not limited to marine traffic, fisheries, and aquaculture (Méndez and Vilas, 2005). Galicia has the largest fishing fleet in Spain, which in 2016 consisted of 4,354 vessels representing 48% of the Spanish and 5.4% of the European fleets (Ministerio de Agricultura, Pesca y Alimentación, 2017). The different cetacean species present along this highly productive locus are therefore vulnerable to a number of direct human impacts such as vessel collisions, by-catch, overfishing, oil spills, pollution and habitat modification (López et al. 2003; Vieites et al. 2004; Díaz López and Methion, 2017, 2018).

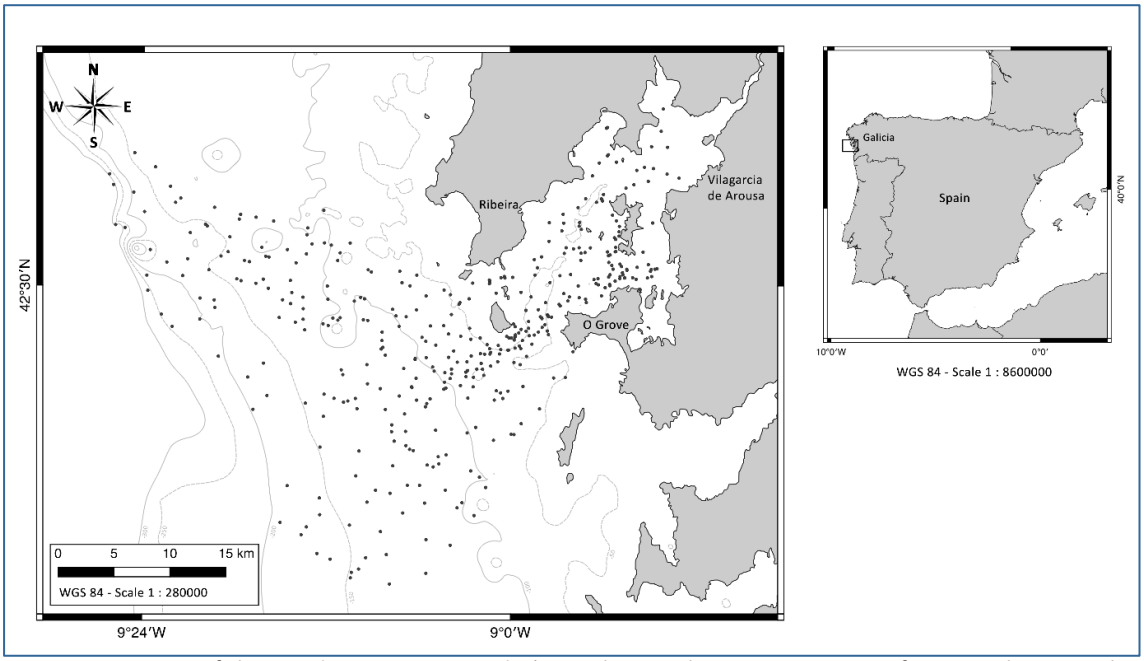


Figure 3.1 *Map of the study area surveyed along the north-western coast of Spain, showing the randomly selected samples collected instantaneously every 20 min.*

3.3.2. Data collection

Data for this study were collected as part of a longitudinal study carried out by the Bottlenose Dolphin Research Institute BDRI (www.thebdri.com) on the ecology of cetacean species inhabiting the Galician waters (Díaz López and Methion, 2017, 2018; Methion and Díaz López, 2018). A 12 m fly-bridge research vessel was used to systematically monitor the study area, recording data on presence and number of common dolphins, anthropogenic and oceanographic variables following the methods described by Díaz López and Methion (2018). Boat-based observation surveys were carried out year-round from March 2014 until October 2017 with systematic transect lines adapted to match the specific conditions of the study area. At least three experienced observers were stationed on the flying bridge (situated at 4 m above the sea level), scanning 360 degrees of the sea surface in search of cetaceans (with the naked eye and 10x50 binoculars). The spatial distribution of the effort varied according to weather conditions and time constraints throughout the study period. Surveys were done when the sea conditions were up to 3 on the Douglas sea state scale, wave height smaller than 1.5 m, and visibility was not reduced by rain or fog.

Following Díaz López and Methion (2018), on each survey, the time, position, vessel speed, presence of cetaceans (within a 1 nm radius of the boat's position), anthropogenic and environmental data were recorded as an instantaneous point sample every 20 minutes (20-minute sample). The spatial resolution of this 20 min interval was 2 nm (given a 6 - 8 kn speed) and the visual detection/nondetection of common dolphins was recorded instantaneously for all 20-minute samples. Upon sighting of common dolphins, searching effort (on effort time) ceased and the vessel slowly manoeuvred towards the animals in order to minimise disturbance during the approach. Group size and composition were estimated before and after common dolphins had been approached based on the total count of individuals observed at one time in the area. A group of common dolphins was defined as one or more dolphins observed within a 500 metres radius. Because the research vessel often stayed with the animals, animals could be observed at close ranges (<50 m) and for long periods of time (>45 min). At the end of an encounter, the searching effort continued along the previously planned route.

Environmental variables

Five environmental predictors were initially considered to have potential ecological significance and were available for each 20-minute sample recorded:

Date, time (UTC in hours), sea surface temperature (SST in ° Celsius), tidal cycle (rising with the flooding tide and falling with the ebbing tide), chlorophyll a (in mg x m^{-3}), and upwelling index (m^3 x s^{-1} x km^{-1}).

Tidal cycle (presence/absence of flood tide) was obtained for the harbour of Ribeira (42° 33' N, 008° 59' W), from the Galician weather service (http://www.meteogalicia.gal). Chlorophyll a data were obtained as daily rasters, with a spatial resolution of 1 km x 1 km, for the position of each instantaneous sample from the COPERNICUS Marine Environment Monitoring Service website (http://marine.copernicus.eu). Upwelling index (Bakun, 1973) was obtained from the Instituto Español de Oceanografía (www.indicedeafloramiento.ieo.es) and was calculated using sea level pressure of the Meteogalicia WRF atmosferic model.

Topographic variables

Five topographic variables were initially considered to have potential ecological significance and were available for each 20-minute sample recorded.

Position (Latitude and longitude coordinates), depth (m), bottom slope gradient (expressed as percent slope), bottom slope aspect (the orientation of the slope with respect to True North in degrees), and distance to the coast (m).

Bottom slope gradient and slope aspect, were computed from the bottom depth obtained from a bathymetric chart data set, with a 500 m x 500 m resolution, digitized from two 1:50,000 scale nautical charts from the Instituto Hidrográfico de la Marina (Spain).

Anthropogenic variables

Four anthropogenic variables were measured within a 1 nm visual range for each 20 min sample recorded:

Number of bottom trawlers, number of purse-seines, number of motor boats (including recreational boats and cargo ships, representative of the marine traffic), and presence of fishing buoys (indicating the occurrence of bottom set gill-nets).

Data analysis and modelling framework

Overall, 3,114 samples were collected instantaneously every 20 min of which 1,207 were on effort (when searching for common dolphins). Of these on effort samples, 634 were in inshore waters (< 150 m depth) and 569 on the continental shelf (between 150 m and 300 m). All samples collected in waters deeper than 300 m were excluded for further analysis because they were unrepresented in the study (n = 20 samples).

Following Díaz López and Methion (2018), a dataset was generated by randomly selecting 35% of the samples (n = 422 samples) searching for common dolphins. By arbitrarily down-sampling the number of on effort 20-minute samples, the lack of independence arising from consecutive samplings was limited, avoiding the influence of variation in the spatial distribution of the observation effort, and limiting pseudo-replication. Date and time were not included as covariates in further analysis, because they were related with other variables (i.e. sea surface temperature and chlorophyll a) which were included instead due to their biological interpretability (Díaz López and Methion, 2018) and to prevent over-parameterization (Forney, 2000). Likewise, latitude and longitude (GPS position) and distance to the coast were not included in further analysis, because they were highly correlated with water depth (Spearman rho > 0.9, $p < 0.001$).

Generalized additive models (GAMs, Hastie and Tibshirani, 1990) were used to explore the environmental, topographic and anthropogenic variables that might have affected the distribution and density of common dolphins. A GAM is a non-parametric generalization of multiple linear regressions, widely-used for interpreting ecological interactions, which enables the estimation of both linear trends as well as non-monotonic responses, within the same model framework (Hastie and Tibshirani, 1990). The GAMs results and diagnostic information about the fitting procedure were implemented from the mgcv package (Wood, 2006) in v. 1.8.1. of the statistics and graphics tool R (R Core Team, 2016). To choose the most appropriate presence-absence model to address an

apparently zero-inflated dataset, three different models such as GAMs with logistic link function, Tweedie or Negative Binomial distributions were compared using the Akaike Information Criterion (AIC) (Virgili et al. 2017). The number of common dolphins seen (given presence) was modelled using a GAM with a negative binomial distribution and logarithmic link function. Even though the best presence-absence model selected did not completely accommodate the elevated number of absences, the use of two types of GAMs in this study, with abundance data and presence–absence data, allowed an accurate prediction of the response variables (Howard et al. 2014). The smooth functions were constructed as cubic splines and their optimal shape was estimated by minimizing the general cross validation (GCV) criterion (Wood, 2006). To limit relationships to plausible simple forms and limit the risk of overfitting the number of knots in the smooth functions was reduced to 5. Model assumptions were checked by visual inspection of the residuals and regression fits were examined using plots of residuals against fitted values. The Variance Inflation Factor (VIFs) was calculated to reveal no signs of collinearity among the explanatory variables, with all values below a cut-off level of 3. To find a set of explanatory variables that does not contain collinearity, variables were removed one at a time and then the VIF values were recalculated. This process was repeated until all VIF values were smaller than 3. The Durbin-Watson test (from the R package "lmtest", Zeileis and Hothorn, 2002) and auto-correlation functions (ACF) were used to check for serial correlation, both in our raw data and in the residuals from the models.

Because of the large number of potential combinations of predictor variables, and as an additional improvement, GAMs simplification and selection were performed using a multi-model inference approach based on the methods and recommendations of Burnham and Anderson (2002) and Grueber et al. (2011). Model averaging can lead to robust predictions accounting for uncertainty in model selection by making inferences from an ensemble of possible solutions (Burnham and Anderson, 2002). This multi-model inference approach enables the response variable (presence or number of common dolphins) to vary as a linear or nonlinear function of the selected model covariates, while accounting for the non-normality.

As a first step in the analysis, an ensemble of competing GAMs to explain the response variable was selected using the R package 'MuMIn' (Barton, 2011). To ensure that the

most parsimonious models were maintained within the best supported model set, models were compared based on their Akaike information criterion corrected for small sample sizes (AICc) (Grueber et al. 2011). The models with a Δ AICc< 2 (the difference in AICc of each model in comparison to the model with the lowest AICc) were selected to identify the relative importance of each model term in predicting the response variable and to estimate the effect sizes of the predictors (Burnham and Anderson, 2002). Ecological conclusions were drawn from the direct comparison of this set of models that provided substantial support. Models were ranked from best to worst using the Δ AICc and the Akaike weights (wi) to give the relative support for a given model compared with the others (Grueber et al. 2011). Furthermore, the relative importance of a predictor variable (RVI) was calculated as the sum of the Akaike weights overall of the models in which the predictor appears (Burnham and Anderson, 2002). Partial predictions with 95% confidence intervals were plotted for each covariate included within the best supported model set.

3.4. *Results*

3.4.1. Survey effort and presence of common dolphins

Overall, 273 daily boat surveys over a period of 38 months and covering 9,417 km were undertaken between March 2014 and October 2017. In total, 1,015 hours were spent in satisfactory conditions (up to 3 on the Douglas sea state scale, wave height smaller than 1.5 m, and absence of rain or fog).

During the study, 91 sightings of common dolphin groups were recorded (average sighting distance = 341 ±60 m) (Figure 3.2). A total number of 4,963 common dolphins were seen on 28 different days at sea (10% of total number of daily surveys) over 14 different months. This species was encountered along the shelf and inshore waters throughout the study area and in all seasons of the year. The size and composition of common dolphin aggregations were examined for the observed groups. Group size ranged from 1 to 700 dolphins (mean = 54.5 ±11, n = 91) with the majority (73% of the groups) having 40 or less individuals. Group composition showed that 81% of the observed common dolphins were considered adults; thus, the remaining 19% were categorized as dependent calves, of which 4% were new-borns. Dependent calves were

present in 69% of the observed groups. Group size was significantly related with the number of dependent calves in the group (Spearman rho = 0.88, $p<0.001$). Likewise, the size of the aggregations was significantly higher in presence of dependent calves (mean $_{\text{with calves}}$ = 75.7 ±15 vs. mean $_{\text{without calves}}$ = 6.9 ±1.4; Mann-Whitney, $p<0.001$). During the study period common dolphins have not been observed in mixed feeding aggregations with other dolphin species.

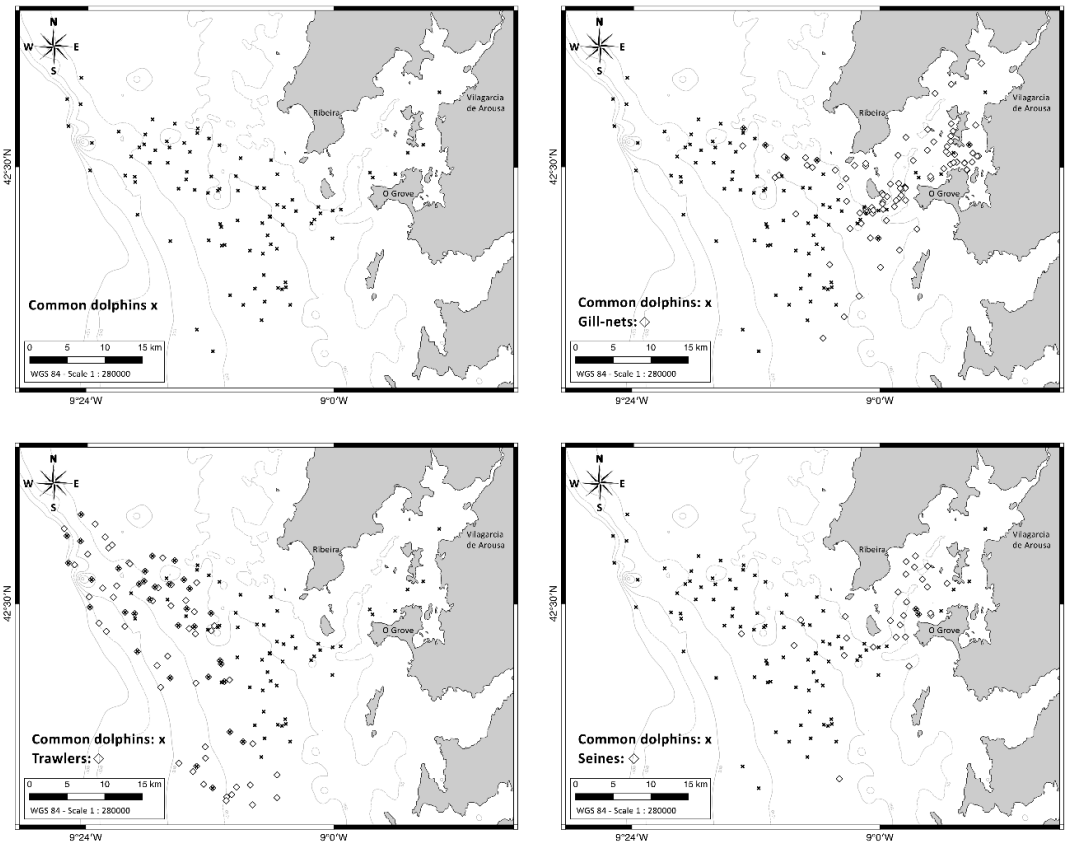


Figure 3.2 *Distribution of common dolphin sightings (crosses) and distribution of commercial fisheries (squares). When sightings were in the presence of fisheries, crosses were included within the squares.*

3.4.2. Environmental, topographic, and anthropogenic factors affecting common dolphin presence

Due to restricted habitat use, low density and poor detection even in good sea state conditions the absence of common dolphins in the dataset was large (78.7%). A GAM with a logistic link function was found to be the most appropriate model to fit the data

(lowest AIC), the GAMs with a negative binomial and Tweedie distributions showed similar predictions but higher AIC scores. A global GAM with a logistic link function was created with 11 selected environmental, topographic, and anthropogenic variables that did not contain collinearity: SST, chlorophyll a, upwelling index, tidal cycle, depth, slope, aspect, number of bottom trawlers, number of purse seine fishing boats, and presence of gill-nets. The GAM explained 21.3% of the variation in common dolphin presence (R-sq = 0.18, UBRE = -0.10, AICc = 379.6). A candidate model set consisting of all 2,048 simplified versions of the global model was produced. The simplified versions were compared based on their AICc. Five models with Δ AICc <2 were used to produce model averaged parameter estimates (Table 3.1).

Table 3.1 *Most likely models explaining the variation in presence of short-beaked common dolphins in relation to environmental, topographic, and anthropogenic variables. Depth, CHL = concentration of chlorophyll a, SST = sea surface temperature, Slope = bottom slope gradient, FN = presence/absence of gill-nets, Trawlers = number of bottom set trawlers. Only five most candidate models (Δi ≤ 2) of the 2,048 are presented, df degrees of freedom, Δi difference between the particular model and the best model, wi Akaike weight showing the relative support of a given model compared to the others.*

Model	df	logLik	AICc	Δi	wi
FN/CHL/Depth/SST	8.20	-175.38	367.52	0.00	0.29
FN/Depth/SST	6.99	-176.76	367.84	0.31	0.24
FN/CHL/Depth/SST/Trawlers	9.26	-174.77	368.53	1.01	0.17
FN/CHL/Depth/SST/Slope	9.56	-174.57	368.75	1.23	0.15
FN/Depth/Trawlers/SST	8.34	-175.92	368.91	1.39	0.14

Depth, water temperature, and presence/absence of gill-nets were retained in each model within the candidate model set having a relative variable importance (RVI) of 1 in the final average model. Concentration of chlorophyll a had an RVI of 0.61 in the final averaged model. Number of bottom set trawlers and bottom slope gradient had a relative variable importance RVI of 0.32 and 0.15 respectively in the final averaged model. Number of purse seine fishing boats, tidal cycle, number of motor boats (as a measure of the marine traffic), upwelling index, and bottom slope aspect, however, were not present in the top model set, indicating that these covariates were not important predictors of the presence of common dolphins.

Common dolphin occurrence was predicted to be more likely at the edge of the continental slope (at 150 – 200 m depth and strong bottom slope gradient), during moderate sea surface water temperatures (around 16°C), in absence of bottom set gill-nets, low concentration of chlorophyll a, and with a high number of bottom trawlers (Figure 3.3, Table 3.2).

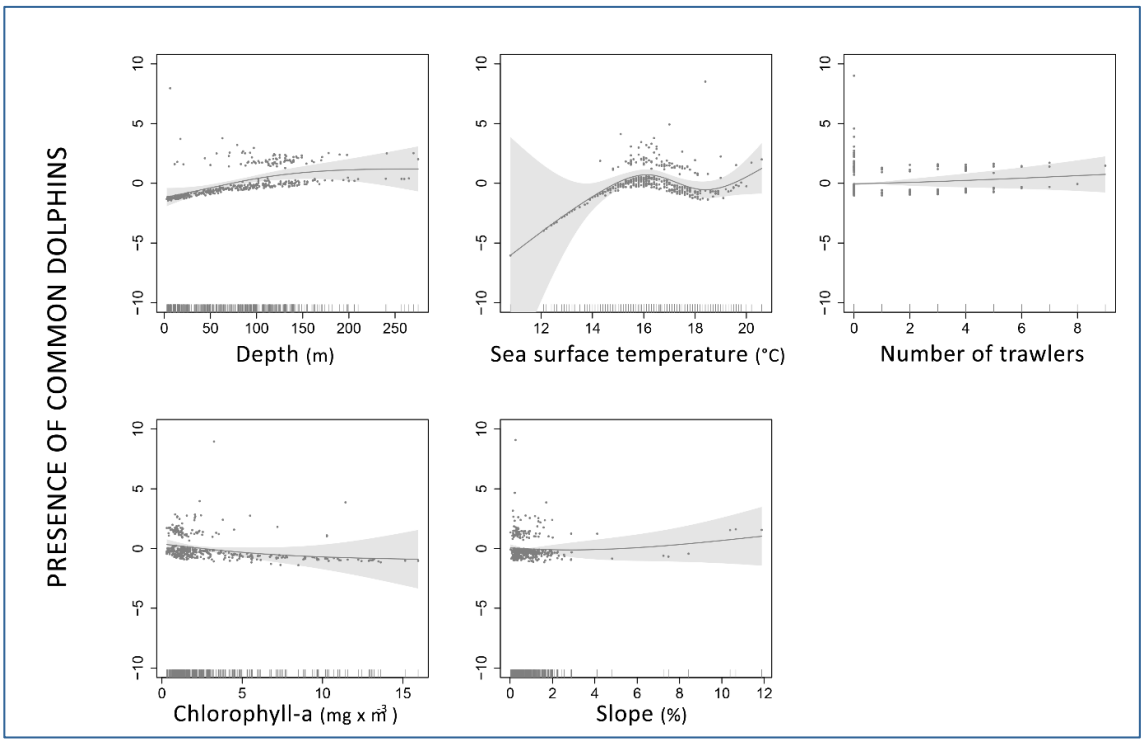


Figure 3.3 *Averaged predictions of common dolphins' presence for each covariate present in the confidence set of models and their 95% confidence limits when all other variables are fixed to their mean value.*

Table 3.2 *Examples of the predicted effect of variables included in the model-averaged model on the presence of short-beaked common dolphins, with the other predictors held at their mean (N=422). SE = standard error. RVI = relative variable importance, N models = number of containing models. SST = sea surface temperature, CHL = concentration of chlorophyll a, Trawlers = number of bottom set trawlers, Slope = bottom slope gradient.*

Predictor		Estimated presence (%) of common dolphins		RVI	N models
Depth	50m	15.66	SE = 3.78	1	5
	100 m	28.84	SE = 4.66		
	150 m	39.96	SE = 7.38		
	200 m	45.60	SE = 12.31		
	250 m	47.38	SE = 19.95		
Gill-nets	Presence	12.65	SE = 5.13	1	5
	Absence	28.05	SE = 4.90		
SST	12	0.26	SE = 0.77	1	5
	14	4.78	SE = 3.25		
	16	23.70	SE = 4.03		
	18	8.94	SE = 3.22		
	20	20.76	SE = 12.35		
CHL	0	32.35	SE = 7.05	0.61	3
	5	19.16	SE = 4.70		
	10	13.90	SE = 6.94		
	15	11.99	SE = 12.04		
Trawlers	0	22.79	SE = 4.16	0.32	2
	4	28.20	SE = 7.58		
	8	36.97	SE = 15.93		
Slope	0	24.97	SE = 4.89	0.15	1
	4	22.44	SE = 8.42		
	8	30.62	SE = 16.43		

3.4.3. Effects of environmental, topographic, and anthropogenic factors on the size of the aggregations of common dolphins

Nine explanatory variables were used to create the GAMs since aspect and number of motor boats were considered collinear and therefore were dropped before starting the analyses. The global GAM explained 39.3% of the variation in the number of common dolphins (R-sq = -0.03, AICc = 833.91, n = 89). Out of 1,024 simplified versions of the global model, four models with Δ AICc <2 were used to generate model averaged parameter estimates (Table 3.3).

Table 3.3 *Most likely models explaining the variation in number of short-beaked common dolphins in relation to environmental, topographic and anthropogenic variables. Depth, CHL = concentration of chlorophyll a, SST = sea surface temperature, Slope = bottom slope gradient, FN = presence/absence of gill-nets, Seines = number of seines, UI = upwelling index. Only four most candidate models (Δi ≤ 2) of the 1,024 are presented, df degrees of freedom, Δi difference between the particular model and the best model, wi Akaike weight showing the relative support of a given model compared to the others.*

Model	df	logLik	AICc	Δi	wi
Slope/UI/Tidal cycle	9.43	-402.07	825.50	0.00	0.31
FN/Slope/UI/Tidal cycle	10.41	-400.97	825.82	0.31	0.26
FN/CHL/Depth/Seines/Slope/UI/Tidal cycle	16.65	-392.29	826.13	0.63	0.23
FN/Depth/Seines/Slope/UI/SST	17.20	-391.55	826.35	0.85	0.20

Slope gradient and upwelling index were both retained in each model within the candidate model set having a relative variable importance (RVI) of 1 in the final average model. Tidal cycle and presence of fishing nets had an RVI of 0.80 and 0.69 respectively in the final averaged model. Depth and number of purse seine fishing boats had an RVI of 0.43 in the final averaged model. CHL a and SST were only present in one model within the candidate model set and had an RVI of 0.23 and 0.20, respectively in the final averaged model. The anthropogenic variable number of bottom trawlers, however, was not present in the top model set, indicating that this covariate was not an important predictor of the size of the aggregations of common dolphins.

The number of common dolphins was predicted to be mostly influenced by the tidal cycle and upwelling events. Common dolphin aggregations were predicted to increase during flood tide and upwelling periods at the edge of the continental slope. Moreover, the size of the aggregations of common dolphins was predicted to increase in absence of gill-nets and with a higher number of purse seines (Figure 3.4, Table 3.4).

Table 3.4. *Examples of the predicted effect of variables included in the model-averaged model on the size of the aggregations of short-beaked common dolphins, with the other predictors held at their mean (N=89). SE = standard error. RVI = relative variable importance, N models = number of containing models. SST = sea surface temperature, CHL = concentration of chlorophyll a, Trawlers = number of bottom set trawlers, Slope = bottom slope gradient.*

Predictor		Estimated number of common dolphins		RVI	N models
Slope	0	33.31	SE = 24.84	1	4
	4	277.62	SE = 225.65		
	8	134.39	SE = 109.20		
UI	-2,000	23.35	SE = 7.64	1	4
	0	26.04	SE = 7.46		
	2,000	33.71	SE = 13.21		
	4,000	53.62	SE = 34.19		
Tidal cycle	Ebb	21.23	SE = 6.44	0.8	3
	Flood	36.78	SE = 12.17		
Gill-nets	Presence	12.65	SE = 5.13	0.69	3
	Absence	28.08	SE = 8.15		
Depth	50m	9.47	SE = 3.80	0.43	2
	100 m	23.98	SE = 7.04		
	150 m	38.63	SE = 12.51		
	200 m	39.26	SE = 18.56		
	250 m	23.16	SE = 18.61		
Seines	0	25.35	SE = 7.32	0.43	2
	1	88.95	SE = 60.49		
	2	312.26	SE = 399.34		
CHL	0	16.87	SE = 6.09	0.23	1
	5	45.12	SE = 20.51		
	10	68.24	SE = 51.04		
	15	87.82	SE = 114.83		
SST	12	0.35	SE = 0.69	0.2	1
	14	3.55	SE = 3.01		
	16	23.09	SE = 6.41		
	18	19.94	SE = 7.92		
	20	5.99	SE = 4.05		

3.5. *Discussion*

Marine top predators, such as common dolphins, can serve as indicators of ecosystem health and are exposed to different levels of anthropogenic impacts (Halpern et al. 2008; Maxwell et al. 2013). A good understanding of the level of interaction between common dolphins and commercial fisheries is critical for marine conservation and management. In this context, our study provides relevant information to assess the common dolphin habitat preferences and its degree of interaction with commercial fishing activities along the north-western coast of the Iberian Peninsula. At the same time these findings

highlight the importance of considering the interaction of multiple variables in ecological studies on fine temporal and spatial scales.

Our results report that common dolphins present a fine-scale pattern of habitat use along the north-western coast of Spain, with an unequal use of available habitat and varying relative abundance, which is mostly related to the variation in environmental, topographic, and anthropogenic drivers. These findings are consistent with previous studies in the region which used data collected from observers on-board fishing vessels (Spyrakos et al. 2011). Furthermore, the boat-based research surveys of this study provide additional information than fishing vessel observer programs by providing data about common dolphin occurrence from areas not covered by the fishing vessels.

Given the oceanographic characteristics of the north-western coast of Spain, variability in common dolphin responses to the environmental and topographic stressors is likely a result of the complex and dynamic interactions of these factors with prey availability. Along this coastal region, the species shows a preference for blue whiting (*Micromesistius poutassou*), sardine (*Sardina pilchardus*) and to a lesser extent, Atlantic horse mackerel (*Trachurus trachurus*) (Santos et al. 2013, 2014). Therefore, the observed influence of oceanographic parameters such as the sea surface temperature on the fluctuations in presence and relative density of common dolphins may be related to seasonal changes in abundance of these demersal and pelagic fish species (Tenore et al. 1995). It is likely distribution aspects of these fish species, not primary productivity aspects, that influence common dolphin presence in the area. Likewise, the relationship with depth could also be associated with the availability of demersal or pelagic fish species (Spyrakos et al. 2011).

Wind driven coastal upwelling events along the north-western coast of Spain take nutrient-rich waters into the photic layer, enhancing primary and secondary productivity and so, after some time, supporting plankton-feeding fish species in shelf waters (Pérez et al. 2010). The availability of these fish species is an important driver for both common dolphins and fisheries presence and distribution. The relatively low chlorophyll a concentration reported in presence of common dolphins could be interpreted as a period of phytoplankton decay mediated by zooplankton grazing and therefore an

abundance of zooplanctivorous fish species. The results of our analysis predicted higher aggregations of common dolphins in deeper waters, in periods of upwelling, and during flood phases, which may be related to the abundance of large aggregations of fish species in offshore waters (Pérez et al. 2010). Indeed, the upwelling events together with strong tidal streams make the study area a suitable foraging habitat for common dolphins, by supporting high prey densities.

Many dolphin species can be both harmed by and benefit from anthropogenic fishing activities and some of the effects of this interaction operate at the population level (Díaz López 2006, 2018; Bearzi et al. 2008; Guinet et al. 2014). While dolphin species depredate on fisheries because the catch is part of their natural diet, the lower probability to find common dolphins in presence of gill-nets supports the idea that this species does not exploit this anthropogenic food source. These observations could be explained by the fact that gill-net fisheries operate mostly in coastal waters targeting demersal, benthic and bentho-pelagic organisms, which are not main prey items in the diet of common dolphins (Santos et al. 2013). This lack of direct interaction between common dolphins and gill-net fisheries does not exclude the existence of incidental captures in this type of fishery. For example, López et al. (2003) estimated an annual mortality of 87 small dolphin species (most of them probably common dolphins) in gill-net fisheries in Galician waters, derived from interview data and observations from fishing vessels.

In addition to incidental captures in gill-net fisheries, common dolphins are also caught in trawl and purse seine fisheries (Morizur et al. 1999; Murphy et al. 2013). In fact, the main fisheries responsible for common dolphin bycatch in Galician waters are bottom trawlers, with estimations ranging from 394 to 900 common dolphins captured per year (López et al. 2003; Fernández-Contreras et al. 2010). Our findings support the idea that the by-catch is related to the frequency of common dolphin interaction with fishing vessels. Indeed, our results predict a higher presence of common dolphins in areas where the trawl fisheries mainly operate. While common dolphins have been reported to feed both on discards and directly from trawl nets (Murphy et al. 2013), the link between the number of bottom trawlers and common dolphin presence does not necessarily imply a direct relationship. Their association may also be due to trawlers and common dolphin sharing the same resources since bottom trawl fisheries target blue

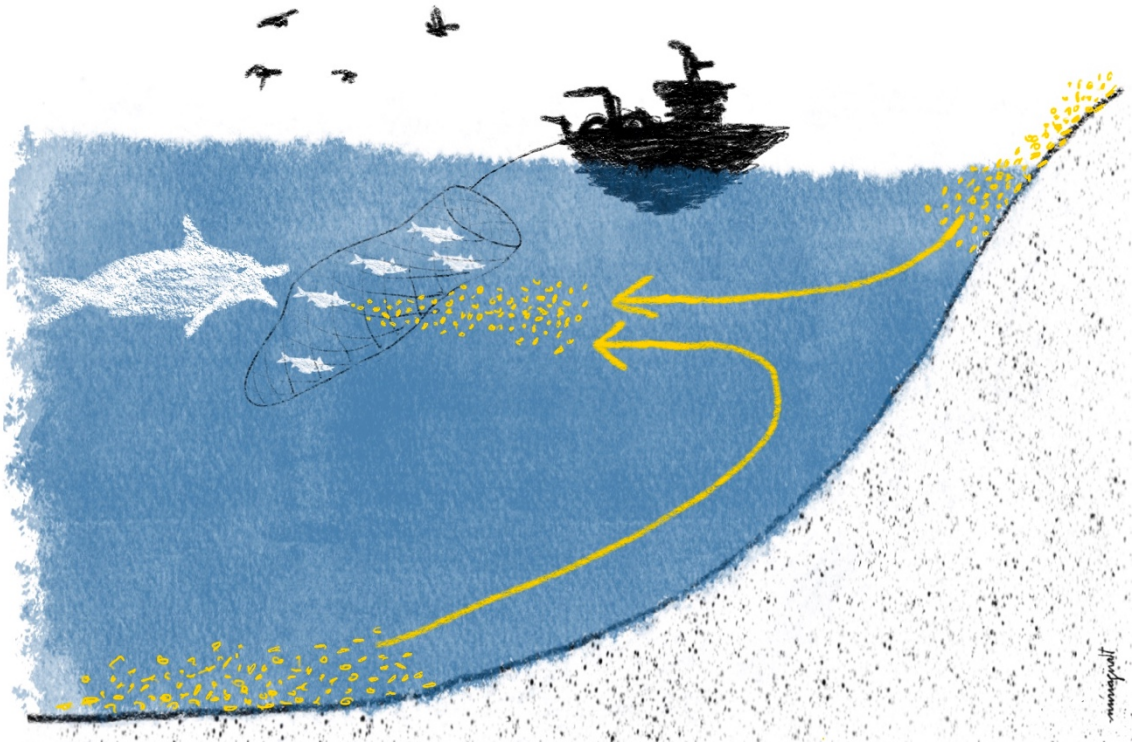
whiting, Atlantic horse mackerel and hake (*Merluccius merluccius*, Linnaeus 1758) (Fernández-Contreras et al. 2010).

Although purse-seine fisheries target sardine, one of the main prey species of common dolphins in the region (Méndez Fernández et al. 2012; Santos et al. 2013; Marçalo et al. 2018), this type of fisheries was not an important predictor of the presence of common dolphins in the area. Common dolphins could target sardine aggregations irrespectively of the presence of purse seiners, as suggested in recent studies along the Portuguese shelf waters (Marçalo et al. 2018). Galician purse seine fishermen claim that common dolphins negatively affect their harvests, so fishers often avoid dropping their nets in presence of common dolphins (Goetz et al. 2014). This operational change could help explain the lack of overlap between common dolphins and purse seine fisheries in the region. Another explanation for the low association between purse seines and common dolphins is the fact that purse seines mainly operate in shallower waters, due to a decline in sardine stocks (Pérez et al. 2010), and therefore target less important common dolphin prey species.

Findings of this study may help concentrate conservation efforts on the interaction of common dolphins with fisheries in areas of highest concern. The observed fine-scale pattern of habitat use of common dolphins in zones characterized by a high bottom trawl fishing pressure supports the idea that this type of fishery is more likely to "attract" common dolphins. As the likelihood of fisheries by-catch is related to opportunity and selectivity of the fishing gear, these results can indirectly be linked to the susceptibility of these marine predators to fisheries. Indeed, trawl fisheries affect common dolphins in a number of ways: (1) increased mortality from entanglement in fishing gear that could compromise common dolphin survival in the region (López et al. 2003; Fernández-Contreras et al. 2010; De Boer et al. 2012; Saavedra et al. 2017) and (2) competition for the same fish species (Bearzi et al. 2003). The latter may represent a subtle and scarcely noticeable threat, as fisheries could reduce the availability of common dolphin prey and this impact may go unobserved given insufficient research effort (e.g. fish abundance estimations, changes in common dolphin survival rates and migration patterns).

Thanks to these findings, it can be concluded that common dolphins are more vulnerable to bottom trawl than to purse-seine and gill-net fisheries along the north-western coast of the Iberian Peninsula. With an increase of 16% of the bottom trawl catches along the continental shelf in the last 10 years (official catches from Ribeira harbour, Xunta de Galicia, Conselleria do Mar, 2020a,b), current harvesting regimes along the study area might exacerbate both fishery-induced by-catch mortalities and fishing pressure on dolphin prey availability, increasing the risk of extinction of this marine predator. Previous studies in the region showed that the percentage of stranded common dolphins due to fishery interactions has increased approximately 18% during the last 20 years (Murphy et al. 2013). From such a perspective, a restriction of bottom trawl fisheries in waters shallower than 250 - 300 m (suggested by Fernández-Contreras et al. (2010) and Goetz et al. (2014)), combined with a reduction of nocturnal trawling (suggested by López et al. (2003)), could ameliorate adverse effects critical for the conservation of this marine top predator in the region.

This study can therefore be used as a relevant indicator of the degree of vulnerability of common dolphins to human pressure providing comprehensive information on which to base conservation and management strategies. Furthermore, the identification of hotspots with the greatest potential for overlap between fisheries and common dolphins might suggest specific areas and conditions in which to concentrate management strategies to protect this vulnerable species.



Drawing by Núria Giralt

Chapter 4

Food-web interactions in a coastal ecosystem influenced by upwelling and terrestrial runoff off North-West Spain

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Contribution to the article:

OGP conceived and designed the study together with BDL and ER, analysed and interpreted the data with inputs from BDL and ER, designed the figures and tables, developed the modelling framework and wrote the manuscript with inputs from BDL, SM and ER. Additionally, OGP contributed to the last year (2017) of data collection.

4.1. *Abstract*

Ecopath with Ecosim has been used to create mass-balance models of different types of ecosystems around the world to explore and analyse their functioning and structure. This modelling framework has become a key tool in the ecosystem approach to fisheries management, by providing a more comprehensive and holistic understanding of the interactions between the different species. Additionally, Ecopath with Ecosim has provided a useful framework to study ecosystem maturity, changes in the ecosystem functioning over time and the impact of fisheries and aquaculture on the ecosystem, among other aspects. The present work explores the ecosystem functioning and structure in an anthropogenically impacted coastal area, influenced by seasonal coastal upwelling and high input of nutrients from rias (ancient drowned tectonic valleys) off North-West Spain. A mass-balance model with 23 functional groups was created using Ecopath to study the trophic interactions in the ecosystem during the post-upwelling period (August to October) in 2017. The model described an immature, wasp-waist ecosystem, that shared characteristics of ecosystems found in upwelling areas and ecosystems found in fjords or coastal embayments. Deeper analyses highlighted the importance of small planktivorous pelagic fish as a keystone functional group, and of zooplankton, blue whiting (*Micromesistius poutassou*) and phytoplankton as structuring groups in the ecosystem. Additionally, the study revealed that the existing fishing pressure on species of intermediate-high trophic levels could alter ecosystem functioning and structure, and ultimately affect top predators in the area. Findings of this study provide baseline information in ecosystem functioning and structure in the area and highlight the need to deeper study the effects of fisheries and their potential impacts on top predators.

Keywords: Ecopath, Mass-balance model, Upwelling, Wasp-waist, North-West Spain, Coastal Waters, Food-web

4.2. *Introduction*

Marine coastal ecosystems, particularly those close to densely populated areas, are heavily impacted by human activities (Halpern et al. 2008). Interestingly, some of the most productive marine ecosystems are located in coastal areas, typically linked to upwelling systems, estuaries or terrestrial runoff (Field et al. 1998; Jarre-Teichmann et al. 1998; Carr, 2001). These areas are of interest, not only due to their high biodiversity and production, but also because they provide important goods and services for coastal communities (Pauly and Christensen, 1995; Worm et al. 2006). Conservation and management strategies that consider the ecosystem as a whole, such as the ecosystem modelling approach, are needed to improve our knowledge of coastal marine ecosystem functioning, ensure their resilience, and make predictions about the effects of human activities (Coll et al. 2009a,b).

Ecopath with Ecosim (EwE) is a modelling software developed to create mass-balance models of exploited aquatic and marine ecosystems (Christensen and Walters, 2004; Heymans et al. 2016). Based on the work of Polovina (1984) and Ulanowicz (1986), EwE evolved to be a software capable of modelling complex ecosystems, considering not only the energy flows within the ecosystem, but also fisheries impact (Pauly et al. 2000). Since its development in the late 1980s, EwE has become a useful and crucial tool to create ecosystem mass-balance models that have been applied to a variety of scenarios in different ecosystems, ranging from oceanic to coastal regions, with emphasis on bays, fjords, estuaries and upwelling areas (Colléter et al. 2015). Although it has been mainly used as a tool for an ecosystem approach to fisheries management (Pauly et al. 2000), EwE has also been successfully applied to study ecosystem maturity (Christensen, 1995), compare similar ecosystems (Torres et al. 2013), analyse the temporal change of ecosystems (Shannon et al. 2003; Heymans et al. 2004; Ruzicka et al. 2012), evaluate the impact of environmental changes (Tam et al. 2008), and to assess the impact of fisheries or aquaculture on ecosystems (Sánchez and Olaso, 2004; Coll et al. 2006; Díaz López et al. 2008; Outeiro et al. 2018). The widespread use of EwE allows for comparisons between different marine ecosystems globally and provides reference information for future mass-balance models (Heymans et al. 2014; Colléter et al. 2015). However, there is also a need to develop fine-scale mass-balance models describing specific productive

coastal areas impacted by human activities at a regional scale. In this regard, studies providing baseline information on ecosystem functioning and structure are crucial to analyse changes in future scenarios and develop enhanced ecosystem management and conservation strategies.

The continental shelf off North-West Spain is a highly productive coastal area, heavily impacted by human activities, such as fisheries and aquaculture (López et al. 2003; Outeiro et al. 2018). Seasonal upwelling events coupled with terrestrial runoff bring nutrients to the photic layer in coastal waters, enhancing primary production (Alvarez et al. 2012). As a consequence, fisheries and aquaculture have become the main economic activities in the area, turning it into one of the most important regions for these activities in Europe (Rodríguez Rodríguez et al. 2011; Surís-Regueiro and Santiago, 2014). Despite the uniqueness of the area, and its influence in the local and regional economies, there is limited information regarding the ecosystem functioning and structure of the waters of the Galician continental shelf (Outeiro et al. 2018). The paucity of information on the ecosystem dynamics in this area poses great uncertainty around the likely responses (such as alteration in primary production and species distribution (Pérez et al. 2010; Casabella et al. 2014; Sousa et al. 2017)) of the studied ecosystem to changes in upwelling regimes triggered by climate change.

The present study aims to understand the functioning of the Rías Baixas shelf ecosystem, located in a coastal area influenced by coastal upwelling and high input of nutrients from rias (ancient drowned tectonic valleys) on the north-western coast of Spain, and to present a mass-balance model that could be used as baseline for future works. Special attention is given to marine top predators (i.e. cetaceans and seabirds) and to the fisheries impact on the ecosystem. The study offers a good opportunity to improve scientific knowledge by creating the first EwE model of the Rías Baixas shelf ecosystem located in a highly productive and impacted coastal area off North-West Spain, providing a new and powerful tool for ecosystem-based management strategies.

4.3. *Material and methods*

4.3.1. Study area and period

Galicia is an autonomous region in North-West Spain, located on the northern limit of the North-West Africa upwelling system (Gonzalez-Nuevo et al. 2014). The region is influenced by wind-driven seasonal coastal upwelling events, which carry deep, cold and nutrient-rich waters to the photic layer, enhancing primary production (Torres et al. 2003; Alvarez et al. 2012). Upwelling events are a consequence of sustained northerly winds (Torres et al. 2003) and typically occur during spring and summer, leading to peaks in chlorophyll a concentration in coastal waters of the continental shelf (Alvarez et al. 2012; Gonzalez-Nuevo et al. 2014). Additionally, terrestrial runoff enhances the production in the study area especially in winter, when rainfall is more important, and thus river discharge is higher (Pitcher et al. 2010; Alvarez et al. 2012).

The 1,498 km of Galician coastline is shaped by a series of drowned tectonic valleys, called rias, that influence the oceanic dynamics and enhance the coastal primary production (Prego et al. 1999; Alvarez et al. 2012). Previous studies emphasised the importance of this area for marine top predators (Pierce et al. 2010; Díaz López and Methion, 2018, 2019; Chapters 2 and 3) and fisheries (Surís-Regueiro and Santiago, 2014). The rias can be divided into Rías Altas, north of Cape Finisterre, and Rías Baixas, south of Cape Finisterre (Prego et al. 1999). The area considered in this study was located West of the entrance of Ría de Arousa, the biggest of the Rías Baixas (Prego et al. 1999) (Figure 4.1). The study area covered 933.13 km^2, extending from the coast of Cape Corrubedo, Sálvora Island and Ons Island in the east (8° 56.69′ W), to the 300 metres bathymetry line in the west (9° 29.07′ W). The southern limit was set at the southern end of Ons island, at the entrance of the Ría de Pontevedra (42° 21.31′ N), and the area extended north to the southern entrance of the Ría de Muros-Noia (42° 38.40′ N).

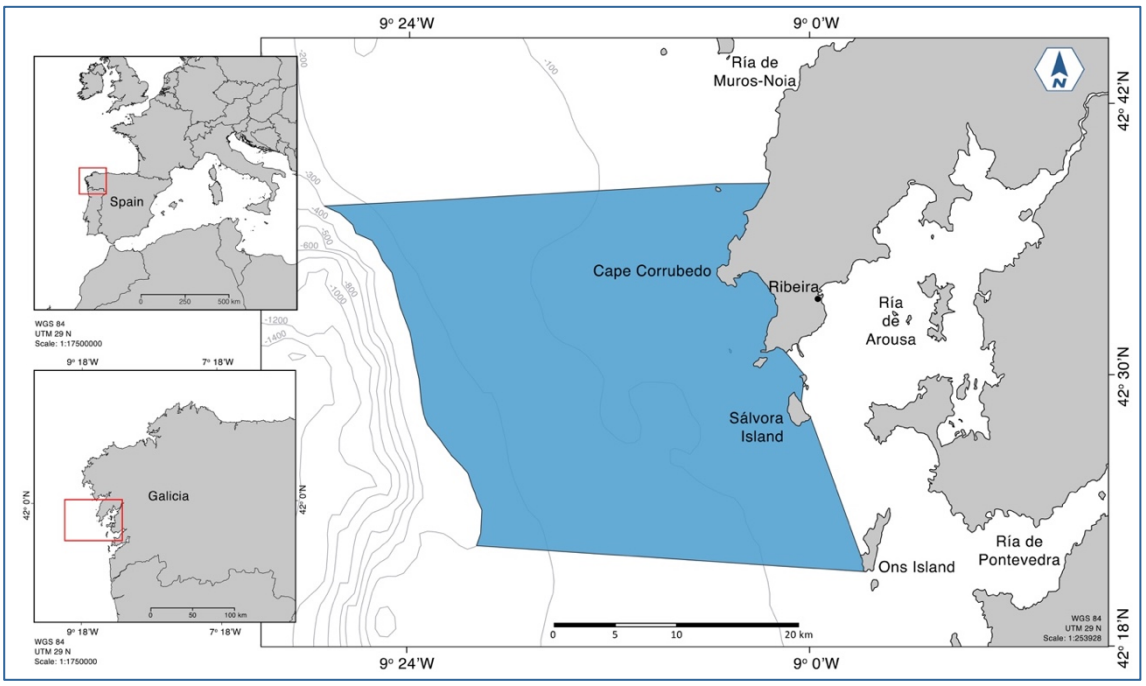


Figure 4.1 *Map showing the Rías Baixas shelf ecosystem selected to create the Ecopath model. This included waters above the continental shelf, to the West of the entrance of Ría de Arousa; Ría de Pontevedra and Ría de Muros-Noia (North-West Spain).*

The study represents a scenario that corresponds to the post-upwelling period in 2017 (late summer: August – October), and was developed to study the dynamics of a coastal ecosystem influenced by coastal upwelling events and coastal primary production in the area.

4.3.2.Modelling framework

Ecopath with Ecosim (EwE) version 6.5.14040.0 (www.ecopath.org) was used to develop a mass-balance model of the study area using the Ecopath functionality of the software. Ecopath creates a model of an ecosystem under the assumption of mass-balance over a specific period of time (Christensen and Walters, 2004). The software integrates routines that are used to estimate biomass, production/biomass ratios and consumption of the different functional groups, and makes them interact with routines that analyse the flows between functional groups based on the theory of Ulanowicz (1986). Ecopath works with two basic equations (Christensen and Pauly, 1992). The first equation explores the

energy transfer in each functional group under the assumption that the inputs will equal the outputs.

Equation 4.1

$$Q = P + R + U$$

or

$$Consumption = Production + Respiration + Unassimilated\ food$$

The second equation explains the production in each functional group (i):

Equation 4.2

$$\boldsymbol{P_i = Y_i + B_i \cdot M2_i + E_i + BA_i + P_i \cdot (1 - EE_i)}$$

where P_i is the production rate of (i); Y_i is the total fishery catch rate of (i); B_i is the biomass of (i); $M2_i$ is the total predation rate for (i); E_i is the net migration rate (emigration – immigration) of (i); BA_i is the biomass accumulation rate of (i); EE_i is the ecotrophic efficiency of (i) and the product $Pi \cdot (1 - EE_i)$ is the other mortality rate of (i) or $M0_i$. This equation can also be expressed as:

Equation 4.3

$$\boldsymbol{B_i \cdot (P/B)_i - EE_i \sum_{j=1}^{n} B_j \cdot (Q/B)_j \cdot DC_{ji} - Y_i - E_i - BA_i = 0} \quad (3)$$

where $(P/B)_i$ is the production/biomass ratio of (i); $(Q/B)_j$ is the consumption/biomass ratio of (j); DC_{ij} is the fraction of prey (i) in the average diet of a predator (j).

From equation 4.3, Ecopath establishes a modelling framework based on a set of linear functions, one per each functional group, to estimate one of the following parameters; biomass, production by biomass ratio, consumption by biomass ratio or ecotrophic efficiency (Christensen and Walters, 2004). The remaining three parameters must be entered for each group. Additional information regarding the catch rate, the net migration rate, the biomass accumulation, the consumption rate and the diet composition of each group is also needed by the modelling package (Christensen and Walters, 2004). Further information on Ecopath working procedures and data requirements can be found in the scientific literature and in the Ecopath manual

(Christensen and Pauly, 1992; Christensen and Walters, 2004; Christensen et al. 2005; Heymans et al. 2011).

4.3.3.Functional groups

To understand the trophic dynamics in this study area a total of 23 functional groups were included in the model. Special emphasis was given to top predator groups, especially cetaceans and seabirds as relative abundance data were obtained for these groups in the study area during the study period. Species with similar ecological roles were considered as functional groups. Additionally, the ecosystem was divided into two domains, the pelagic domain and the non-pelagic domain and each functional group was assigned to one of the domains (Table 4.1). In total, four groups of cetaceans, two of seabirds, ten of fish, three of invertebrates, a zooplankton group and a phytoplankton group were created. Detritus and discards were also included as separate functional groups.

Table 4.1 *The 23 functional groups included in the model and their distribution in the pelagic and non-pelagic domains.*

Pelagic domain	Non-pelagic domain
Common dolphin (*Delphinus delphis*)	Blue whiting (*Micromesistius poutassou*)
Harbour porpoise (*Phocoena phocoena*)	Atlantic horse mackerel (*Trachurus trachurus*)
Bottlenose dolphin (*Tursiops truncatus*)	Benthopelagic fish
Baleen whales	Bathydemersal piscivorous fish
Seabirds I, pursuit and plunge divers	Demersal piscivorous fish
Seabirds II, surface and aerial feeders	Non-planktonic crustaceans
Sardine (*Sardina pilchardus*)	Macrobenthos
Large piscivorous pelagic fish	Detritus
Other piscivorous pelagic fish	Discards
Large planktivorous pelagic fish	
Small planktivorous pelagic fish	
Cephalopods	
Zooplankton	
Phytoplankton	

Cetaceans

Systematic data collection on cetaceans since 2014 led to the identification of up to nine species of cetaceans in Galician waters (Díaz López and Methion, 2017, 2018, 2019). Only species regularly found in the area were included in the model, including common

dolphin (*Delphinus delphis*), harbour porpoise (*Phocoena phocoena*), bottlenose dolphin (*Tursiops truncatus*), and four species of baleen whales.

Common dolphin: Common dolphins are the most commonly seen cetacean in the north-western coast of Spain and are widely distributed in the study area (Saavedra et al. 2018), which includes optimal habitat for the species (Chapter 2). Data on relative abundance were calculated from direct observations at sea along 14 surveys carried out between August and October 2017. A total of 46 common dolphin groups with an average size of 49 ±10 individuals were recorded and the relative abundance in the modelled area was estimated at 0.21 individuals/km2. Information on the diet, mean body weight, daily food intake and mortality rates was obtained from previous studies conducted in the North-East Atlantic (Table A1.1).

Harbour porpoise: The smallest of the cetaceans species in the region, harbour porpoise, is commonly seen in the study area, mainly associated with coastal and continental shelf waters, where its relative abundance was estimated at 0.021 individuals/km2 (Díaz López and Methion, 2018). Information on the diet of harbour porpoise, mean body weight and daily food intake was obtained from scientific literature (Table A1.2).

Bottlenose dolphin: Bottlenose dolphins are the most commonly seen cetacean in inshore Galician waters, although they are also sighted in deeper waters above the continental shelf (López et al. 2004; Methion and Díaz López, 2018). Data on relative abundance were calculated from direct observations (number of sightings) at sea between August and October 2017. The average group size was estimated at 43 ±10 individuals, and the relative abundance was 0.042 individuals/km2. Information on the diet, average body weight, daily food intake and mortality rates was obtained from previous studies (Table A1.3).

Baleen whales: Four species of baleen whales have been recorded off the Galician coast, where feeding events occur, especially after the upwelling periods (Díaz López and Methion, 2019). This functional group included the four species of baleen whales most commonly seen in the area, namely fin whales (*Balaenoptera physalus*), blue whales

(*B. musculus*), minke whales (*B. acutorostrata*) and humpback whales (*Megaptera novaeangliae*, Borowski 1781). Data on relative abundance were calculated from previous studies carried out in the area with data collected between August and October 2017 (Díaz López and Methion, 2019). Information to calculate the total biomass and the P/B and Q/B ratios was obtained from previous studies on diet, average weight, daily food intake and mortality rates (Table A1.4).

Seabirds

Systematic data collection on seabirds since 2014 led to the identification of up to 26 different species of seabirds in Galician waters (BDRI, 2018a). These include several species of gulls, shearwaters, terns and skuas among others. Only the species commonly seen in the study area were included in the analysis and they were divided into two different groups depending on their feeding ecology and behaviours described by Camphuysen and Webb (1999). For each functional group, the most abundant species, based on the number of individuals, was selected as the representative of the group. The average weight for each seabird group was calculated taking into consideration the mean weight and the relative abundance of all the species included in the group. Information on the P/B and Q/B ratios was obtained from previous studies (Table A1.5 and A1.6).

Seabirds I, pursuit and plunge divers: This functional group included species that used deep plunging, deep diving or pursuit diving as feeding techniques, mainly shags (*Phalacrocorax aristotelis*, Linnaeus 1761), great cormorants (*P. carbo*, Linnaeus 1758), northern gannets (*Morus bassanus*, Linnaeus 1758) and shearwaters (*Calonectris diomedea*, Scopoli 1769, *Puffinus mauretanicus*, Lowe 1921, *P. gravis*, O'Reilly 1818, *P. griseus*, Gmelin 1789, *P. puffinus* Brünnich 1764). Direct observations at sea were used to calculate the relative abundance of each species. Northern gannets were the most commonly seen species and consequently were selected as the representative of the group.

Seabirds II, surface and aerial pursuit feeders: This functional group included species that used surface feeding, shallow plunging and aerial pursuit as feeding techniques, mainly gulls (*Larus fuscus*, Linnaeus 1758, *L. marinus*, Linnaeus 1758, *L. melanocephalus*,

Temminck 1820, *L. michahellis* Naumann 1840, *Xema sabini*, Sabine 1819), terns (*Sterna sandvicensis*, Latham 1787) and skuas (*Stercorarius parasiticus* Linnaeus 1758, *S. pomarinus*, Temmick 1815, *S. skua*, Brünnich 1764). Direct observations at sea were used to calculate the relative abundance of each species. Yellow legged gulls (*Larus michahellis*) were the most commonly seen species and consequently they were selected as the representative of the group.

Fish

To have a better understanding of the different fish species in the area, landings data from Ribeira harbour in 2017 provided by the Galician government (Xunta de Galicia, Consellería do mar, 2020a) were examined. This data included only commercially exploited fish species, as these were the best locally available data. Ribeira harbour is located at the entrance of the Ría de Arousa, on its northern coast (Figure 4.1), and is considered the third most important European harbour for small-scale fisheries, in terms of landings (Cruz Pazos and Pizarro Alcalde, 2013). A total of 81 fish species caught within the area were landed, comprising species of Osteichthyes and Chondrichthyes. This information was used to create the different fish functional groups that were included in the model. Three species were considered as three separate functional groups, namely blue whiting (*Micromesistius poutassou*), sardine (*Sardina pilchardus*) and Atlantic horse mackerel (*Trachurus trachurus*), given their importance in terms of fishing (Xunta de Galicia, Consellería do mar, 2020a). The other species were allocated to seven functional groups depending on their habitat and trophic ecology (Table 4.2).

Table 4.2 *Description of the fish functional groups included in the Rías Baixas shelf ecosystem model.*

Functional group	Definition
Large piscivorous pelagic fish	Fish whose diet mainly consists of other fish species, feed in the top 200 metres of the water column and are more than 100 cm long.
Other piscivorous pelagic fish	Fish whose diet mainly consists of other fish species, feed in the top 200 metres of the water column and are less than 100 cm long.
Large planktivorous pelagic fish	Fish whose diet mainly consists of zoo- and/or phytoplankton and feed in the top 200 metres of the water column and are more than 25 cm long.
Small planktivorous pelagic fish	Fish whose diet mainly consists of zoo- and/or phytoplankton and feed in the top 200 metres of the water column and are less than 25 cm long.
Benthopelagic fish	Fish whose diet consists mainly of fish and feed in the benthopelagic zone.
Bathydemersal piscivorous fish	Fish whose diet consists mainly of fish and feed in the bathydemersal zone.
Demersal piscivorous fish	Fish whose diet consists mainly of fish and feed in the demersal zone.

Biomass values for each functional group were calculated by combining information on biomass and landings from ICCAT, ICES and information on landings in Ribeira harbour (Appendix 1, Table A1.24). P/B ratios were obtained from previous models in nearby areas, and Q/B ratios were obtained from either models created in nearby areas or from previous studies (Appendix 1, Tables A1.7 to A1.16).

Blue whiting: This species was allocated as a separate group due to its economic and ecological importance in the area (Villasante, 2012). The species is widely distributed in the North-East Atlantic, from the Barents Sea to the Strait of Gibraltar, and it plays an important ecological role as a predator of zooplankton and small fish, and as prey items for larger fish species and marine mammals (Villasante, 2012; ICES, 2018a). Furthermore, this species is of great economic importance in the area, as it represents approximately 39% of the total landed fish biomass in Ribeira harbour (Xunta de Galicia, Consellería do mar, 2020a) (Appendix 1, Table A1.7).

Sardine: Despite the decreasing trend since the 1980s (Cabrero et al. 2019) sardine has historically been important for Galician fisheries (Vázquez-Rowe et al. 2014). Sardine is distributed along the North-East Atlantic Ocean, from the North Sea to Senegal and the

Mediterranean Sea (Cabrero et al. 2019). This species plays an important ecological role in the area by feeding on lower trophic levels, mainly phytoplankton and zooplankton (Garrido et al. 2008), and is an important part of the diet of marine top predators (Santos et al. 2014). In 2017, sardine represented around 1.5% of the total fish biomass landed in Ribeira harbour (Xunta de Galicia, Consellería do mar, 2020a) (Appendix 1, Table A1.8).

Atlantic horse mackerel: The species is widely distributed along the North-East Atlantic, from the North Sea to the Strait of Gibraltar (Murta et al. 2008). Atlantic horse mackerel is an important species for local fisheries, comprising 25% of the total landed fish biomass in Ribeira harbour in 2017, becoming the second most landed species in that harbour (Xunta de Galicia, Consellería do mar, 2020a) (Appendix 1, Table A1.9).

Large piscivorous pelagic fish: This functional group was created to represent the different species of pelagic fish longer than 100 cm that feed predominantly on other fish. Several species of sharks, tuna and other pelagic fish have been recorded in the study area since 2014 (BDRI, 2018b). For instance, blue sharks (*Prionace glauca*, Cantor 1849) have been recorded year round in both inshore waters and waters above the continental shelf, and Atlantic bluefin tuna (*Thunnus thynnus*, Linnaeus 1758) have been recorded feeding on garfish (*Belone belone*, Linnaeus 1761*)* during the period of the year considered in this study (Appendix 1, Table A1.10).

Other piscivorous pelagic fish: This functional group was mostly composed of piscivorous species of the family Scombridae, that were smaller than 100 cm, such as the Atlantic bonito (*Sarda sarda*, Bloch 1793) or the skipjack tuna (*Katsuwonus pelamis*, Linnaeus 1758). Additionally, other species such as John Dory (*Zeus faber*, Linnaeus 1758) or garfish were also included (Appendix 1, Table A1.11).

Large planktivorous pelagic fish: Fish that mostly feed on plankton and measure more than 25 cm formed this functional group. Among others fish species, the group included several planktivorous species of the family Scombridae such as the Atlantic mackerel (*Scomber scombrus*, Linnaeus 1758) and the Atlantic chub mackerel (*Scomber colias*, Gmelin 1789), which together represent around 25% of the landed fish biomass in Ribeira harbour (Xunta de Galicia, Consellería do mar, 2020a) (Appendix 1, Table A1.12).

Small planktivorous pelagic fish: Small species of pelagic planktivorous fish (less than 25 cm), such as sandeels (*Ammodytes* spp.) and European anchovy (*Engraulis encrasicolus*) are an important intermediate trophic level in upwelling ecosystems, that transfer energy from lower trophic levels (plankton) to top predators (Cury et al. 2000) (Appendix 1, Table A1.13).

Benthopelagic fish: This functional group was composed mainly of fish species of the families Sparidae and Gadidae, and included species such as poor cod (*Trisopterus minutus*, Linnaeus 1758) and bogue (*Boops boops*, Linnaeus 1758), both relatively important commercial species in the area (Xunta de Galicia, Consellería do mar, 2020a; Alonso-Fernández et al. 2008) (Appendix 1, Table A1.14).

Bathydemersal piscivorous fish: Piscivorous fish species inhabiting bathydemersal habitats, such as angler fish (*Lophius piscatorius*, Linnaeus 1758), blackbellied angler (*Lophius budegassa*, Spinola, 1807) or the alfonsino (*Beryx decadactylus*, Cuvier 1829) were included in this functional group (Appendix 1, Table A1.15).

Demersal piscivorous fish: This was the most species rich functional group and included several species of importance in terms of fisheries, such as the European hake (*Merluccius merluccius*), the European conger (*Conger conger*, Linnaeus 1758), the white seabream (*Diplodus sargus*, Linnaeus 1758) and the European seabass (*Dicentrarchus labrax*, Linnaeus 1758), among others (Appendix 1, Table A1.16).

Invertebrates

Cephalopods: These invertebrates play a crucial role in ecosystems, in which they act as links between different trophic levels and between different habitats (de la Chesnais et al. 2019). Squids and benthic cephalopods were included in the same group, as only very limited information about cephalopod distribution and abundance was available. The total cephalopod landings in Ribeira harbour during 2017 (Xunta de Galicia, Consellería do mar, 2020a) were used to select the species that were included in the model. The group was mainly composed of neritic cephalopods such as lesser flying squid (*Todaropsis eblanae*, Ball 1841) or European squid (*Loligo vulgaris*, Lamarck 1758) (Appendix 1, Table A1.17).

Non-planktonic crustaceans: Information about non-commercial crustaceans in the area is scarce. Therefore, data on total crustaceans' landings in Ribeira harbour in 2017 were combined with data on demersal trawl surveys (Fariña et al. 1997) to determine the species composition that would be included in the functional group and to estimate their total biomass (Appendix 1, Table A1.18).

Macrobenthos: Benthic communities in Galician waters are formed by a wide variety of species (Serrano et al. 2006). However, this functional group was conceived to represent the detritivorous communities and included mainly echinoderms such as the spiny starfish (*Marthasterias glacialis*, Linnaeus 1758) and sea urchins (*Spatangus purpureus*, Müller 1776) among others (Appendix 1, Table A1.19).

Zooplankton

The zooplankton biomass shows interannual and seasonal variation in the study area (Buttay et al. 2016). This variation is caused by a combination of several processes, such as seasonal upwelling events, oceanic currents and coastal runoff (Buttay et al. 2016). The highest abundance of zooplankton in the area typically occurs at the end of summer, coinciding with the upwelling season (Buttay et al. 2016). Copepods are the most abundant and persistent group in the zooplankton in the area, representing around 72% of the zooplankton community (Buttay et al. 2016). In the present study, P/B and Q/B ratios and the ecotrophic efficiencies were obtained from a similar, nearby area (Sánchez and Olaso, 2004) (Appendix 1, Table A1.20).

Phytoplankton

Primary production peaks in the area have been linked to increased nutrients from both river runoff and seasonal upwelling events (Alvarez et al. 2012). The latter are especially important in late summer, a period in which they enhance primary production, causing the highest phytoplankton peaks of the year (Alvarez et al. 2012). Information on phytoplankton biomass and the P/B ratio was obtained from a similar, nearby area (Torres et al. 2013) (Appendix 1, Table A1.21).

Detritus

Information on detritus was obtained from a nearby area on the western coast of Spain (Torres et al. 2013).

Landings and discards

Detailed information on fish, cephalopods and crustacean landings in Galician harbours was provided by the Galician government (Xunta de Galicia, Consellería do mar, 2020a). An analysis of the marine species landed in the different harbours located in the area was conducted prior to creating the model and concluded that Ribeira harbour accounted for 94% of the total landings in the area. Therefore, only the landings reported for Ribeira harbour were included in the model. In total, 34,337 t of fish, 216 t of cephalopods and 98 t of crustaceans were landed in Ribeira harbour in 2017. These data were used to calculate the total biomass caught per km^2 in the area (Appendix 1, Table A1.24). To understand the combined effect of the different fishing techniques used in the area on the Rías Baixas shelf ecosystem, all fisheries were included as one group in the model. Additionally, recent studies estimated that 16.9% of the total fish caught by the Galician fishing fleet was discarded (Vázquez-Rowe et al. 2011). Hence, this value was applied to the study area to calculate the total amount of discards for each of the fish functional groups (Appendix 1, Tables A1.22, A1.24).

4.3.4.Diet

EwE requires quantitative diet information to calculate the consumption of the functional groups (Christensen et al. 2005). Several methodologies have been used to study the diet of marine species (Barrett et al. 2007; Ahlbeck et al. 2012; Bowen and Iverson, 2013). The diet of most of the marine mammals, fish and cephalopods groups included in the model (70% of the functional groups) was obtained from quantitative studies derived from stomach content analysis. The diet of both seabirds groups (10% of the functional groups) was obtained from studies that reconstructed diet using pellets. Scientific literature was used to obtain the diet of the remaining groups (20% of the functional groups). For groups containing more than one species, the diet of the most representative species was selected (See supplementary material). Diet variability among regions can be important for some marine species, thus quantitative diet studies

carried out in Galicia were prioritised (Appendix 1, Table A1.25). Indeed, the diet of 25% of the functional groups was obtained from studies carried out in Galician waters, and another 25% from studies conducted in Portugal. The diet of the remaining functional groups was obtained from studies that took place in the North-East Atlantic (20%), in the Mediterranean Sea (20%), in the North Atlantic (5%) and in other areas (5%).

4.3.5.Model quality, balancing and analysis

The pedigree index was used to categorise the uncertainty of the inputs. This routine takes into account the origin of the data entered in the model to determine how well this is rooted in local data (Christensen and Walters, 2004). The index varies from 0, when data do not have a local origin, to 1, when inputs are fully rooted in local data (Christensen and Walters, 2004).

Using estimates of biomass, production/biomass ratios, consumption/biomass ratios and diet compositions as input parameters can result in unbalanced models in which ecotrophic efficiency values for some functional groups exceed unity (Kavanagh et al. 2004). The balancing process requires the modification of such input parameters in order to obtain a balanced model, in which the ecotrophic efficiencies of all groups do not exceed unity (Christensen and Walters, 2004). The PREBAL assessment technique (Link, 2010) checks several aspects on the biomass across groups, biomass ratios and vital rates, among others. This technique was used to analyse all the input parameters for each functional group, and to establish priorities during the balancing process.

Several of the ecological indicators described by Odum (1969), such as total net primary production, total primary production/total respiration, total primary production/biomass, biomass/total system throughput and net system production were used to evaluate the system's maturity (Christensen, 1995). The complexity and connectivity were evaluated using the system omnivory index, which is a measure of the variance of the prey's trophic level (Christensen and Pauly, 1993b), and is calculated as a weighted average of the omnivory index of each functional group (Libralato, 2013). Another measure of system maturity and stability is the Finn's cycling index, which quantifies the proportion of cycling in a system compared to the total system throughput (Finn, 1976). This index ranges between 0, when there is no cycling in the system, and

infinite, when there is no straight through flow. The Finn's cycling index has been linked to the recovery time after perturbations and thus, to the stability of ecosystems (Vasconcellos et al. 1997). Finally, ascendancy and overhead were used to evaluate the organisation and the "strength in reserve" of the food web respectively (Ulanowicz, 1986).

Network analysis was used to examine the relationship between the different functional groups and the importance of the different domains of the ecosystem using different parameters. One of these parameters was the trophic aggregation, a routine that aggregates the different functional groups in discrete trophic levels (Ulanowicz, 1995). This was displayed in the form of the Lindeman spine (Lindeman, 1942), a diagram that shows the flows and the transfer efficiency between discrete trophic levels. The transfer efficiency can be described as the proportion of the input trophic flows that are transferred to the next trophic level or that are exported (Lindeman, 1942; Christensen and Walters, 2004). Additionally, the flows between functional groups together with their consumption on other trophic levels were used to establish the main flows in the ecosystem and to assess the importance of each domain in the modelled food web.

Keystone species and keystone functional groups have a disproportionately strong effect on the ecosystem despite their low biomass (Power et al. 1996) and have become crucial elements in the development of conservation strategies that intend to preserve ecosystems and their functioning (Valls et al. 2015). Therefore, identifying these crucial keystone species or keystone functional groups within the ecosystems is critical. In this regard, the keystoneness index (Libralato et al. 2006) was used to determine if there were any species or functional group that could be considered as a keystone species or keystone functional group.

4.4. *Results and discussion*

The model resulting from the balancing process had a pedigree index of 0.532, which is above the mean pedigree index value calculated from previously constructed models for which such information was available, and falls within the higher end of the variation range (Morissette, 2007; Colléter et al. 2015).

4.4.1. Balancing the model

The first model obtained was unbalanced, as nine groups had an ecotrophic efficiency greater than 1, meaning that their biomass was insufficient to sustain the trophic demand of their predators. These groups included several high commercial valuable species such as blue whiting and sardine, but also other groups of fishes and invertebrates. Following Link (2010), a PREBAL assessment was conducted prior to balancing the model. The method detected several groups, the biomass of which was notably greater or notably smaller than the one expected for a group of a given trophic level in a balanced ecosystem. All the groups with a biomass higher than expected included highly commercially valuable species such as blue whiting, sardine, Atlantic horse mackerel and Atlantic mackerel. These high biomass values could be explained by the method used to estimate the biomass of the fish groups, which relied on the landings data from Ribeira harbour. Because these species are preferentially targeted in the area, this approach could have led to an overestimation of their biomass. In order to obtain a better estimate for the biomass, the ecotrophic efficiencies estimated for the same groups in other Ecopath models created in similar and nearby areas were used to modify the input parameters of these groups.

Once the biomass of all groups had been corrected, the subsequent balancing steps focussed on adjusting the diet of the different functional groups and especially the top predators. For instance, direct feeding observations recorded by researchers in the area since 2014 (Díaz López and Methion, 2017, 2019; Methion and Díaz López, 2019b) were used as complementary information to adjust the diet of cetacean species. Additionally, scientific literature was used to gather additional information to adjust the diet of several cetaceans, seabirds and fish groups. The final diet included in the model is shown in Table 4.3.

The input parameters obtained after the balancing process are shown in Table 4.4, together with basic parameters calculated by Ecopath. The respiration/assimilation, production/respiration and respiration/biomass ratios as well as the net efficiencies were within the expected values (Christensen et al. 2005).

Table 4.3 *Diet composition (% of prey biomass) of the different functional groups (FG). Columns show the predators and rows show the prey. Functional groups: 1. Common dolphins; 2. Harbour porpoise; 3. Bottlenose dolphins; 4. Baleen whales; 5. Seabirds I; 6. Seabirds II; 7. Blue whiting; 8. Sardine; 9. Atlantic horse mackerel; 10. Large piscivorous pelagic fish; 11. Other piscivorous pelagic fish; 12. Large planktivorous pelagic fish; 13. Small planktivorous pelagic fish; 14. Benthopelagic fish; 15. Bathydemersal piscivorous fish; 16. Demersal piscivorous fish; 17. Cephalopods; 18. Non-planktonic crustaceans; 19. Macrobenthos; 20. Zooplankton; 21. Phytoplankton; 22. Discards; 23. Detritus.*

FG	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1																				
2																				
3																				
4																				
5																				
6																				
7	0.309		0.337			0.055	0.01								0.46	0.656				
8	0.114	0.029				0.029					0.239					0.151				
9	0.071	0.355	0.025			0.023					0.002				0.44	0.043				
10			0.05							0.027										
11	0.051		0.143		0.004	0.006				0.025	0.031									
12	0.112		0.152		0.016	0.007				0.261										
13	0.11	0.254	0.012	0.15	0.772		0.04			0.093	0.727	0.158				0.064	0.805			
14	0.04	0.208	0.102		0.008	0.016				0.063					0.05	0.054				
15	0.059	0.063	0.004				0.01			0.103						0.011				
16	0.059	0.001	0.1							0.012							0.03			
17	0.075	0.09	0.075				0.01			0.214		0.026			0.04	0.011	0.014			
18						0.462				0.155	0.001				0.01	0.005				
19						0.185				0.004							0.016	0.028	0.05	
20				0.85			0.93	0.7	1	0.043		0.816	1	0.527		0.005	0.135	0.886	0.05	0.268
21								0.3						0.273						0.583
22					0.2	0.217													0.003	
23														0.2				0.086	0.897	0.149
Total	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Table 4.4 *Modified input and output parameters of the Rías Baixas shelf ecosystem model. Values in bold show the modified input parameters, whereas the rest of the values were calculated by Ecopath. Header abbreviations are defined as: D: Domain (PL: Pelagic; NPL: Non-Pelagic); TL: Trophic Level; B: Biomass (t km-2); P/B: Production/Biomass ratio (year-1); Q/B: Consumption/Biomass ratio (year-1); EE: Ecotrophic Efficiency; P/Q: Production/Consumption ratio (year-1); F: Instantaneous fishing mortality rate (year-1); M2: Instantaneous predation rate (year-1); M0: Instantaneous "other mortality" rate (year-1).*

Functional Group	D	TL	B	P/B	Q/B	EE	P/Q	F	M2	M0
Common dolphin	PL	4.58	**0.019**	**0.09**	**23**	0	0	0	0	0.09
Harbour porpoise	PL	4.37	**0.001**	**0.11**	**28.08**	0	0	0	0	0.11
Bottlenose dolphin	PL	4.73	**0.008**	**0.05**	**19.08**	0	0	0	0	0.05
Baleen whales	PL	3.52	**0.061**	**0.06**	**6.46**	0	0.01	0	0	0.06
Seabirds I:	PL	3.89	**0.001**	**0.32**	**82.79**	0	0	0	0	0.32
Seabirds II:	PL	3.56	**0.001**	**0.25**	**182.12**	0	0	0	0	0.25
Blue whiting	NPL	3.46	34.346	**1.06**	**6.52**	**0.99**	0.16	0.5	0.55	0.01
Sardine	PL	2.96	14.089	**0.58**	**8.8**	**0.61**	0.07	0.09	0.27	0.23
Atlantic horse mackerel	NPL	3.37	33.3	**0.64**	**6.47**	**0.8**	0.1	0.33	0.18	0.13
Large piscivorous pelagic fish	PL	4.68	**0.085**	**0.82**	**7.8**	0.45	0.11	0.07	0.3	0.45
Other piscivorous pelagic fish	PL	4.3	**0.745**	**0.82**	**6.5**	0.43	0.13	0.06	0.29	0.47
Large planktivorous pelagic fish	PL	3.57	11.903	**1.14**	**6.28**	**0.85**	0.18	0.95	0.02	0.17
Small planktivorous pelagic fish	PL	3.37	22.364	**1.98**	**9.13**	**0.83**	0.22	0.01	1.63	0.34
Benthopelagic fish	NPL	2.72	5.931	**0.68**	**3.62**	**0.71**	0.19	0.21	0.27	0.2
Bathydemersal piscivorous fish	NPL	4.41	2.936	**1.09**	**4.04**	**0.82**	0.27	0.03	0.86	0.2
Demersal piscivorous fish	NPL	4.34	**4.458**	**0.67**	**3.81**	1	0.18	0.57	0.1	0
Cephalopods	PL	4.25	1.794	**3.2**	**7.5**	**0.95**	0.43	0.13	2.91	0.16
Non-Planktonic Crustaceans	NPL	3.24	**10.221**	**2.35**	**6.33**	0.02	0.37	0.01	0.04	2.3
Macrobenthos	NPL	2.12	**7.845**	**2.5**	**6.5**	0.24	0.38	0	0.59	1.91
Zooplankton	PL	2.37	86.435	**39.08**	**80**	**0.8**	0.49	0	31.26	7.82
Phytoplankton	PL	1	31.061	**158.04**	0	**0.83**	0	0	131.17	26.87
Discards		1	**7.608**	0	0	0	0	0	0	0
Detritus		1	**70**	0	0	0.34	0	0	0	0

Table 4.4 continued *Header abbreviations are defined as: F/Z: Instantaneous fishing mortality/Total mortality ratio (year-1); R: Respiration (t km-2 year-1); A: Assimilation (t km-2 year-1); R/A: Respiration/Assimilation ratio; P/R: Production/Respiration ratio; R/B: Respiration/Biomass ratio; FTD: Flow to detritus (t km-2 year-11); NE: Net Efficiency; OI: Omnivory Index; Q: Consumption (t km-2 year-1).*

Functional Group	F/Z	R	A	R/A	P/R	R/B	FTD	NE	OI	Q
Common dolphin	0	0.36	0.36	1	0	18.31	0.09	0	0.22	0.45
Harbour porpoise	0	0.02	0.02	0.99	0.01	22.35	0.01	0.01	0.23	0.03
Bottlenose dolphin	0	0.12	0.12	1	0	15.21	0.03	0	0.29	0.14
Baleen whales	0	0.31	0.31	0.99	0.01	5.11	0.08	0.01	0.13	0.39
Seabirds I:	0	0.07	0.07	1	0	65.92	0.01	0	0.91	0.09
Seabirds II:	0	0.19	0.19	1	0	145.45	0.01	0	0.87	0.24
Blue whiting	0.47	142.74	179.15	0.8	0.26	4.16	45.15	0.2	0.12	223.94
Sardine	0.15	91.02	99.19	0.92	0.09	6.46	27.98	0.08	0.39	123.98
Atlantic horse mackerel	0.52	151.05	172.37	0.88	0.14	4.54	47.35	0.12	0	215.46
Large piscivorous pelagic fish	0.09	0.46	0.53	0.87	0.15	5.42	0.17	0.13	0.35	0.66
Other piscivorous pelagic fish	0.08	3.26	3.87	0.84	0.19	4.38	1.32	0.16	0.06	4.84
Large planktivorous pelagic fish	0.83	46.23	59.8	0.77	0.29	3.88	16.99	0.23	0.21	74.75
Small planktivorous pelagic fish	0.01	119.07	163.35	0.73	0.37	5.32	48.36	0.27	0	204.18
Benthopelagic fish	0.31	13.14	17.18	0.77	0.31	2.22	5.46	0.23	0.47	21.47
Bathydemersal piscivorous fish	0.03	6.29	9.49	0.66	0.51	2.14	2.95	0.34	0.05	11.86
Demersal piscivorous fish	0.84	10.6	13.59	0.78	0.28	2.38	3.41	0.22	0.08	16.98
Cephalopods	0.04	5.02	10.76	0.47	1.14	2.8	2.98	0.53	0.19	13.46
Non-Planktonic Crustaceans	0	27.74	51.76	0.54	0.87	2.71	36.43	0.46	0.15	64.7
Macrobenthos	0	21.18	40.79	0.52	0.93	2.7	25.19	0.48	0.14	50.99
Zooplankton	0	2,153.97	5,531.86	0.39	1.57	24.92	2,058.54	0.61	0.37	6,914.82
Phytoplankton	0	0	0	0	0	0	834.52	0	0	0
Discards	0	0	0	0	0	0	0	0	0	0
Detritus	0	0	0	0	0	0	0	0	0.49	3,157.04

4.4.2. Description of the balanced model and system maturity

The model obtained after the balancing process presents several characteristics of trophic models from upwelling areas (Table 4.5). These systems can be usually described as immature and are characterised by high nutrient inputs and a dependence on high system throughput (Christensen, 1995). The system modelled here had a total biomass excluding detritus of 268 t km^{-2}, 63% of which was contained in the pelagic domain and the remaining 37% in the non-pelagic domain. The total system throughput, a measure of the size of the ecosystem in terms of flows between functional groups, was 16,025.89 t km^{-2} per year. Both total biomass and total system throughput values fell within the lower range of the values estimated for other upwelling systems around the

world (Shannon et al. 2003; Heymans et al. 2004; Tam et al. 2008). Additionally, several other ecological indicators (Table 4.5) were used to assess the maturity of the ecosystem modelled here (following Odum, 1969; Christensen 1995). These included total net primary production, total primary production/total respiration, total primary production/biomass, biomass/total system throughput, net system production. The values found for each of the parameters confirmed that the Rías Baixas shelf ecosystem described here is in a low-intermediate developmental stage sensu Odum (1969) and that the ecosystem is immature.

Table 4.5 *Summary statistics of the model.*

Parameter	Value	Units
Statistics and flows		
Sum of all consumption	7,943.450	t km^{-2} $year^{-1}$
Sum of all exports	2,124.402	t km^{-2} $year^{-1}$
Sum of all respiratory flows	2,792.846	t km^{-2} $year^{-1}$
Sum of all flows into detritus	3,165.196	t km^{-2} $year^{-1}$
Total system throughput	16,025.890	t km^{-2} $year^{-1}$
Sum of all production	8,470.828	t km^{-2} $year^{-1}$
Mean trophic level of the catch	3.485	
Gross efficiency (catch/net p.p)	0.009	
Shannon diversity index	2.125	
System energetics		
Calculated total net primary production	4,908.915	t km^{-2} $year^{-1}$
Total primary production/total respiration	1.758	
Net system production	2,116.069	t km^{-2} $year^{-1}$
Total primary production/total biomass	18.344	
Total biomass/total throughput	0.017	Year
Total biomass (excluding detritus)	267.607	t km^{-2}
Total catch	45.113	t km^{-2} $year^{-1}$
Network flow indices		
Connectance index	0.234	
System Omnivory Index	0.205	
Throughput cycled (excluding detritus)	1860	t km^{-2} $year^{-1}$
Predatory Cycling Index (PCI)	19.18	% of throughput without
Throughput cycled (including detritus)	3107	detritus
Finn's cycling index	19.4	t km^{-2} $year^{-1}$
Finn's mean path length	3.257	% of total throughput
System thermodynamics sensu Ulanowicz (1986)		
Ascendency (Total)	12,318	Flowbits
Ascendency	22.36	%
Overhead (Total)	42,763	Flowbits
Overhead	77.64	%
Capacity (Total)	55,081	Flowbits
Quality of the model		
Ecopath pedigree index	0.532	
Measure of fit, t*	2.738	

This aspect was also confirmed by the system omnivory index, which was low-intermediate (Table 4.5) indicating that the system had moderate complexity and maturity (Libralato, 2013). These results are in line with what has been found in other upwelling regions (Tam et al. 2008), and are lower than the values of models created in nearby areas (Cantabrian Sea, Sánchez and Olaso, 2004; and Ría de Arousa, Outeiro et al. 2018). Additionally, system omnivory indices have been found to be sensitive to fishing activities, being lower in areas subjected to intensive fishing pressure (Libralato et al. 2010). Hence, the low values obtained in this study could indicate that the moderate complexity and maturity of the ecosystem was a consequence of intense fishing pressure in the area (Surís-Regueiro and Santiago, 2014).

The omnivory indices for each functional group show the variance of the prey's trophic level of a given consumer (Libralato, 2013). The index varies between 0, when consumers feed on just one trophic level and 1, when they feed on a variety of trophic levels. The results showed that the omnivory index for each functional group varied between 0 for Atlantic horse mackerel and small planktivorous pelagic fish and 0.905 for seabirds I (Table 4.4). In general, functional groups of the pelagic domain tended to have a higher omnivory index (mean = 0.30 ±0.07) than those in the non-pelagic domain (mean = 0.14 ±0.06). Similarly, pelagic top predators (dolphins, porpoises, seabirds and large pelagic pisicivorous fish) had higher omnivory indices (mean = 0.44 ±0.12) than non-pelagic top predators (bathydemersal piscivorous fish and demersal piscivorous fish, mean = 0.07 ±0.02).

The Finn's cycling index value for the present study was 19.4%, and indicated that the ecosystem had a shorter recovery time and a higher stability than other upwelling areas (Heymans et al. 2004; Tam et al. 2008), but a longer recovery time and lower stability than nearby, highly productive, inshore areas (Ría de Arousa, Outeiro et al. 2018). These results are in line with earlier studies that showed that coastal lagoons and fjords have higher stability than upwelling systems (Vasconcellos et al. 1997), and that Finn's cycling index tends to decrease with increasing ecosystem size (Heymans et al. 2014). This would indicate that the study area has shared characteristics of upwelling and estuarine ecosystems.

In terms of general system homeostasis, ascendancy and overhead have been used as indices to explain the degree of organisation and the "strength in reserve" of food webs, respectively (Ulanowicz, 1986). These parameters provide insights on the organisation of the food web and the potential recovery of the system (Ulanowicz, 1986; Christensen, 1995). The low ascendancy (22.36%) and the high overhead (77.64%) of the system modelled here denoted a low organisational level and at the same time a high resilience. This is in line with findings in other upwelling systems, where overhead values tend to be high, indicating that the systems are capable of coping with external perturbations (Shannon et al. 2003; Heymans et al. 2004).

4.4.3. Flows and network analysis

The functional groups in the model were organised into four integer trophic levels. In essence, the system could be organised into effective trophic levels (Field et al. 1989), such as primary producers (phytoplankton), primary consumers (zooplankton, macrobenthos, sardine and benthopelagic fish), secondary consumers (including the rest of the fish groups and the cephalopods), and top predators (including cetaceans and seabirds). Eight groups had a trophic level (TL) > 4, and among them, bottlenose dolphins, large piscivorous pelagic fish and common dolphins, had a TL close to 5. All cetaceans except for baleen whales had a TL > 4. Among the fish groups, large piscivorous pelagic, bathydemersal piscivorous, demersal piscivorous and other piscivorous pelagic had a TL > 4, whereas the rest of the fish groups had TL between 2.72 and 3.46. Both seabird groups had TL > 3, close to 4. Among the invertebrates, cephalopods was the group with the highest TL (4.25) and macrobenthos was the group with the lowest TL (2.12).

TLs of delphinids and porpoises, were slightly higher than those recorded by Pauly et al. (1998) and in other upwelling systems (Heymans et al. 2004; Tam et al. 2008), but were in accordance with previous models developed in the North-East Atlantic and in other upwelling regions (Shannon et al. 2003; Lassalle et al. 2011; Torres et al. 2013). These differences among models can be explained by differences in prey availability and in diet differences between populations. Baleen whales had similar TL than those previously reported (e.g. Pauly, et al. 1998, Morato et al. 2016). Conversely, both groups

of seabirds had a slightly lower TL than those previously recorded (Lassalle et al. 2011; Outeiro et al. 2018). This difference might be due to a higher contribution of discards in the seabirds diet. The TL of the fish groups, invertebrates and zooplankton were in line with those found in the North-East Atlantic (Sánchez and Olaso, 2004; Lassalle et al. 2011; Torres et al. 2013).

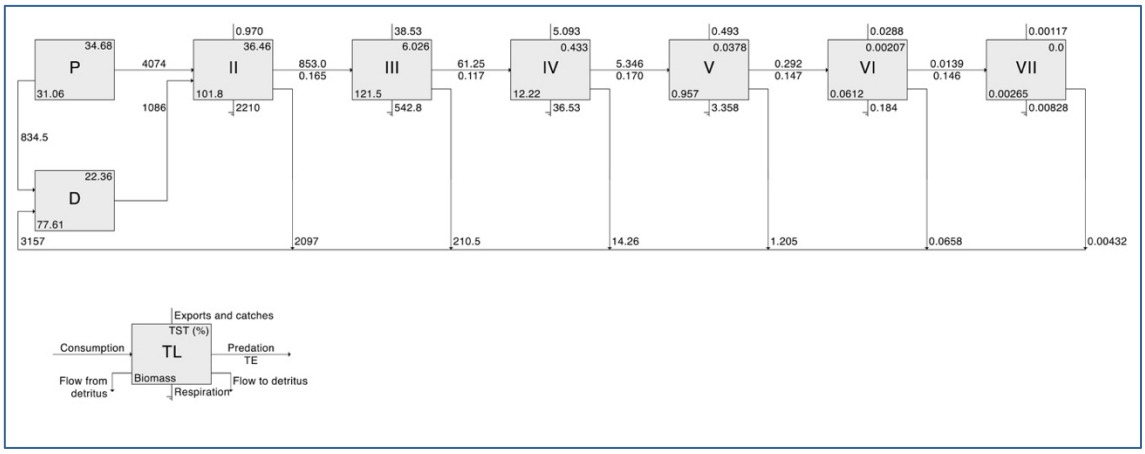


Figure 4.2 *Trophic aggregation showing the different integer trophic levels of the Rías Baixas shelf ecosystem, their transfer efficiencies and the flows between them. D denotes detritus, and P denotes phytoplankton.*

The Lindeman spine (Figure 4.2) aggregates the different functional groups in discrete trophic levels and gives information about different aspects such as the flows between the trophic levels (Lindeman, 1942; Ulanowicz, 1995). The first trophic level is shared by both primary producers and detritus. The system here modelled shows that the majority of the flows (57.04% of the total system throughput) occurred between the TL I and TL II, and secondly between TL II and TL III (36.46% of the total system throughput). Conversely, flows from the TL III and above were insignificant (<7% of the total system throughput).

Figure 4.2 also provides information about the transfer efficiency between successive discrete trophic levels. This ranged between 11.7% (TL III) and 17% (TL IV). The highest values were found in TL IV (17%) and TL II (16.5%) and these might be explained by different factors. While the high transfer efficiency in TL II suggested a good link between phytoplanktivorous and detritivorous organisms and their predators (Coll et al. 2006), the

high transfer efficiency in TL IV was determined by a higher contribution of the exports (Figure 4.3A). Indeed, the proportion of exports in relation to the total transfer efficiency increased with increasing TL. Two elements determine the exports of each TL, the emigration to adjacent ecosystems and the catches by fisheries (Christensen and Pauly, 1993). Since the emigration rate was considered 0 in the present model, the higher proportion of the export in the total transfer efficiency of TL IV could be directly linked to a more intense fishing pressure focussing on species of that trophic level, as it has been seen in other regions (Shannon et al. 2003; Coll et al. 2009b; Libralato et al. 2010).

The mean transfer efficiency, calculated as the geometric mean for TL II, III and IV (Christensen et al. 2005) was 14.89%, and was higher than the mean transfer efficiency found in other upwelling systems (Baird et al. 1991; Jarre-Teichmann et al. 1998; Heymans et al. 2004). Higher than usual efficiencies in the transfer of biomass have been explained by several factors, such as anomalous performances of key species (Baird et al. 1991), bottleneck effect and food limitation (Shannon et al. 2003). However, the high transfer efficiency in the present model could be explained by two main factors, the importance of catches in TL III and above (Shannon et al. 2003; Coll et al. 2009a; Libralato et al. 2010) and the good coupling between zooplankton and its predators (Baird et al. 1991; Coll et al. 2006). Regarding the first factor, 94% of the total biomass landed in Ribeira harbour in 2017 was represented by eight species of fish: European conger, sardine, bogue, European hake, Atlantic mackerel, Atlantic chub mackerel, Atlantic horse mackerel and blue whiting (Xunta de Galicia, Consellería do mar, 2020a). Seven of these species were classified by the model in TL III and IV. As a consequence, the high fishing pressure on these species doubled the TE for TL III and IV, and contributed to an increase of the mean transfer efficiency of the system (Figure 4.3A). With regard to the second factor, the transfer efficiency of TL II was mainly determined by predation (Figure 4.3). The zooplankton was the main component of the TL II in terms of biomass and it was efficiently predated by a series of groups, namely small planktivorous pelagic fish, blue whiting, Atlantic horse mackerel and sardine, which control the transfer of energy into higher trophic levels. These aspects were reinforced by the fate of the total system throughput (Figure 4.3B), which showed the importance of predation in TL I and

II, as well as an increasing importance of the exports in higher trophic levels (III and above).

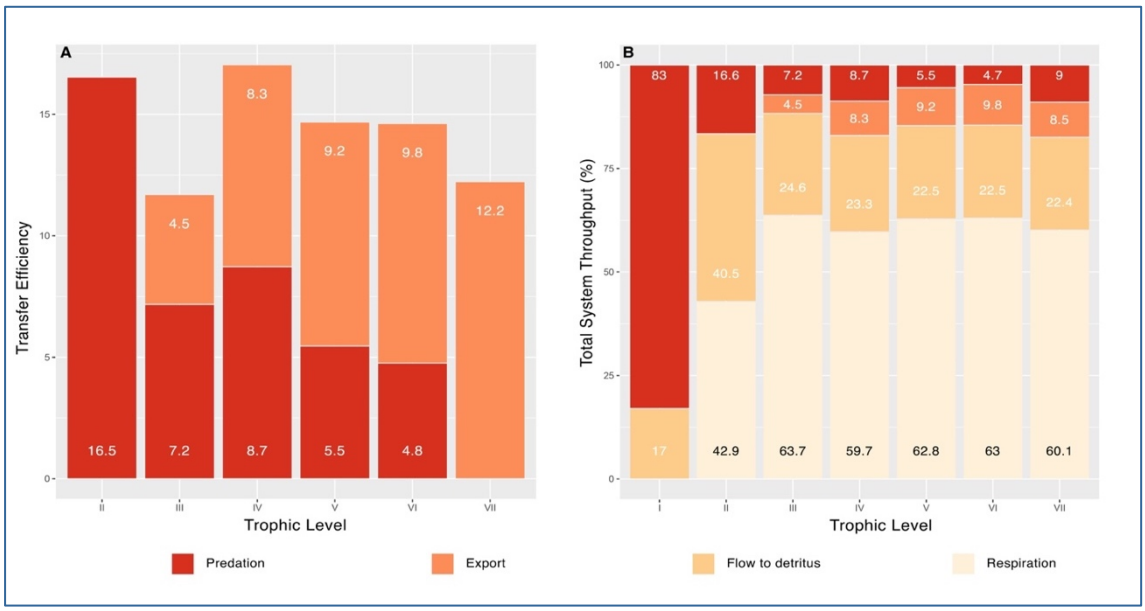


Figure 4.3 *Shows the contribution of the exports and predation on the indicated trophic level to the Transfer Efficiency for each trophic level (A), and the contribution of the exports, predation on the indicated trophic level, flow to detritus and respiration, to the total system throughput (B).*

The modelled system showed that most of the biomass excluding detritus (63%) was contained within the pelagic domain, whereas the remaining 37% was held in the non-pelagic domain. Additionally, the model revealed the importance of the pelagic domain in the system as well as some differences between domains (Figure 4.4). For instance, most of the consumption (86%) of the functional groups in the pelagic domain originated within the same domain, phytoplankton and zooplankton being the most important groups (Appendix 1, Table A1.26). The remaining 14% originated in the non-pelagic domain, where detritus was the most important group. Conversely, 85% of the consumption in the non-pelagic domain originated in the pelagic domain, in which zooplankton was the most important group. The remaining 15% originated within the same domain.

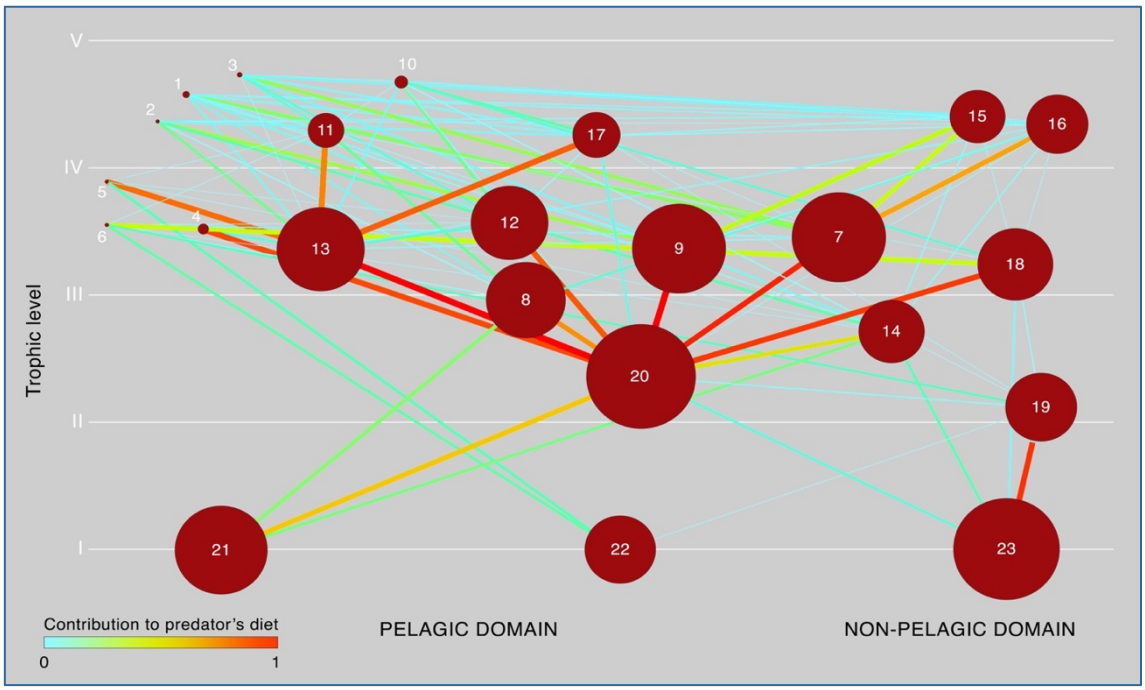


Figure 4.4 *Flow diagram showing the main flows between the functional groups of the ecosystem. Circles represent the different functional groups (scaled to their biomass) and lines the flows between them (colours representing the contribution of each prey to the predator's diet). The functional groups are: 1. Common dolphin; 2: Harbour porpoise; 3: Bottlenose dolphin; 4: Baleen whales; 5: Seabirds I: Pursuit and plunge divers; 6: Seabirds II: Surface and aerial pursuit feeders; 7: Blue whiting; 8: Sardine; 9: Atlantic horse mackerel.; 10: Large piscivorous pelagic fish; 11: Other piscivorous pelagic fish; 12: Large planktivorous pelagic fish; 13: Small Planktivorous pelagic fish; 14: Benthopelagic fish; 15: Bathydemersal piscivorous fish; 16: Demersal piscivorous fish; 17: Cephalopods; 18: Non-planktonic crustaceans; 19: Macrobenthos; 20: Zooplankton; 21: Phytoplankton; 22: Discards; 23: Detritus.*

Zooplankton played an important role in the system by linking the lower levels with the higher levels from the pelagic and the non-pelagic domains, as the main flows from the lower levels towards higher levels passed through it. For instance, blue whiting, Atlantic horse mackerel and, to a lesser extent, non-planktonic crustaceans, fed on zooplankton and determined the energy transfer from the lower to the higher trophic levels in the non-pelagic domain. Similarly, sardine, small planktivorous pelagic fish and large planktivorous pelagic fish were the main predators of zooplankton in the pelagic domain and determined the energy transfer from the lower to the higher trophic levels in that domain.

A deeper analysis showed that most of the flows in the pelagic domain were determined by the interactions between zooplankton, phytoplankton, and planktivorous pelagic fish (Appendix 1, Table A1.26). Some functional groups exclusively fed within the pelagic domain (baleen whales, sardine, large planktivorous pelagic fish and small planktivorous pelagic fish), others primarily fed on functional groups of the pelagic domain (seabirds I, large piscivorous pelagic fish, other piscivorous pelagic fish, cephalopods and zooplankton) and the remaining groups primarily fed on functional groups of the non-pelagic domain (common dolphins, harbour porpoises, bottlenose dolphins and seabirds II). The non-pelagic domain was especially dominated by the interactions between zooplankton, detritus and blue whiting. Some functional groups in the non-pelagic domain mainly fed on functional groups of the same domain (bathydemersal piscivorous fish, demersal piscivorous fish and macrobenthos), while others primarily or exclusively fed on groups of the pelagic domain (blue whiting, Atlantic horse mackerel, benthopelagic fish, and non-planktonic crustaceans). Both domains were connected at low levels through the zooplankton, which was consumed by a wide variety of fish and invertebrate groups of both domains. At intermediate levels, several functional groups, such as the blue whiting, the Atlantic horse mackerel and the benthopelagic fish of the non-pelagic domain and the small planktivorous pelagic fish of the pelagic domain, connected the lower and upper levels of both domains. At higher levels, small cetaceans, seabirds II and large piscivorous pelagic fish connected the pelagic domain with the non-pelagic domain.

4.4.4. Keystoneness Index

The functional group with the highest keystoneness was small planktivorous pelagic fish (group 20 in Figure 4.5). Additional functional groups that ranked high in this index were zooplankton, blue whiting and phytoplankton, however, their biomass was higher than the small planktivorous pelagic fish biomass (Table 4.6). These results indicate that the small planktivorous pelagic fish played a crucial role in the ecosystem structure and functioning, despite its relative low biomass, thus it could be considered as a keystone group (Libralato et al. 2006). Conversely, the dominant role in the ecosystem of the remaining three groups derived from their higher biomass, especially the zooplankton biomass, and therefore they could be considered important structuring groups (Libralato

et al. 2006; Heymans et al. 2011). Furthermore, the results show that the keystone and the structuring functional groups had intermediate trophic levels and variable top-down effects (Table 4.6), suggesting that the Rías Baixas shelf ecosystem is regulated by a mix of top-down and bottom-up controls, and could be described as a wasp-waist ecosystem (Cury et al. 2000; Bakun, 2006; Hunt and McKinnell, 2006; Libralato et al. 2006).

Table 4.6 *The first four functional groups ranked in decreasing order of keystoneness index. Top-down effects (TD), biomass and trophic level are also shown for each functional group.*

Functional group	Keystoneness	TD	Biomass	Trophic level
Small planktivorous pelagic fish	-0.0717	28.51%	22.36	3.37
Zooplankton	-0.18	70.85%	86.44	2.37
Blue whiting	-0.192	82.03%	34.35	3.46
Phytoplankton	-0.212	47.87%	31.06	1

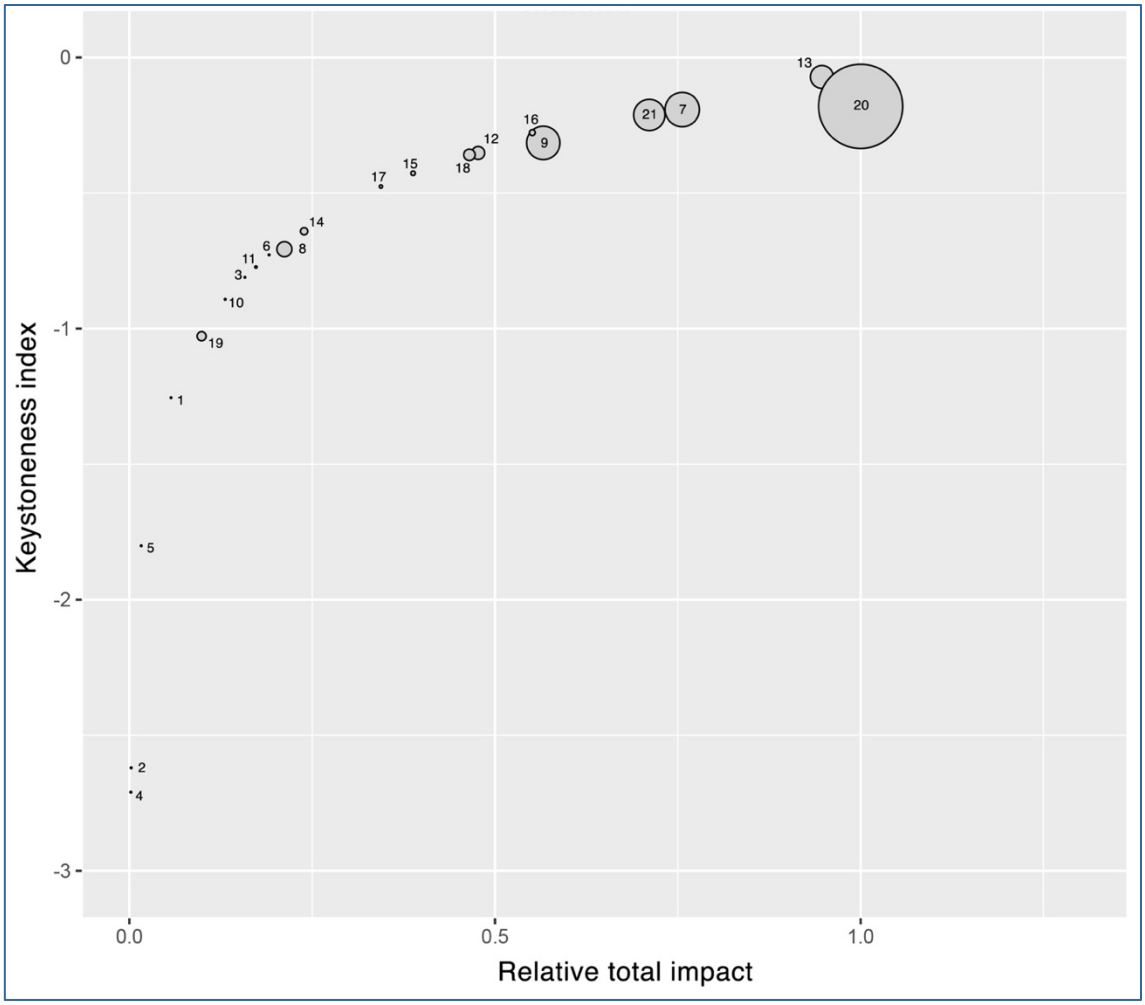


Figure 4.5 *Keystoneness index of the food web modelled in this study sensu Libralato et al. (2006). The size of the circles is scaled according to the biomass of each functional group. The functional groups are: 1. Common dolphin; 2: Harbour porpoise; 3: Bottlenose dolphin; 4: Baleen whales; 5: Seabirds I: Pursuit and plunge divers; 6: Seabirds II: Surface and aerial pursuit feeders; 7: Blue whiting; 8: Sardine; 9: Atlantic horse mackerel.; 10: Large piscivorous pelagic fish; 11: Other piscivorous pelagic fish; 12: Large planktivorous pelagic fish; 13: Small planktivorous pelagic fish; 14: Benthopelagic fish; 15: Bathydemersal piscivorous fish; 16: Demersal piscivorous fish; 17: Cephalopods; 18: Non-planktonic crustaceans; 19: Macrobenthos; 20: Zooplankton; 21: Phytoplankton; 22: Discards; 23: Detritus.*

These findings were reinforced by the flows between functional groups, which show two main energy transfer pathways from lower to higher trophic levels (Figure 4.4). Both pathways originate in the zooplankton, and transfer the energy to higher trophic levels through the small planktivorous pelagic fish (group 13 in Figure 4.4) on one hand, and the blue whiting (group 7 in Figure 4.4) on the other hand. Indeed, small planktivorous pelagic fish have been found to play an important role for predators, becoming an energy-rich source to their diet (Spitz et al. 2018). In North-West Spain, small planktivorous pelagic fish are subjected to recurrent changes in recruitment and biomass that are mostly driven by environmental changes (Santos et al. 2007; Garrido et al. 2017; Cabrero et al. 2019). Furthermore, blue whiting is primarily targeted by Galician fisheries and represented the higher landings biomass in Ribeira harbour in 2017 (Xunta de Galicia, Consellería do mar, 2020a). Consequently, changes in environmental regimes, coupled with fishing pressure of both small planktivorous fish and blue whiting, could have drastic effects on the ecosystem structure and functioning (Santos et al. 2007; Coll et al. 2009c; Valls et al. 2015).

4.5. *Conclusions*

This study presents the first comprehensive mass-balance model of the Rías Baixas shelf ecosystem, a coastal ecosystem located in a highly productive area influenced by coastal upwelling and terrestrial runoff, and heavily impacted by human activities off North-West Spain. EwE proved to be a useful tool to create a mass-balance model describing the trophic interactions among the different functional groups and species in the area which could be used as baseline information for future work focused on coastal management and conservation. Local and detailed information was available for marine top predators, such as cetaceans and seabirds, providing high reliability to the results obtained for these specific functional groups. Data on the fish and cephalopod functional groups were calculated from regional fisheries landing statistics, assuming that the fishing vessels operated within the limits of the study area. These assumptions could have led to an underrepresentation of the non-commercial species in the model. However, since biomass estimates of non-commercial species are not available in the area, landing statistics were considered the best locally available data in order to create the fish

functional groups. Additionally, findings for these groups should be considered carefully, as official landing statistics might underrepresent the real catches in the area (Pauly and Zeller, 2016), leading to an underestimation of the fisheries impacts. Parameter estimates for benthic invertebrates in the area were scarce, highlighting the need to further study these communities if more detailed ecosystem models were to be created. In summary, this study presents a realistic mass-balance model with higher reliability for the results obtained on marine top predators.

In general terms, the Rías Baixas shelf ecosystem shows a wasp-waist control and can be described as immature, moderately complex, stable, with a low organisational level and high resilience, characteristics that apply to upwelling systems worldwide (Christensen, 1995; Jarre-Teichmann and Christensen, 1998 ; Heymans et al. 2004). However, some of the parameters of the model suggest that the ecosystem includes some attributes of ecosystems typically found in fjords or coastal embayments (Vasconcellos et al. 1997). The adjacent rias (Ría de Pontevedra, Ría de Arousa and Ría de Muros-Noia) seem to play an important role in influencing the dynamics of the studied continental shelf ecosystem.

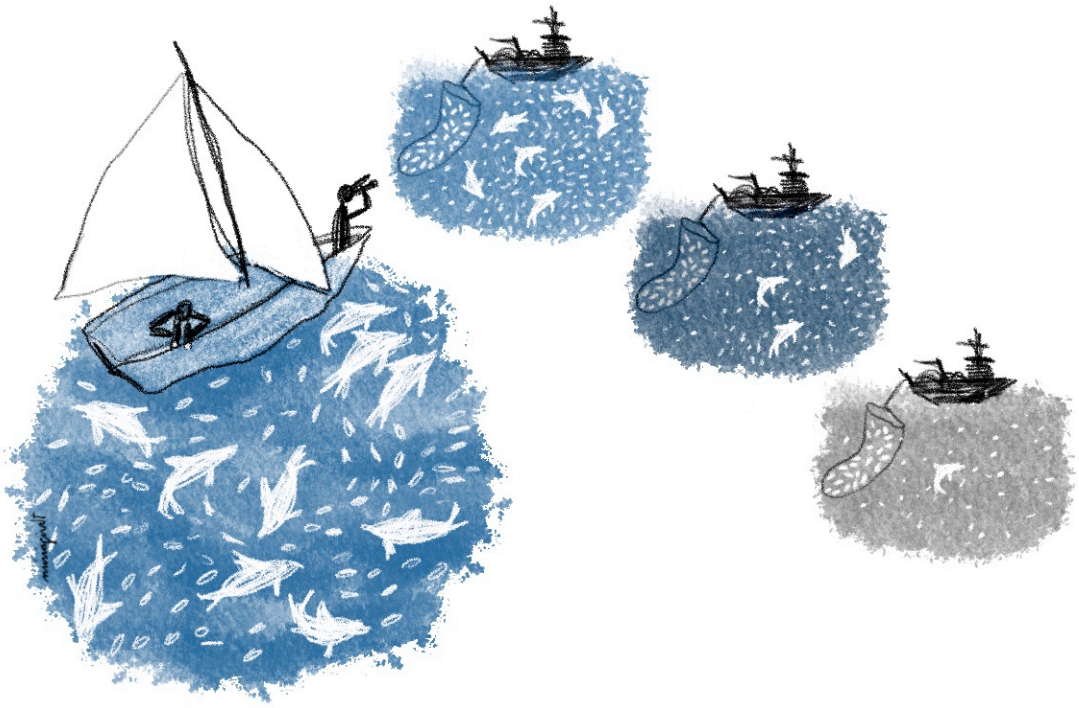
Some of the parameters and indicators used in the model, such as the transfer efficiency and system omnivory index, suggest that the ecosystem functioning and structure could be impacted by the fisheries operating in the area. Indeed, several studies have linked intense fishing pressure to drastic changes in species abundance, evolutionary characteristics of the populations and ultimately alterations in the ecosystem structure and functioning (Pauly et al. 2002; Spitz et al. 2018). Higher than usual transfer efficiencies found in the ecosystem modelled here suggested that fisheries were mainly targeting fish species with a trophic level higher than III. These findings agree with regional catch statistics that state that 94% of the fish biomass caught and landed in the area included fish species of trophic level III or higher (Xunta de Galicia, Concelleria do Mar, 2020a). These landings included mostly three species, blue whiting, Atlantic horse mackerel and Atlantic chub mackerel, which respectively accounted for 38%, 24% and 20% of the total landed biomass (Xunta de Galicia, Concelleria do Mar, 2020a), and are mainly targeted by pair-trawlers operating in the area (Fernandez-Contreras et al. 2010).

The fishing pressure on blue whiting, coupled with the fluctuations in small pelagic fish biomass, might have caused a dual impact on the ecosystem functioning. On one hand, blue whiting was found to have a crucial structuring role by feeding on zooplankton and serving as prey for top predators of both the pelagic and the non-pelagic domains, thus linking the lower and higher trophic levels. Similarly, small planktivorous pelagic fish were considered a keystone functional group, linking lower with higher trophic levels. On the other hand, both functional groups were abundant prey items in the diet of top predators such as common dolphins, bottlenose dolphins and harbour porpoises. Additionally, the wasp-waist nature of the Rías Baixas shelf ecosystem makes it particularly vulnerable to climate variability and to drastic changes in the trophic groups that link lower and higher trophic levels (Cury et al. 2000). Consequently, the fishing pressure, especially on blue whiting, and environmental changes could lead to drastic changes in the ecosystem structure and in the energy flows, ultimately affecting top predators.

Indeed, the study area has been found to be important for some of the marine top predators included in this model, such as common dolphins, bottlenose dolphins, harbour porpoises (Díaz López and Methion, 2018; Chapter 2) or Atlantic bluefin tuna. For instance, Atlantic bluefin tuna, is listed as Endangered by the IUCN, as a consequence of intensive fishing (Collette et al. 2011). Harbour porpoise commonly seen in the area belong to a distinct ecotype, which is already affected by vessel traffic in the area (Fontaine et al. 2014; Díaz López and Methion, 2018). Bottlenose and common dolphins are regularly observed in the area, where they face several threats such as fisheries bycatch, water pollution, and microplastics (López et al. 2002; Hernandez-Gonzalez et al. 2018; Methion and Díaz López, 2019b). As a consequence, drastic changes in the ecosystem functioning and structure could imply an added stress on these and other top predator species, compromising their conservation in the area.

Results of this study provide baseline information on the Rías Baixas shelf ecosystem structure and functioning, located in a coastal area influenced by coastal upwelling and the presence of rias. Moreover, this study provides insights on the potential impacts of intense fishing pressure on the ecosystem in the region. However, given the unique

characteristics of the area and its importance for marine top predators, a deeper and comprehensive understanding of the effects of fisheries is needed to ensure the ecosystem conservation. The combination of this holistic approach with previous studies focused on marine top predator distribution could lead to the development of management plans that ensured sustainable exploitation of fishery resources and conservation strategies focused on these vulnerable species.



Drawing by Núria Giralt

Chapter 5

Modelling ecosystem dynamics to assess the effect of coastal fisheries on three cetacean species

Adapted from the article in review:

Giralt Paradell, O., Methion, S., Rogan, E., Díaz López, B. Modelling ecosystem dynamics to assess the effects of coastal fisheries on three cetacean species. Journal of Environmental Management. In press.

Contribution to the article:

OGP conceived and designed the study together with BDL and ER, analysed and interpreted the data with inputs from BDL and ER, designed the figures and tables, developed the modelling framework and wrote the manuscript with inputs from BDL, SM and ER. Additionally, OGP contributed to the last year (2017) of data collection.

5.1. *Abstract*

The expansion of fisheries and its increased efficiency are causing severe detrimental impacts on marine species and ecosystems, that can be categorised into operational and ecological effects. While impacts directly caused by fishing activities have been extensively documented, it is difficult to set an empirical link between fisheries and changes in predator biomass and abundance. Therefore, exploring the functioning of ecosystems as a whole, the interactions between the different species within them and the impact of human activities, is key to understanding the ecological effects of fisheries on top predators and ecosystems, and to develop effective conservation measures, while ensuring a more sustainable exploitation of fishing resources. For instance, mass balance models, such as Ecopath with Ecosim, have proven to be a useful tool to develop more holistic fisheries management and conservation strategies. In this study, Ecopath with Ecosim was used to investigate the temporal dynamics of the Rías Baixas shelf ecosystem (North-West Spain) between 2005 and 2017. Additionally, nine 30-year forward projecting simulations covering the period 2018 – 2047 were developed to examine the effects of differing fisheries management strategies on common dolphins (*Delphinus delphis*), bottlenose dolphins (*Tursiops truncatus*) and harbour porpoises (*Phocoena phocoena*). Results from these models suggest that when intense fishing increases it poses a major threat to the conservation of these top predators in the area, by reducing the variety of their available prey and potentially enhancing competition amongst them. The study highlights the applicability of Ecopath with Ecosim to develop cetacean conservation measures and despite its small spatial scale, it provides a general framework that can be used to assess cetacean conservation in larger and impacted areas.

Keywords: Ecopath with Ecosim, North-West Spain, ecological effects, fisheries impact, cetaceans, food web interactions

5.2. *Introduction*

Technological improvements and the expansion of fisheries over the second half of the 20th century have led to an increase in the detrimental impacts of fishing activities on marine ecosystems (Pauly et al. 2005; Bell et al. 2017). This is particularly evident in marine mammals for which fisheries impacts can be divided into operational effects and ecological effects (Northridge, 2009). Operational effects are direct impacts from fisheries, that imply the dead, unintentional capture or the injury of marine mammals as a result of a physical contact with fishing gear (Matthiopoulus et al. 2008), and have been extensively documented (Bearzi, 2002; Díaz López, 2006; Read et al. 2006; Rogan and Mackey, 2007; Fernández-Contreras et al. 2010; Breen et al. 2017). Ecological effects include direct competition for the same resources, indirect competition for different resources that are linked through food web dynamics, behaviour alteration, and habitat modification, degradation and loss (DeMaster, 2001; Bearzi, 2002; Plagányi and Butterworth, 2005; Díaz López et al. 2008; Matthiopoulus et al. 2008; Northridge, 2009; Northridge et al. 2017; Díaz López, 2018). As opposed to operational effects, ecological effects are more difficult to detect and evaluate accurately mainly due to insufficient knowledge of food-web dynamics of the affected ecosystems (Matthiopoulus et al. 2008; Moore, 2013). Despite these difficulties, recent studies have documented ecological effects of fisheries on a number of marine mammal species and have predicted an increase of such impacts in the future (DeMaster, 2001; Piroddi et al. 2010; Morissette et al. 2012). Owing to the indirect nature of ecological effects, it is crucial that studies that aim to elucidate the interactions between marine mammals, fisheries, shared resources and the ecosystem in general, include detailed biological information of all the groups in a given ecosystem (Matthiopoulus et al. 2008).

Mass-balance ecosystem modelling software packages, such as Ecopath with Ecosim (EwE), can be used to understand the nature of ecological effects and their impact on marine mammals. By integrating information from different sources, mass-balance ecosystem models offer an opportunity to have a better understanding of complex ecosystem dynamics (Christensen and Walters, 2004). EwE, in particular, combines information on the biomass and production of the different trophic groups in an

ecosystem (including fisheries), the flows between them and the consumption among them (Christensen and Pauly, 1992), with dynamic, time-varying simulations of the prey-predator relationships among the trophic groups (Walters et al. 1997; Gascuel and Pauly, 2009). Due to these characteristics, it has been successfully applied not only to assess the impact of fisheries on the ecosystems under different fishing pressures (Sánchez and Olaso, 2004; Coll et al. 2006; Gascuel et al. 2011; Gasche and Gascuel, 2013; Torres et al. 2013; Bentorcha et al. 2017), but also to evaluate the impact of fishing activities on particular trophic groups, such as marine mammals (Díaz López et al. 2008; Piroddi et al. 2010; Lassalle et al. 2012; Morissette et al. 2012).

Several studies highlight that bycatch and interaction with fisheries represent a high risk on marine megafauna, specially cetaceans, in European waters (Díaz López, 2006; Rogan and Mackey, 2007; Fernández-Contreras et al. 2010; Breen et al. 2017; Chapter 3). As a consequence, cetacean species such as the common dolphin (*Delphinus delphis*), the bottlenose dolphin (*Tursiops truncatus*), and the harbour porpoise (*Phocoena phocoena*) may suffer cumulative impacts derived from operational and ecological effects (Dolman et al. 2016; Murphy et al. 2019). This is particularly relevant in areas with intense fishing activity, such as the continental shelf off North-West Spain (Surís-Regueiro and Santiago, 2014), where the presence and distribution of these three cetacean species have been documented (Spyrakos et al. 2011; Díaz López and Methion, 2018; Methion and Díaz López, 2018; Saavedra et al. 2018; Chapter 2), and result in the spatial and temporal overlap with different fishing operations (Chapter 3). This overlap has been suggested to be as a consequence of cetaceans and purse-seine and trawl fisheries competing for the same resources (Chapters 3 and 4), and it can cause a dual impact on the cetacean species. Common dolphins, bottlenose dolphins and harbour porpoises are most frequently bycaught species in the region (López et al. 2002, 2003; Fernández-Contreras et al. 2010) and they are also susceptible to competition for resources with fisheries (Morissette et al. 2012). Even though operational effects on these species of cetaceans have been studied in the area (López et al. 2002, 2003; Fernández-Contreras et al. 2010; Goetz et al. 2015), the scarce information on ecosystem dynamics coupled with the difficulty in accurately detecting ecological effects has led to a lack of knowledge on the ecological effects of fisheries on dolphins and porpoises. Therefore, studies that

combine information on ecosystem functioning and dynamics with fisheries information to better understand the ecological effects of fisheries on cetaceans in the area are key to formulating and promoting conservation strategies to help protect these vulnerable species.

This becomes increasingly important in areas where conservation measures are already in place, as new information on the ecological effects of fisheries on these species of cetaceans could result in improvements to these measures. In Europe, the Natura 2000 network is the largest coordinated network of protected areas and currently protects around 6% of the European marine territory (https://ec.europa.eu/environment/nature/natura2000/index_en.htm, last visited on February, 18 2020). This network is based on the Birds (Council Directive 79/409/EEC) and Habitats (Council Directive 92/43/EEC) Directives of the European Union, and aims to protect crucial areas for the species and habitats listed in both Directives. Three Natura 2000 network sites are located in the study area (information from EUNIS: https://eunis.eea.europa.eu/sites.jsp, last accessed on February 18th 2020). In this regard, studies that combine different sources of information to better understand the ecological effects of fisheries on these cetacean species could bring new perspectives to the conservation needs of the species in the area and could be an additional tool to improve the already existing protection measures.

The present work builds on previous studies that highlighted the spatial overlap and the resource overlap between cetaceans and fisheries in the coastal waters off North West Spain (Díaz López and Methion, 2018; Chapters 2-4). Based on a mass-balance model created to understand the Rías Baixas shelf ecosystem (Chapter 4), the present study uses dynamic simulations between 2005 and 2017 to explore the ecological effects of fisheries on common dolphins, bottlenose dolphins and harbour porpoises. Additionally, 30-years forward projecting simulations covering the period 2018 – 2047 were developed to examine the responses of the ecosystem, and more particularly these three species, to different fishing pressures. In total, nine scenarios were developed and divided into three categories: (1) two scenarios recreated the same trend in fishing effort and landings between 2005 and 2017; (2) two further scenarios recreated important fishing effort

reductions, such as fishing at maximum sustainable yield (MSY) or a 30-year total fishing ban; (3) five scenarios recreated sustained annual increases in fishing effort between 5 and 25%. With these 30-year forward simulations the study aims to better understand the ecological effects of fisheries on cetacean species in the area. This better comprehension of the potential impacts caused by fishing activities could lead to the improvement of already existing conservation measures and management plans and to the proposal of new ones with the ultimate aim of protecting, not only the cetacean species present in these waters, but also the ecosystem they inhabit.

5.3. *Methods*

5.3.1. Study area, fisheries and period

The study area (hereafter referred to as "Rías Baixas shelf ecosystem", Chapter 4) is located in the continental shelf waters west from the entrance of the Ría de Arousa (North-West Spain), extending to the 300 metres bathymetry line, and has a total area of 933.13 km2 (Figure 5.1). This coastal area exhibits a high marine primary productivity because of the combination of two factors; the seasonal upwelling events caused by northerly wind regimes that carry deep, nutrient-rich waters masses to the photic layer, and the terrestrial runoff caused by river discharge, that inputs nutrients into the coastal areas (Torres et al. 2003). Additionally, the study area includes the Atlantic Islands National Park, protecting an area of 75.82 km2 and three Natura 2000 sites. Two of these cover approximately 130 km2 of coastal marine waters, protecting, among other species, bottlenose dolphins and harbour porpoises. The third area covers 2,219 km2 of marine coastal waters and focuses exclusively on the protection of birds (Figure 5.1).

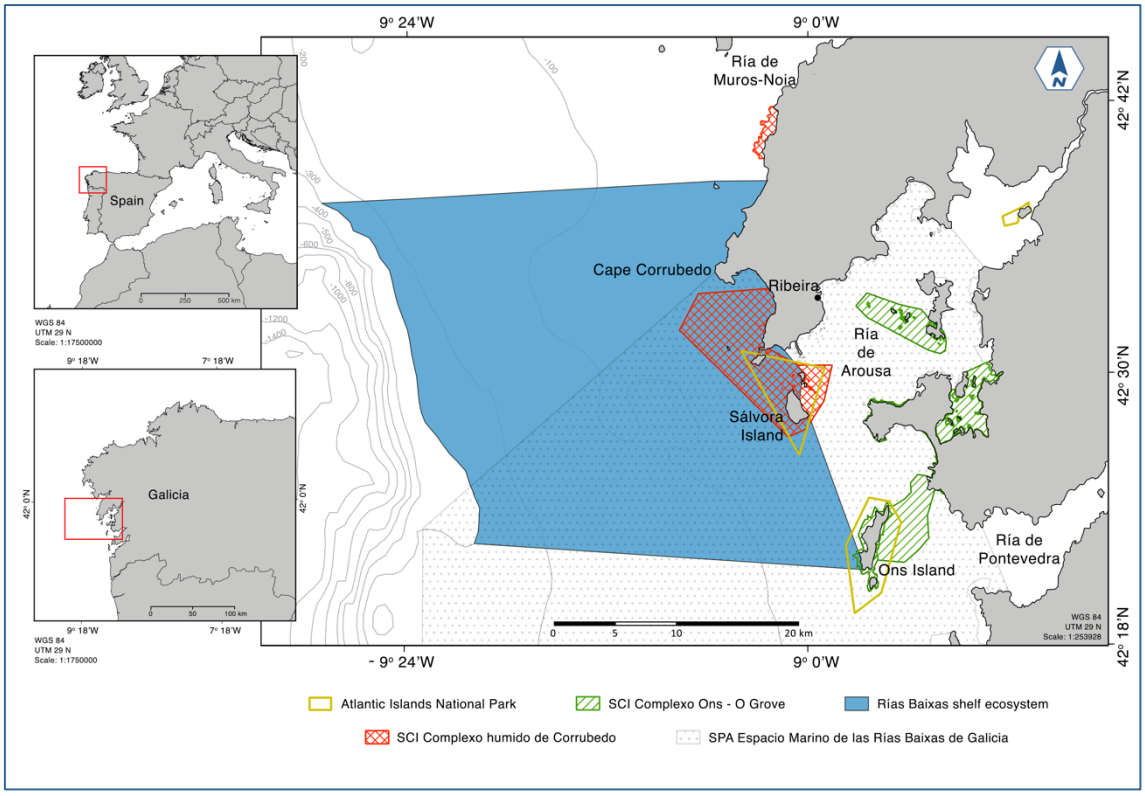


Figure 5.1 *Map of the study area, showing the Rías Baixas shelf ecosystem selected to create the Ecopath model, the Atlantic Islands National Park and the three Natura 2000 protected sites (SCI Complexo Ons – O Grove, SCI Complexo humido de Corrubedo and SPA Espacio Marino de las Rías Baixas de Galicia.*

There are predominantly two types of fishing fleets operating within the study area: (1) the artisanal fleet (88.87% of the total number of fishing boats in Galicia in 2017) is a mixed-gear fleet that targets different species depending on the season; (2) the coastal fleet (7.33% of the total number of fishing boats in Galicia in 2017) is the second largest fleet and uses several fishing techniques, such as trawling, purse-seine, gill-net and long-line, targeting several fish species, such as blue whiting (*Micromesistius poutassou*), sardine (*Sardina pilchardus*), Atlantic horse mackerel (*Trachurus trachurus*) and hake (*Merluccius merluccius*), among others (Surís-Regueiro et al. 2014; Xunta de Galicia, Consellería do Mar, 2020a). For the purposes of this study, only the fishing boats belonging to these two categories and that were registered in the fishing harbour of Ribeira were incorporated into the model. With a total of 240 boats (5.6% of the Galician fishing fleet), Ribeira harbour is the most important harbour in terms of landings, of the area (Xunta de Galicia, Consellería do Mar, 2020a). As seen in the rest of Galicia, the

fishing fleet in Ribeira harbour and its aggregated fishing power have been steadily declining since 2005 (Figure A2.1). Conversely, the volume of landings shows a positive trend since 2005 (Figure A2.1).

The present study investigates the trophic dynamics in the Rías Baixas shelf ecosystem between 2005 and 2017. Although historical regional fisheries data would allow for a longer study period, a major oil spill affected the Galician coast in November 2002, causing severe alterations in all ecosystems (Penela-Arenaz et al. 2009). Significant recovery of shellfish, fish and marine birds were not reported until one to three years after the disaster (Martínez-Gómez et al. 2009; Viñas et al. 2009; Moreno et al. 2011). Therefore, the period between 2005 and 2017 was chosen, as it was the longest time period that allowed the study of the trophic dynamics of the Rías Baixas shelf ecosystem, ruling out the effects of the oil spill, and thus focussing on the trophic dynamics and the effects of fisheries.

5.3.2.Modelling framework

Different components of the Ecopath with Ecosim (EwE) software version 6.6.16540.0 (www.ecopath.org) were used to create a mass balance representation of the Rías Baixas shelf ecosystem and to analyse its temporal dynamics between 2005 and 2017. The resulting model was then used to perform 30-years forward projecting simulations to analyse the response of the ecosystem, and more particularly that of common dolphins, bottlenose dolphins and harbour porpoises, to nine future scenarios simulating different fishing pressures.

5.3.3.Mass-balance model

A "Back to the Future" approach (Pitcher, 2001) was implemented to create a new model of the Rías Baixas shelf ecosystem in 2005 based on the mass balance model created to represent the state of the ecosystem in 2017 (Chapter 4). The 2005 model was created with the Ecopath module, that ensures the energy balance between the functional groups by assuming that consumption of the functional group (i) equals the sum of its production, its respiration and the unassimilated food (Christensen and Walters, 2004). Ecopath takes into account several parameters, such as the fishery catch rate (Yi),

biomass (Bi), natural predation rate (M2i), net migration rate (Ei), biomass accumulation rate (BAi), ecotrophic efficiency (EEi), and other mortality (Pi · (1-EEi)) to calculate the production rate (Pi) of each functional group (i) included in the model:

Equation 5.1

$$P_i = Y_i + B_i \cdot M2_i + E_i + BA_i + P_i \cdot (1 - EE_i)$$

This equation can be re-expressed as:

Equation 5.2

$$B(P/B)_i = \sum_{j=1}^{n} B_j(Q/B)_j DC_{ij} + Y_i + E_i + BA_j + B_i(P/B)_i(1 - EE_i)$$

where $(P/B)_i$ is the production by biomass ratio of (i), $(Q/B)_j$ is the consumption by biomass ratio of (j), and DC_{ij} is the fraction of prey (i) in the average diet of a predator (j). From this second equation (5.2), a modelling framework based on a series of linear functions, one for each functional group, is developed and solved for one of the following parameters, biomass, production by biomass ratio, consumption by biomass ratio or ecotrophic efficiency (Christensen and Walters, 2004). The remaining three parameters need to be entered in the software for each of the functional groups. Detailed information on the Ecopath working procedures, capabilities and limitations has been extensively documented (Christensen and Pauly, 1992; Christensen and Walters, 2004; Plagányi and Butterworth, 2004; Heymans et al. 2011).

The 2005 Rías Baixas shelf ecosystem was formed by the same 23 functional groups that comprised the 2017 model from Chapter 4 (Table 5.1). The ecosystem was divided into the pelagic domain and the non-pelagic domain and each functional group was assigned to one of the domains. Species with a similar ecological role were aggregated in the same functional group. Biomass was only calculated for the groups for which reliable information from the early 2000s was available. For the rest of the groups, biomass was assumed to be the same as in the 2017 model or was estimated by Ecopath (Appendix 2, Table A2.1). Production by biomass ratio was calculated from abundance estimates for common dolphin (López et al. 2004) and harbour porpoise (Hammond et al. 2013). A precautionary approach was used when no reliable information was available

to calculate production by biomass or consumption by biomass ratios, and these were assumed to be the same as in the 2017 model (Appendix 2, Table A2.1). Information on landings, discards and fisheries was obtained using the same data sources and procedures as in the 2017 model from Chapter 4 (Appendix 2, Table A2.2). The artisanal and the coastal fleet were included into a single group to better understand the combined effect of fisheries on the ecosystem. As no major changes of species have been reported in the area, diet of the different groups was also assumed to be the same as in 2017.

Table 5.1 *The 23 functional groups included in the 2005 model divided into pelagic and non-pelagic domains. Further details on the group composition are included in Appendix 2, Table A2.1.*

Pelagic domain	Non-pelagic domain
Common dolphin (*Delphinus delphis*)	Blue whiting (*Micromesistius poutassou*)
Harbour porpoise (*Phocoena phocoena*)	Atlantic horse mackerel (*Trachurus trachurus*)
Bottlenose dolphin (*Tursiops truncatus*)	Benthopelagic fish
Baleen whales	Bathydemersal piscivorous fish
Seabirds I, pursuit and plunge divers	Demersal piscivorous fish
Seabirds II, surface and aerial feeders	Non-planktonic crustaceans
Sardine (*Sardina pilchardus*)	Macrobenthos
Large piscivorous pelagic fish	Detritus
Other piscivorous pelagic fish	Discards
Large planktivorous pelagic fish	
Small planktivorous pelagic fish	
Cephalopods	
Zooplankton	
Phytoplankton	

To assess the ecological role of the different functional groups, the mixed trophic impact (MTI) routine and the keystoneness index were calculated. By quantifying the direct and indirect effects of each functional group on the rest of functional groups, the MTI routine provides information about the ecological role of each group within the ecosystem (Ulanowicz and Puccia, 1990). The keystoneness index (Libralato et al. 2006) relates the overall effect of a functional group in the food web to its biomass. This index was used to detect keystone functional groups (groups that have a strong impact on the ecosystem despite their small biomass (Power et al., 1996)) and structuring functional groups. (groups that have a strong impact on the ecosystem and a high biomass (Libralato et al., 2006)). Two methods were used to calculate this index. The first one,

proposed by Libralato et al., 2006, is based on the overall effect and biomass of each functional group and focuses on finding the groups that have both low biomass and high effect. The second method is based on the impact of each functional group multiplied by the biomass in a descending order and focuses on highlighting the importance of top predators as keystone species (Valls et al., 2015).

A PREBAL (Link, 2010) assessment was performed prior to the balancing process to detect the groups where modelled biomass diverged significantly from the expected biomass according to their trophic level. To address the anomalies detected by this process, the ecotrophic efficiency obtained in the 2017 model was used as an input parameter instead of the biomass for the functional groups with a higher than expected biomass.

5.3.4. Dynamic simulations

Once the 2005 model was balanced, the Ecosim module (Walters et al. 1997) of EwE was used to analyse and calibrate the temporal dynamics of the Rías Baixas shelf ecosystem between 2005 and 2017.

Ecosim takes the static ecosystem model generated by Ecopath and creates time-varying dynamic simulations of the same ecosystem (Walters et al. 1997, 2000), based on a set of differential equations derived from the Ecopath master equation (Equation 2) and can be expressed as follows:

Equation 5.3

$$dB_i/dt = (P/Q)_i \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - (M_i + F_i + e_i)B_i$$

where dB_i/dt is the change in biomass of group (i) over time, $(P/Q)_i$ is the net growth efficiency, M_i is the non-predation mortality rate, F_i is the fishing mortality rate, e_i is the emigration rate, I_i is the immigration rate, B_i is the biomass of group (i), $\sum_j Q_{ji}$ is the total consumption rate by group (i) and $\sum_j Q_{ij}$ is the predation by all predators on the same group (i). These dynamic simulations assume that prey and predator biomasses determine the flows between functional groups (Walters et al. 2000). This idea is based on the foraging arena theory (Walters and Korman, 1999) that states that prey alternates

between a vulnerable and an invulnerable state with respect to predators. These concepts are incorporated in the model through the consumption rates (Q_{ij}), which can be calculated as:

Equation 5.4

$$Q_{ij} = \frac{v_{ij} \cdot a_{ij} \cdot B_i \cdot B_j \cdot T_i \cdot T_j \cdot S_{ij} \cdot M_{ij} / D_j}{v_{ij} + v'_{ij} \cdot T_i \cdot M_{ij} + a_{ij} \cdot M_{ij} \cdot B_j \cdot S_{ij} \cdot T_j / D_j}$$

where v_{ij} is the rate at which prey move from the invulnerable to the vulnerable state or vulnerability, a_{ij} is the effective search rate for predator j feeding on prey type i, T_i and T_j are the prey and predator relative feeding times respectively, S_{ij} are the seasonal or long term forcing effects, M_{ij} are the mediation forcing effects and D_j are the effects of handling time as a limit to consumption rate. The vulnerabilities explain how a substantial increase of predator biomass impacts on the predation mortality and they determine the mechanism that controls the biomass of the different groups in the ecosystem (Christensen et al. 2005). In this regard, bottom-up control is expressed by low vulnerability values ($v_{ij} = 1$), top-down control is represented by high vulnerability values ($v_{ij} \gg 1$), and mixed flow control is achieved when $v_{ij} = 2$. Detailed information on the Ecosim assumptions and working procedures has been documented extensively (Walters et al. 1997, 2000; Christensen and Walters, 2004).

5.3.5.Time series data and fitting

To adjust the model to the ecosystem historical dynamics, a time series on biomass, catches, fishing effort and mortality for different functional groups were incorporated (Appendix 2, Table A2.3). Partial biomass time series were calculated for common dolphins, harbour porpoises and two groups of seabirds from relative abundances derived from direct observations at sea (BDRI 2018a, b; Chapter 4). Bottlenose dolphin was the only odontocete species not included in the fitting process, as there are no reliable historical biomass data. Time series on absolute biomass, catches and fishing mortalities for most fish groups, cephalopods and non-planktonic crustaceans, were obtained by combining regional landing statistics (Xunta de Galicia, Consellería do Mar, 2020a) with information from pelagic surveys (ICES, 2018b,c 2019a,b,c,d,e). Aggregated engine horsepower (expressed as HP) of the small-scale and coastal fleets operating in

Ribeira harbour was obtained from regional statistics (Xunta de Galicia, Consellería do Mar, 2020b), and was used as a proxy for fishing effort. To do so, the number of boats in 2005 was used to set the starting relative fishing effort value (1). Then this value was changed by calculating the percentage of variation in the number of fishing boats from one year to the next. Daily time series on chlorophyll a concentration in waters above the Rías Baixas continental shelf (Beca-Carretero et al. 2019) were used as a proxy to recreate historical changes in primary production in the area.

Once the time series data are included in the model, a measure of goodness of fit consisting of a weighted sum of squared (SS) deviations of log observed biomasses from log predicted biomasses is calculated for each model run (Christensen et al. 2005). Changes in fishing impact, vulnerability settings, primary productivity, will alter the fit of the model to the time series and thus several hypothetical models need to be tested in order to find the best fit (Heymans et al. 2016). To consider all the possible hypothetical models the "fit to time series" procedure (Tomczak et al. 2012) was applied. This method consists of systematically changing the number of vulnerabilities and primary productivity anomalies used to fit the model to the time series (Tomczak et al. 2012). To reduce human error in this critical process the automated "stepwise fitting" procedure of Ecosim was used (Scott et al. 2016). Vulnerability parameters were searched by predator for all iterations. Eight different groups of hypothetical models were tested (Table 5.3). The SS and the Akaike Information Criterion (AIC), which penalises for overparameterization (Akaike, 1974), were used to find the model with the best fit for each group of hypothetical models. In this regard, the models with the lowest SS, AIC and AICc, which corrects for small sample sizes (Burnham et al. 2004), were considered the best fits for each group of hypothetical models.

5.3.6.Assessing model uncertainty

Monte-Carlo simulations can be used to evaluate the uncertainty of Ecopath input parameters on Ecosim simulations (Heymans et al. 2016). The model that showed the best fit to the time series data after the automated stepwise fitting procedure was used to run 100 Monte-Carlo simulations. Ecopath input parameters (biomass, production by biomass and consumption by biomass ratios and ecotrophic efficiency) were randomly

selected with a coefficient of variation of 0.1 around them giving 100 different outcomes. These results were used to assess the uncertainty of the input data and to plot the 5th and 95th percentile confidence intervals for the fitted biomass (Corrales et al. 2017).

5.3.7.Future scenarios

The model with the best fit was used to perform the 30-year forward projecting simulations after the time-series period to predict the impact of fishing on the ecosystem in general, and, more particularly, on common dolphins, bottlenose dolphins and harbour porpoises. To do so, nine scenarios representing different plausible fishing effort levels were examined and are detailed below. To prioritise the effects of fishing pressure and minimise the influence of seasonal and annual primary production fluctuations, the forcing function was left constant throughout the 30-year forward projecting simulations.

Base scenario: This scenario was conceived to assess the impact of fishing if the 2017 conditions were kept throughout the forward simulation. To do so, the 2017 fishing effort and fishing mortalities for the different functional groups were kept constant throughout the 30-year forward projecting simulation.

Same trend scenario: The times series used to fit the model showed a 2.6% annual decrease in fishing effort and a 3% increase in landings between 2005 and 2017. This scenario reproduces those trends throughout the 30 year forward simulation.

Fisheries ban scenario: A temporal 30-year fisheries closure was considered in this scenario. To simulate this closure, both fishing effort and fishing mortalities were set to 0 throughout the 30 year forward simulation.

Fishing mortality at maximum sustainable yield (FMSY) scenario: According to the United Nations Convention on the Law of the Sea, coastal states should manage fisheries aiming to achieve maximum sustainable yield (UNCLOS, 1982). The Member States of the European Union agreed to achieve this goal for all depleted stocks by 2015, at the World Summit on Sustainable Development held in Johannesburg in 2002 (WSSD, 2002). This agreement was then further regulated within the Common Fisheries Policy (CFP) of the European Union that extended the deadline to 2020 (EC, 2013). The fishing mortality

at maximum sustainable yield (FMSY) for each functional group was calculated for 2017 (Appendix 2, Table A2.3). Fishing effort was set at the same value as in 2017. Both fishing mortalities at MSY and fishing effort were kept constant throughout the forward simulation.

Increased fishing effort scenarios: Five additional scenarios (e1, e2, e3, e4, e5) were conceived to evaluate the effects of a sustained annual increase in fishing effort on the ecosystem. Five different annual increases (e1 = 5% increase, e2 = 10% increase, e3 = 15% increase, e4 = 20% increase and e5 = 25% increase) were considered. Fishing mortality was increased accordingly for each scenario.

5.4. *Results*

5.4.1. Balancing the mass-balance model

The Ecopath model resulting from the "Back to the Future" approach had a pedigree index of 0.532, which was above the mean pedigree index calculated for other studies (Morissette et al. 2007, Colléter et al. 2015). The model was unbalanced and had to be readjusted. Six groups, including blue whiting, Atlantic horse mackerel, large piscivorous pelagic fish, other piscivorous pelagic fish, small planktivorous pelagic and demersal piscivorous fish, showed an ecotrophic efficiency higher than one. The PREBAL assessment (Figure A2.2) showed that these species had a biomass notably higher than the one expected from a group of their trophic level. In addition, six groups showed cannibalism within their diets, although this represented less than 5% of their diets, except for the zooplankton. Although cannibalism can constitute a problem, especially if it represents more than 10% of a groups diet (Christensen et al. 2005), no adjustments were made as percentages for most groups were lower than 5% (Heymans et al. 2016). The same precautionary approach as in Chapter 4 was applied to balance the model. The results of the balanced model are shown in Table 5.2.

Table 5.2 *Results of the balanced Ecopath 2005 model using the "Back to the Future" approach. Input parameters are shown in bold letters and stars show Ecotrophic Efficiencies taken from the 2017 model to balance the model.*

Group	TL	B	P/B	Q/B	EE	P/Q
Common dolphin	4.58	**0.036**	**0.05**	**23**	0	0
Harbour porpoise	4.37	**0.001**	**0.11**	**28.08**	0	0
Bottlenose dolphin	4.73	**0.076**	**0.05**	**19.08**	0	0
Baleen whales	3.52	**0.061**	**0.06**	**6.46**	0	0.01
Seabirds 1: Pursuit and plunge divers	3.89	**0.001**	**0.32**	**82.79**	0	0
Seabirds 2: Surface and aerial pursuit feeders	3.56	**0.001**	**0.25**	**182.12**	0	0
Blue whiting	3.46	29.892	**1.06**	**6.52**	**0.99***	0.16
Sardine	2.96	**78.695**	**0.58**	**8.8**	0.24	0.07
Atlantic horse mackerel	3.37	27.434	**0.64**	**6.47**	**0.80***	0.1
Large piscivorous pelagic fish	4.68	0.502	**0.82**	**7.8**	**0.45***	0.11
Other piscivorous pelagic fish	4.3	2.357	**0.82**	**6.5**	**0.43***	0.13
Large planktivorous pelagic fish	3.57	**9.349**	**1.14**	**6.28**	0.85	0.18
Small planktivorous pelagic fish	3.37	25.185	**1.98**	**9.13**	**0.83***	0.22
Benthopelagic fish	2.72	4.868	**0.68**	**3.62**	**0.71***	0.19
Bathydemersal piscivorous fish	4.41	3.269	**1.09**	**4.04**	**0.82***	0.27
Demersal piscivorous fish	4.34	4.224	**0.67**	**3.81**	**0.99***	0.18
Cephalopods	4.25	1.906	**3.2**	**7.5**	**0.92***	0.43
Non-Planktonic Crustaceans	3.24	21.849	**2.35**	**6.33**	**0.02***	0.37
Macrobenthos	2.12	15.14	**2.5**	**6.5**	**0.24***	0.38
Zooplankton	2.37	128.32	**39.08**	**80**	**0.80***	0.49
Phytoplankton	1	47.246	**158.04**	**0**	**0.83***	0
Discards	1	**5.062**	0	**0**	0	0
Detritus	1	**70**	0	**0**	0.34	0

Similar to what was found in the 2017 ecosystem model (Chapter 4), the functional group with the highest keystoneness index was small planktivorous pelagic fish (Figure 5.2 and Appendix 2, Table A2.4). Other groups such as zooplankton, phytoplankton and blue whiting had a high keystoneness index, but they showed a higher biomass, especially zooplankton. Hence, these groups could be considered as important structuring groups of the ecosystem (Libralato et al. 2006). Common dolphins and harbour porpoises had a lower keystoneness index than bottlenose dolphins, suggesting that their impact on the ecosystem was lower (Figure 5.2 and Appendix 2, Table A2.4). The second method used to assess the keystone species (Valls et al., 2015) ranked three species of top predators (large piscivorous pelagic fish, bathydemersal piscivorous fish and bottlenose dolphin) and small planktivorous pelagic fish among the four functional groups with a higher keystoneness. This method confirmed small planktivorous pelagic fish as a key functional

group, and highlighted the importance of top predators in the Rias Baixas shelf ecosystem. In contrast, both methods ranked other top predators such as common dolphins, harbour porpoise and both groups of seabirds among the groups with lower keystoneness.

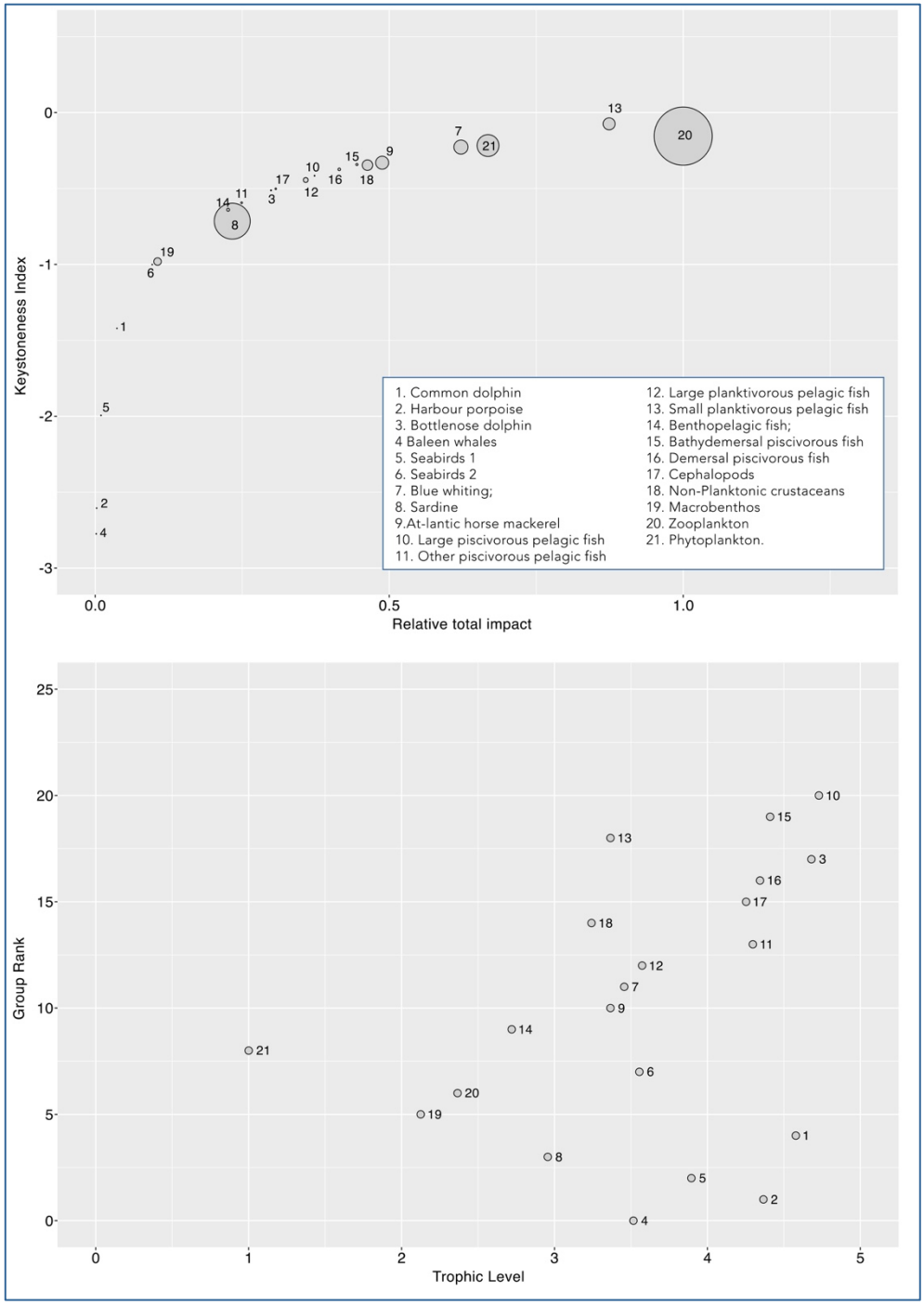


Figure 5.2 *Results of the two methods used to calculate the Keystoneness (top, Libralato et al., 2006; bottom, Valls et al., 2015) of the 2005 Rías Baixas ecosystem model. Circles on the top plot are scaled to the biomass of the group. Functional groups on the bottom plot are ranked according to their keystoneness in ascending order.*

The MTI routine showed that the functional groups with high keystoneness indices were also crucial groups in supporting the ecosystem (Figure 5.3). For instance, small pelagic fish, zooplankton and phytoplankton had a positive impact on most functional groups, whereas blue whiting had a negative impact. This highlights the importance of these groups in the ecosystem, and suggests a mix of top-down and bottom-up ecosystem control, as seen in the 2017 ecosystem model (Chapter 4). Therefore, the 2005 Rías Baixas shelf ecosystem could be described as a wasp-waist ecosystem (Cury et al. 2000). Additionally, small planktivorous pelagic fish, zooplankton and phytoplankton, together with blue whiting, Atlantic horse mackerel and to a lesser extent benthopelagic fish, had positive effects on common dolphins, harbour porpoises and bottlenose dolphins.

The routine also allowed the identification of the impact of the coastal fisheries on the different functional groups. The results show that the largest negative impacts were exerted on demersal piscivorous fish and large planktivorous fish. However, lower impacts were caused to Atlantic horse mackerel, sardine and bathydemersal piscivorous fish. These functional groups included species that are components of common dolphin, harbour porpoise and bottlenose dolphin diet. In addition, coastal fisheries showed an indirect impact on the three species of cetaceans, in particular on common and bottlenose dolphins.

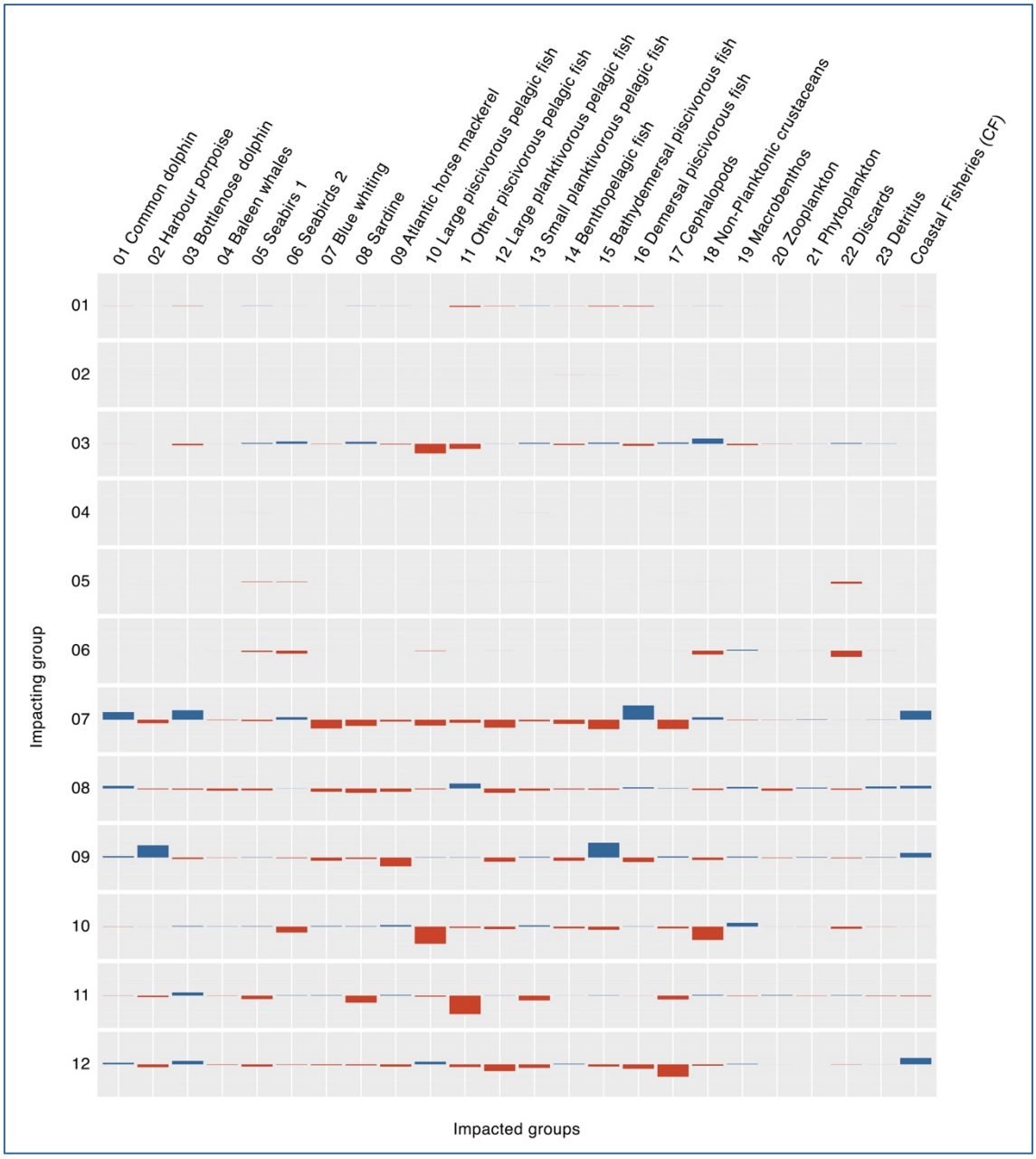


Figure 5.3 *Mixed Trophic Impact (MTI) plot of the 2005 Rías Baixas shelf ecosystem. The plot indicates the relative impacts caused by the impacting functional groups (rows) on the impacted functional groups (columns). Blue boxes indicate positive impacts whereas red boxes show negative impacts. The size of the box shows the degree of the impact with bigger boxes showing more important impacts. The functional groups are: 1. Common dolphin; 2: Harbour porpoise; 3: Bottlenose dolphin; 4: Baleen whales; 5: Seabirds I: Pursuit and plunge divers; 6: Seabirds II: Surface and aerial pursuit feeders; 7: Blue whiting; 8: Sardine; 9: Atlantic horse mackerel.; 10: Large piscivorous pelagic fish; 11: Other piscivorous pelagic fish and 12: Large planktivorous pelagic fish.*

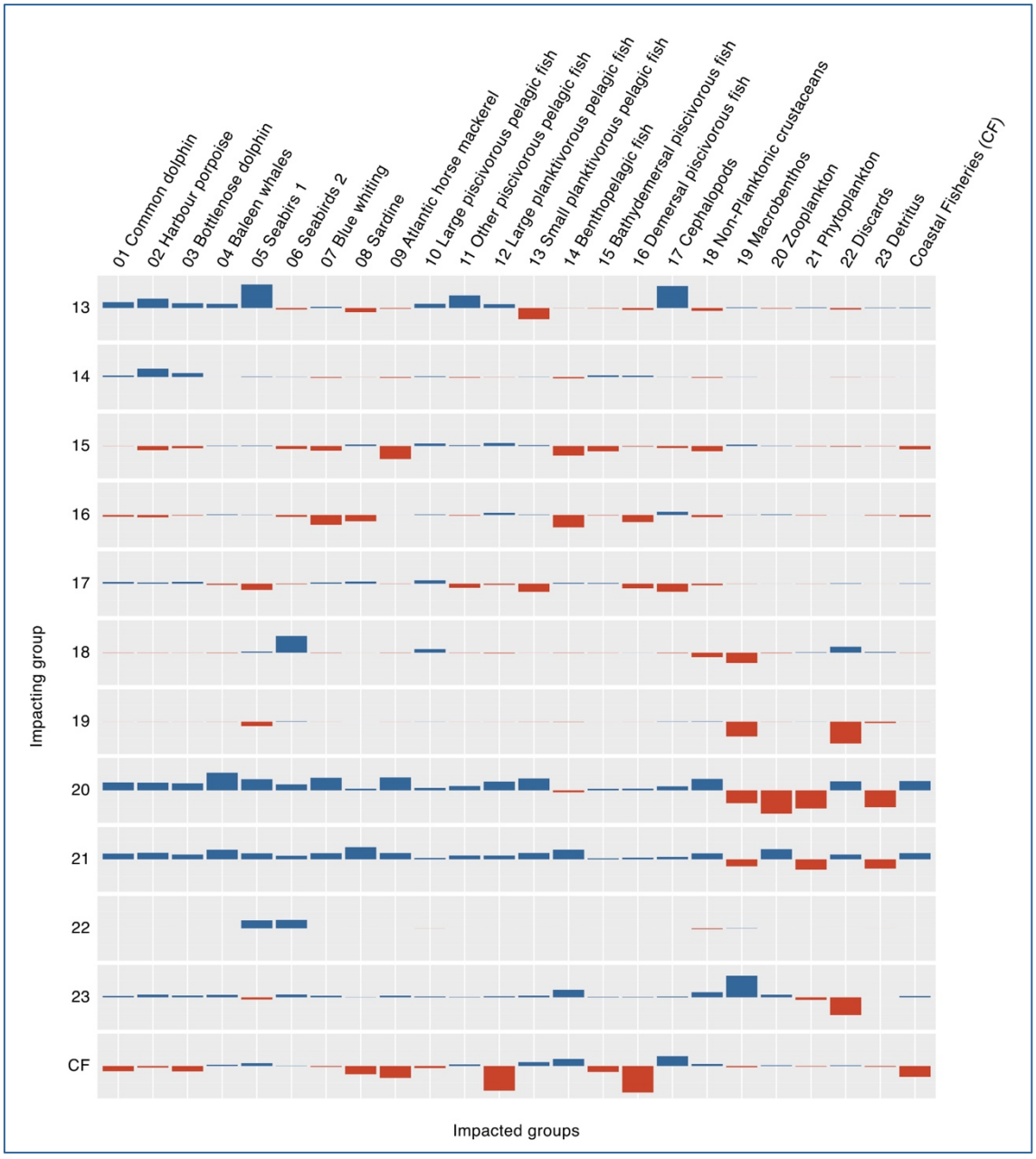


Figure 5.3 continued. *Mixed Trophic Impact (MTI) plot of the 2005 Rías Baixas shelf ecosystem. The plot indicates the relative impacts caused by the impacting functional groups (rows) on the impacted functional groups (columns). Blue boxes indicate positive impacts whereas red boxes show negative impacts. The size of the box shows the degree of the impact with bigger boxes showing more important impacts. The functional groups are: 13: Small planktivorous pelagic fish; 14: Benthopelagic fish; 15: Bathydemersal piscivorous fish; 16: Demersal piscivorous fish; 17: Cephalopods; 18: Non-planktonic crustaceans; 19: Macrobenthos; 20: Zooplankton; 21: Phytoplankton; 22: Discards; 23: Detritus and CF: Coastal Fisheries.*

5.4.2.Fitting the model to time series

The automated stepwise fitting procedure analysed 398 hypothetical models (Table 5.3). This process was used to choose the model with the lowest AICc and the lowest SS for each group of hypothetical models, which corresponded to the best fit for that particular group. The model with the best fit (lowest AICc = 16.6) was achieved when trophic effects and forcing function were included in the stepwise fitting procedure. This model included 11 trophic effects and 4 spline points in the environmental forcing function, and improved the fit by 58.7% compared to the baseline model (AICc = 59).

Table 5.3 *Results of the automated "stepwise fitting" procedure, showing the best fit for each of the eight groups of hypothetical models tested. The model with the best overall fit is highlighted in bold letters. N shows the number of hypothetical models tested in each group. The number of parameters (K) equals the number of vulnerability parameters (TE) plus the number of primary production spline points (PP). The fit improvement shows the percentage of reduction of SS compared to the baseline hypothetical model.*

Group	Hypothetical models	N	TE	PP	K	Min SS	AICc	Fit improvement
1	Baseline	1	0	0	0	323.4	59	-
2	Baseline + trophic effects	22	7	0	7	275	32.2	45.4%
3	Baseline + primary productivity anomalies	11	0	3	3	318.7	61.5	-4.2%
4	**Baseline + trophic effects and primary productivity anomalies**	**165**	**11**	**4**	**15**	**240.4**	**16.6**	**58.7%**
5	Fishing	1	0	0	0	339.9	71.9	-21.9%
6	Fishing + trophic effects	22	6	0	6	292.5	45.8	22.4%
7	Fishing + primary productivity anomalies	11	0	2	2	339.9	75.9	-28.6%
8	Fishing + trophic effects and primary productivity anomalies	165	6	2	8	266.5	26.4	55.3%

The best model was used to fit the data to the time series covering the period from 2005 to 2017. In general, the historical biomass trends for most of the functional groups included in the time series were well reproduced by the model (Figure 5.4). Comparing the observed biomass data with the model predictions, the functional groups with the best fit were sardine, Atlantic horse mackerel and bathydemersal piscivorous fish. The uncertainty addressed with the Monte-Carlo simulations was lowest for Atlantic horse mackerel, small planktivorous pelagic fish and bathydemersal piscivorous fish, which showed very narrow confidence intervals throughout the time series period, and highest for demersal piscivorous fish (Figure 5.4). The best fitting model reproduced catch trends

differently depending on the functional group. For instance, benthopelagic fish, bathydemersal piscivorous fish and cephalopods were the functional groups for which the predicted catches better replicated the observed trends, whereas catches were underestimated or overestimated for other functional groups (Figure A2.3).

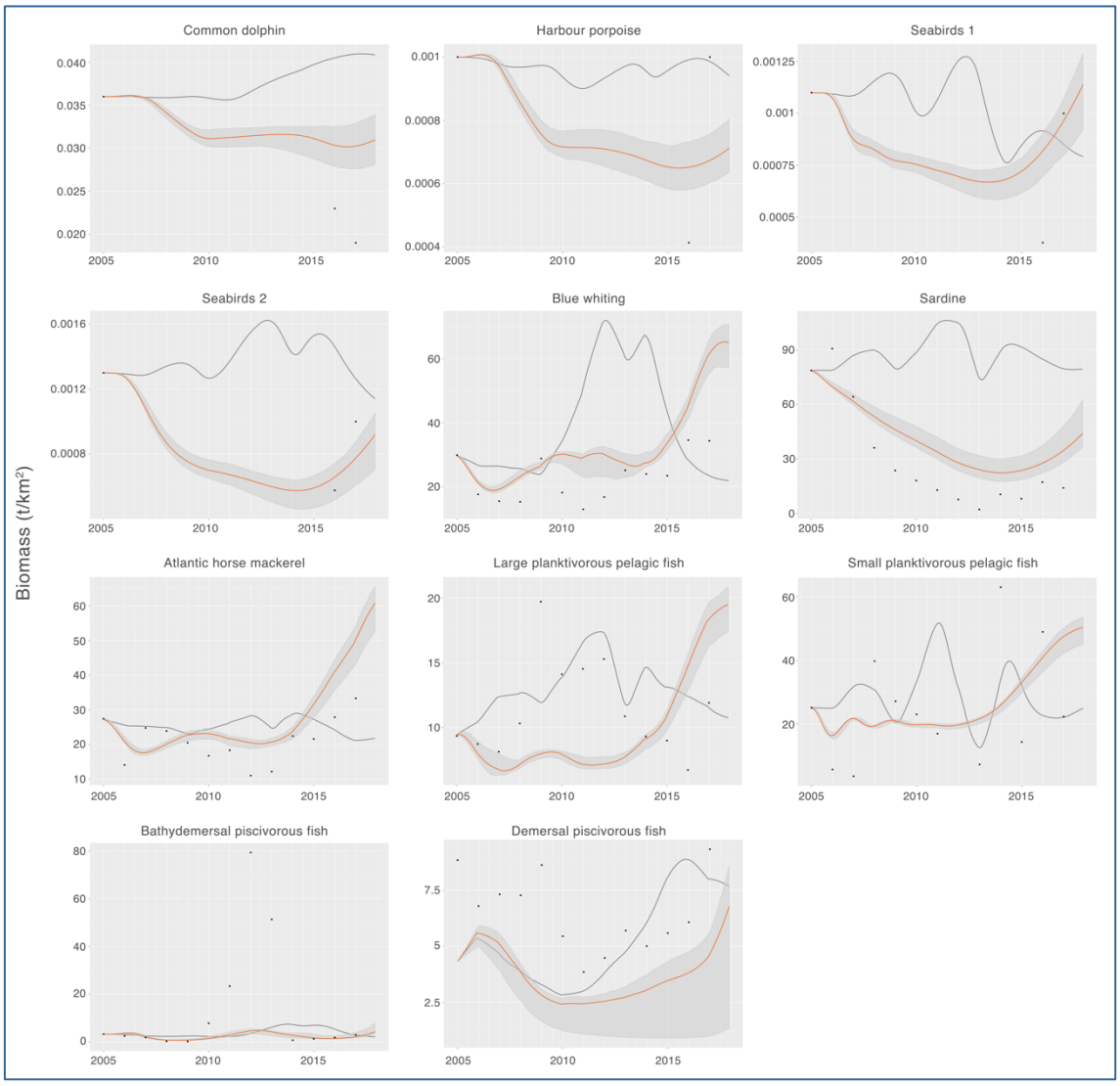


Figure 5.4 *Biomass trends obtained for the Ecosim model prior to the automated stepwise fitting process (grey line) and the model with the lowest SS and lowest AICc (orange line). The grey shaded area represents the 5th and 95th percentiles obtained during the Monte-Carlo simulations. Black dots show the observed biomass.*

5.4.3.Analysing the forward simulations

The results of the 30-year forward projecting simulations, created to assess the impact of different fishing efforts on common dolphins, bottlenose dolphins and harbour porpoises, showed different results for the different species. The evolution of the relative biomass over the modelled period was assessed for these species under the nine scenarios (Figure 5.5). None of the models accounted for bycatch mortalities. In general, all three species showed a decreasing biomass trend in the simulations in which fishing effort was increased and a steady increasing trend in the FMSY scenario. Some particularities were found for each species.

5.4.4.Forward simulations for common dolphins

In general terms, the common dolphin's biomass was predicted to increase steadily in the base, same trend, no fishing and FMSY scenarios. However, this increase was lower if conditions were kept at a similar level to those found in 2017. Conversely, scenarios that simulated an increase in fishing effort, predicted mostly a decrease in common dolphin's biomass throughout the 30-year forward projecting simulation. In these cases, biomass was predicted to have halved by 2043 compared to the start of the simulation.

5.4.5.Forward simulations for harbour porpoises

Predicted biomass trends for harbour porpoises showed a similar pattern for most scenarios. With the exception of the FMSY scenario, which exhibited a steady increase in biomass throughout the 30-year forward projecting simulation, the predictions for this species showed an increasing trend until 2025 – 2030 followed by a decrease until the end of the forward simulation. Harbour porpoise relative biomass was predicted to be less than 1 at the end of the forward simulation in all scenarios except for the FMSY. The biggest decreases in biomass were shown by the no fishing, the same trend scenarios and when fishing effort was increased by at least 15%, for which relative biomass would be lower than 0.5 by 2043.

5.4.6.Forward simulations for bottlenose dolphins

Two contrasted general trends in bottlenose dolphin relative biomass could be identified throughout the nine 30-year forward projecting simulations. On the one hand,

biomass was predicted to increase at different rates in the four scenarios that simulated similar conditions to 2017 or a reduction in fishing effort. The most optimistic scenario, predicted a 4-fold biomass increase by 2043. On the other hand, the biomass was predicted to decrease in the scenarios with a more intense fishing effort, dropping to less than half the biomass of 2005.

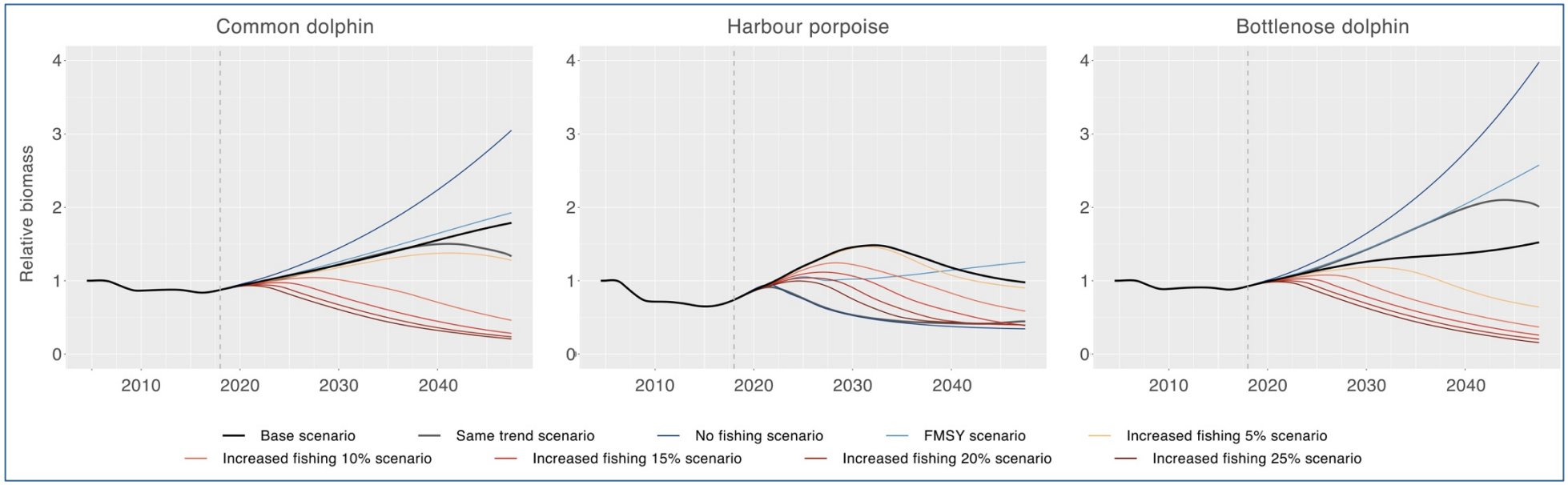


Figure 5.5 *Common dolphin, harbour porpoise and bottlenose dolphin relative biomass evolution between 2005 and 2043 under the nine future scenarios. The grey vertical dashed line represents the end of the time series period and the start of the 30-year forward projecting simulations. The black line to the left of the grey vertical dashed line represents the model with the best fit to the time series. The lines to the right of the dashed line represent the predicted relative biomasses under the different scenarios.*

5.4.7.Changes in diet composition

When comparing the evolution of the predicted diet composition between the different scenarios of common dolphin, harbour porpoise and bottlenose dolphins, three main patterns could be identified (Figure 5.6, Table 5.4 and Figures A2.4-A2.6). First, in those scenarios that kept conditions similar to 2017 or that simulated a decrease in fishing effort, the three species tended to show more diverse diets. In these cases, the predominant group were predicted to be demersal piscivorous fish for both dolphin species and Atlantic horse mackerel for harbour porpoises, although they were never predicted to exceed 60% of the diet composition. Secondly, diets tended to be less varied when the fishing effort was increased. In the most extreme cases, common and harbour porpoises were predicted to feed only on one functional group. Thirdly, increasing the fishing effort resulted in common dolphins and harbour porpoises, and to a lesser extent bottlenose dolphins, feeding almost exclusively in small pelagic planktivorous fish.

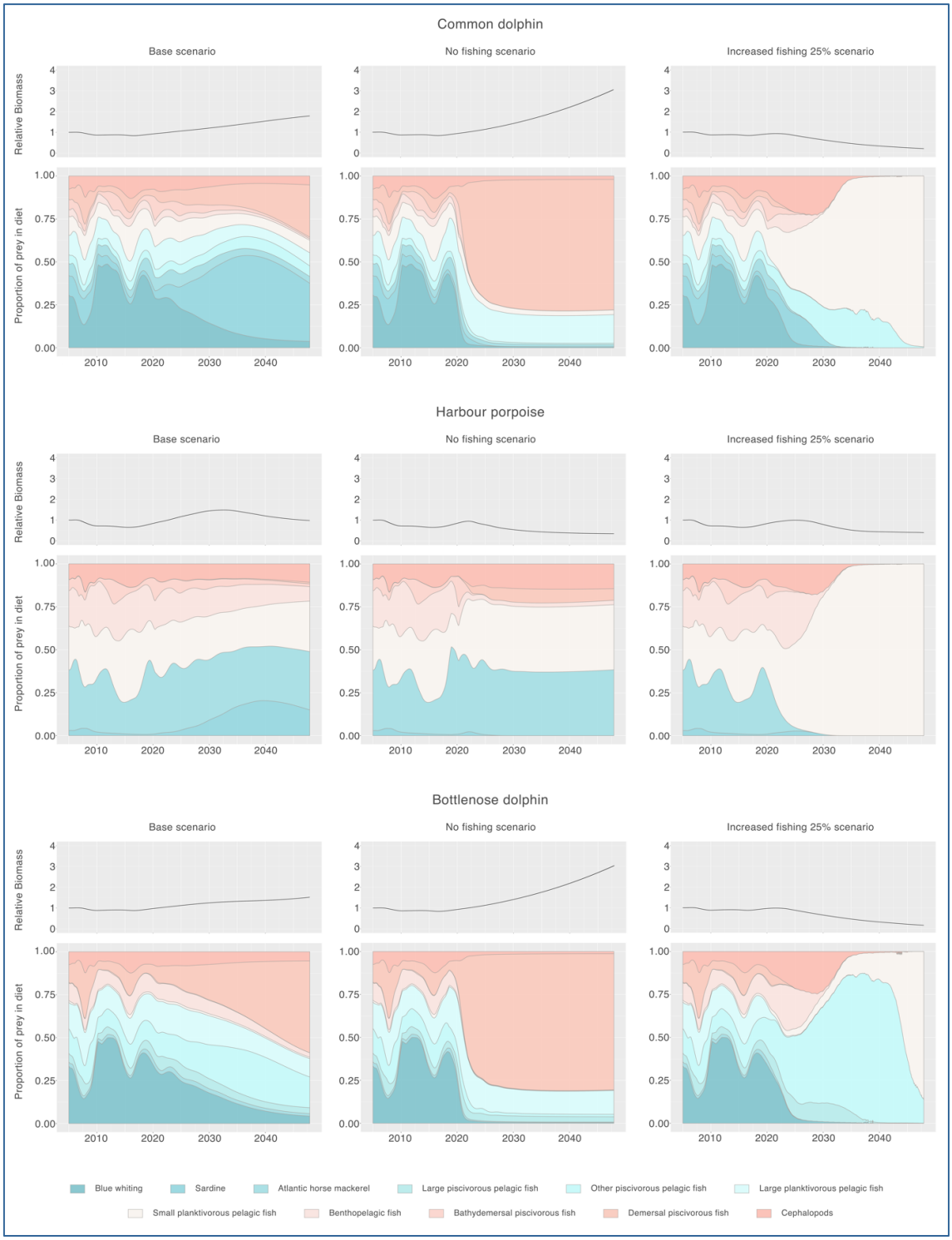


Figure 5.6 *Evolution of the contribution of the different functional groups in the diet of common dolphins, harbour porpoises and bottlenose dolphins for the base, no fishing and increased fishing 25% scenarios. The black lines on the graphs above show the common dolphin's relative biomass trends for each scenario.*

Table 5.4 *Percentage of contribution of the different functional groups (only the most relevant functional groups are shown) to the diet of common dolphin, harbour porpoise and bottlenose dolphin at the end of each scenario. The group with a higher percentage is shown in bold letters. Abbreviations can be understood as follows: S: Sardine; AHM: Atlantic horse mackerel; LPPF: Large piscivorous pelagic fish; OPP: Other piscivorous pelagic fish; LPLP: Large piscivorous pelagic fish; SPLP: Small piscivorous pelagic fish; BP: Benthopelagic fish; BDP: Bathydemersal piscivorous fish; DP: Demersal piscivorous fish; C: Cephalopods.*

	Common dolphin						Harbour porpoise					Bottlenose dolphin						
Scenario	S	OPP	LPLP	SPLP	DP	C	S	AHM	SPLP	BP	C	LPPF	OPP	LPLP	SPLP	BP	DP	C
Base	**33.8**	6.2	7.6	7.3	30.5	5.2	14.9	**34.0**	29.4	8.5	10.8	3.5	17.9	10.7	0.8	2.5	**53.4**	5.4
Same trend	0.0	10.3	1.0	22.4	**48.4**	15.0	0.0	1.6	**63.4**	12.4	21.7	6.0	19.9	0.9	1.7	2.8	**57.6**	10.3
No Fishing	0.0	0.8	16.6	2.7	**75.9**	2.0	0.0	**38.4**	37.9	2.5	14.4	3.1	1.4	13.9	0.2	0.1	**79.3**	1.3
FMSY	0.0	2.0	28.8	8.2	**44.0**	5.5	0.0	**57.4**	28.2	3.2	9.8	4.3	4.1	28.1	0.6	0.8	**53.6**	4.0
Increased Fishing 5	**57.3**	11.0	0.2	14.2	0.0	9.3	16.0	0.7	35.1	**36.2**	12.0	6.3	**48.1**	0.4	2.4	25.8	0.0	14.5
Increased Fishing 10	0.7	19.7	0.1	**58.3**	0.0	20.0	0.1	0.0	**83.4**	1.4	15.0	11.0	**58.4**	0.2	6.7	1.2	0.0	21.5
Increased Fishing 15	0.0	20.3	0.0	**78.4**	0.0	1.0	0.0	0.0	**99.3**	0.0	0.7	2.6	**83.0**	0.0	12.4	0.0	0.0	1.5
Increased Fishing 20	0.0	10.9	0.0	**88.8**	0.0	0.2	0.0	0.0	**99.9**	0.0	0.1	0.3	**75.7**	0.0	23.5	0.0	0.0	0.6
Increased Fishing 25	0.0	0.6	0.0	**99.4**	0.0	0.0	0.0	0.0	**100.0**	0.0	0.0	0.1	13.6	0.0	**86.2**	0.0	0.0	0.0

5.5. *Discussion*

Food-web dynamics models can help elucidate the extent of operational and ecological impacts of fisheries on cetaceans, as a first step towards more effective ecosystem conservation and management plans. In this regard, findings of this study provide insights on the ecological effects of fisheries on common dolphins, bottlenose dolphins and harbour porpoises in a coastal area, impacted by fishing activities, and highlight the applicability of EwE models to cetacean conservation. This work could serve as a starting point to develop comprehensive tools that could be used to better realise an ecosystem approach to fisheries management, while ensuring the conservation of top predators.

5.5.1. Assumptions and limitations of the model

The 2005 and 2017 Ecopath models and the time series used in this study were built prioritising the best available local data. High resolution abundance data were obtained for common dolphin, harbour porpoise and both seabird functional groups for the last two years of the simulation. However, a complete biomass time series for these species could not be obtained due to the lack of regular biomass and population trend assessments in the area prior to 2015. Similarly, bottlenose dolphin were not included in the time series due to the lack of data on the species abundance in the area between 2005 and 2017. Another limitation of the models was that 70% of the fish functional groups resulted from aggregating several species with similar trophic ecology, which could have led to an underrepresentation of species interactions (Alexander et al. 2015). Additionally, biomass estimates and catches for the fish and cephalopods functional groups were obtained from official regional landing statistics, potentially leading to an underrepresentation of the non-commercial species. However, commercial species comprised 98% and 90% of the demersal and pelagic fish communities' biomass, respectively (Fariña et al. 1997; Santos et al. 2013), confirming the representativeness of the fish and cephalopod functional groups used in this study. A further potential side effect of using official landing statistics is that they tend to underrepresent real catches (Coll et al. 2014), and therefore, findings for the fish and cephalopod functional groups should be considered carefully. However, in the absence of more reliable data, regional

landing statistics were the best local available data to use as input parameters for both Ecopath models and Ecosim time series.

Another constraint relates to the Ecosim dynamic simulations. These simulations did not address the potential real diet variations over time. However, since the dynamic simulations covered 13 years, local, quantitative diet studies conducted in a similar time frame to the present study were prioritised (Chapter 4), and assumed to be representative for the whole period. Despite these limitations and pitfalls, Ecopath with Ecosim proved to be a useful tool to represent the time-dynamic variations of the Rías Baixas shelf ecosystem and to assess the impact of fishing activities on marine top predators.

5.5.2.Time series fitting

The duration of the time series period was determined by the Prestige oil spill, that occurred in November 2002. The starting point of the dynamic simulations was set to 2005, to minimize the influence of the oil spill in the ecosystem dynamics and to focus on the effects of fishing activities on common and bottlenose dolphins, harbour porpoises and the ecosystem.

The best model explained 59% of the variability of the data and suggested that trophic interactions were the main driver influencing the Rías Baixas shelf ecosystem. These results are in line with what has been seen in other areas (Coll et al. 2008; Corrales et al. 2017). The trophodynamic model captured the overall biomass and catches variations over time for most functional groups. However, it was unable to reproduce the fluctuating biomass trend or the observed catches of small and large planktivorous pelagic fish. This could be explained because these functional groups included species such as the European anchovy (*Engraulis encrasicolus*) and the Atlantic mackerel (*Scomber scombrus*), which may be subjected to migratory and seasonal patterns that extend beyond the scope of the area studied here (Uriarte et al. 1996; Murta et al. 2008). Additionally, yearly fluctuations have been documented for small pelagic fish in other areas (Coll et al. 2006; Lindegren et al. 2013; Van Beveren et al. 2016). These have been linked to recruitment variability determined by environmental factors such as upwelling intensity and density-dependent processes (Borja et al. 2008; Lindegren et al. 2013;

Bakun et al. 2015), ultimately affecting fisheries (Uriarte et al. 1996; Van Beveren et al. 2016). The uncertainties addressed with the Monte-Carlo simulations showed a narrow confidence interval around the model predictions with a slight increase at the end of the time series period for most groups, giving strength to the prediction outcomes.

5.5.3. Analysing the scenarios

The 30-year forward projecting simulations highlighted the vulnerability of common dolphins, bottlenose dolphins and harbour porpoises to fishing activities. The model drew different general predictions for harbour porpoises and both dolphin species, dividing the three cetaceans species into two groups. In this regard, harbour porpoise biomass was predicted to decrease in all scenarios except when fishing effort was set to ensure MSY, whereas common and bottlenose dolphins showed increasing trends for all scenarios in which fishing effort was not increased. This became especially apparent in the no fishing scenario, which predicted a biomass increase for both dolphin species, but forecasted the biggest decrease in harbour porpoise biomass. With no fishing boats operating in the area and an increase in bottlenose dolphins biomass, other mechanisms such as interference competition or trophic competition between these species could take place (Spitz et al. 2006; Fernández et al. 2013; Méndez-Fernandez et al. 2013), despite the spatial separation that both species show in the area (Díaz López and Methion, 2018), and cause the decrease of this small cetacean.

Similarly, both same trend and base scenarios predicted an increase in common and bottlenose dolphin biomass but a decrease for harbour porpoise. Accurate data on fishing effort and catches in Galicia are difficult to obtain (Villasante et al. 2010). As a result of the CFP, the European Union urged Member States to adjust their fishing capacity to the fishing opportunities over time by decommissioning specific types of fishing vessels (EC, 2002). However, these measures have been proven insufficient due to inadequate methods to calculate the real fishing effort and capacity of the fleets, ineffective implementation of the measures to reduce the fishing effort, and misreporting of fishing power (European Court of Auditors, 2011; European Union, 2019). These aspects could explain inconsistencies found in the regional statistics (Xunta de Galicia, Conselleria do Mar, 2020a,b) that showed an increasing trend for landings

between 2005 and 2017, while the number of boats and the fishing power decreased steadily (Figure A2.1). Additionally, illegal, unreported and unregulated (IUU) fishing has been estimated at around 40% in North-West Spain (Villasante et al. 2015), hampering the understanding of the effects of fisheries on the ecosystem (Coll et al. 2014). Since fishing effort and catches included in this study come from official statistics, IUU fisheries were not accounted for, and as a consequence, these two scenarios might be overly optimistic when predicting cetaceans biomass throughout the simulation(s).

Only the FMSY scenario suggested that achieving the CFP objective of exploitation at MSY level would also benefit the small cetaceans in the Rías Baixas shelf ecosystem. However, a number of assumptions were made here. First, MSY was assumed to be constant throughout the simulation and therefore, a constant fishing mortality value was applied to this scenario, not accounting for probable future changes that may occur as a result of fluctuating environmental conditions or management decisions, which could result in substantially different results (Serpetti et al. 2017). Second, although it seems that adopting an MSY approach to fisheries management would be a first step in the right direction, this would not necessarily ensure the conservation of the species and the ecosystem (Moore, 2013; Prellezo and Curtin, 2015). Traditional MSY approaches build on single stock fisheries management methods and aim to obtain the maximum sustainable yield of different fish stocks. However, they do not consider fish stocks as part of an ecosystem, failing to capture the multispecific nature of ecosystems, and the relationships among the different trophic groups (Walters et al. 2005). Recently, multispecies MSY approaches have been developed to account for the interactions between different fish species in mixed fisheries (Stäbler et al. 2016; Thorpe, 2019). However, these might not be sufficient to ensure both sustainable fishing and ecosystem conservation (Legović et al. 2010; Smith et al. 2011).

5.5.4.Ecological effects of fisheries

Competition for resources between fisheries has been suggested to be one of the main drivers of cetacean disappearance in some areas (Bearzi et al. 2008; Piroddi et al. 2011), and has been suggested to occur in the North-East Atlantic (Lassalle et al. 2012; Santos et al. 2014). Additionally, spatial overlap between cetaceans and fishing activities

targeting shared resources (Díaz López and Methion, 2018; Chapters 2 and 3) and operational effects (López et al. 2002, 2003; Goetz et al. 2015) have been documented previously in the Rías Baixas shelf ecosystem. However, resource overlap is not a sufficient condition for interactions between cetaceans and fisheries, unless negative or positive impacts can be proven (Santos et al. 2014). In this regard, the MTI routine showed that fisheries had negative impacts on common dolphins, harbour porpoise and bottlenose dolphins. Fisheries also had a negative impact on functional groups that included key components of the cetaceans' diet, such as demersal piscivorous fish, large planktivorous pelagic fish and to a lesser extent, Atlantic horse mackerel and sardine. These results would support the idea that, indeed detrimental effects of fisheries on common dolphins, harbour porpoises and bottlenose dolphins are occurring in the area, as has been reported in other regions (Piroddi et al. 2011).

Although the MTI routine refers to a specific moment in time (in this case, the 2005 Rías Baixas shelf ecosystem, Valls et al. 2015), the scenarios with increased fishing effort, further explored the effects of the impacts of the fishing activities on the different cetacean species. These analyses involved two main aspects, decreasing cetacean biomass trends and a tendency towards less varied diets with increased fishing effort, suggesting an indirect effect of fisheries on all three cetacean species included in the model through their diet (Walters et al. 2005).

The predicted generalised collapse of most fish stocks caused by higher fishing efforts would result in a trend towards less varied diets for the three cetacean species, especially in the scenarios with higher fishing efforts. In these cases, their diet would be almost exclusively composed by small pelagic planktivorous fish, which is the keystone functional group of the Rías Baixas shelf ecosystem (Chapter 4). Small pelagic fish are energy rich species, capable of meeting the energetic requirements of common dolphins, harbour porpoises and bottlenose dolphins (Spitz et al. 2010). However, collapses in multiple fish stocks could hinder the ability of generalist cetacean species, such as the ones studied here, to switch to another prey if their preferred prey becomes unavailable (Jennings et al. 2001). As a result, they would depend upon a reduced group of fish species the recruitment and biomass of which have shown important fluctuations in the past, and are highly determined by environmental changes that influence primary

production (Cabrero et al. 2019). Indeed, climate change makes the evolution of primary productivity in shelf waters off North-West Spain in the coming years unclear, and some studies predict an important decrease (Pérez et al. 2010), while others predict an increase (Casabella et al. 2014). Therefore, these fluctuations, which were not considered in the 30-year forward projecting simulations, could strongly influence small pelagic fish, ultimately determining the presence of common dolphins, harbour porpoises and bottlenose dolphins in the area.

5.5.5.Fishing pressure, an additional threat on cetacean species

Currently, bycatch and marine traffic are major threats for cetacean populations in Galicia (Díaz López and Methion, 2018; Murphy et al. 2019). Bycatch, for instance, has been estimated to kill around 1,623 dolphins annually in Galicia (López et al. 2003). Of those, 3% are bottlenose dolphins, and 97% are small cetaceans, mostly common dolphins and, to a much lesser extent, harbour porpoises. These high bycatch numbers are already likely to exceed the limits set to achieve Good Environmental Status for common dolphins in Galician waters (Fernández-Contreras et al. 2010; Saavedra et al. 2018), and could have a similar impact on bottlenose dolphins and harbour porpoises (Llavona Vallina, 2018). Additionally, concerns raised about the increase in bycatch of common dolphins in the Bay of Biscay and adjacent areas, suggest that real bycatch mortality could be underestimated (Peltier et al. 2019; ICES, 2020), and led the European Commission to urge Spain to implement effective bycatch control measures (European Commission, 2020). However, these previous studies focussed only on the effects of bycatch and did not consider other aspects. Recently, fisheries were found to target fish species of intermediate-high trophic levels in the Rías Baixas shelf ecosystem, potentially altering ecosystem functioning and ultimately affecting top predators (Chapter 4). This aspect was further investigated in the present study, showing that the ecological effects of fisheries on common dolphins, bottlenose dolphins and harbour porpoises probably pose the major threat to these species, adding to already existing threats and seriously endangering their conservation.

The situation would be especially critical for harbour porpoise, as the 30-year forward projecting simulations predicted a decrease in the species biomass in almost all

scenarios. Harbour porpoises in the Iberian coast form a distinct ecotype and population (Fontaine et al. 2014). Despite a significant gene flow, genetic characteristics and habitat preferences differentiate the Iberian ecotype from other North-East Atlantic populations (Fontaine et al. 2014, Llavona Vallina, 2018). Additionally, the seasonality and the relatively small extension of the upwelling region along the Iberian coast, may reduce available food resources for the species and trigger emigration from the area (Fontaine et al. 2014). Although no competition between bottlenose dolphins and harbour porpoise has been reported in the Rías Baixas (Méndez-Fernandez et al. 2013; Díaz López and Methion, 2018), the present study predicts a reduction in fish resources due to fishing activities, which could ultimately lead to competition for prey, particularly among these two top predators. Harbour porpoise conservation status in the area is already delicate due to their reduced population size and the impact of boat traffic (Díaz López and Methion, 2018). The combination of previous findings with results of the present study pose a very pessimistic future for the species, in which the cumulative effect of boat traffic, intrinsic characteristics of the species, competition with other top predators and ecological effects caused by fisheries seriously threaten harbour porpoise conservation in the short term.

5.5.6.Implications for conservation and management

Several measures have been proposed to improve cetacean conservation in Galicia, including seasonal closures, operational changes, spatial redistribution of certain fisheries, the designation of Special Areas of Conservation or the development of improved legislative frameworks (López et al. 2003; Fernández-Contreras et al. 2010; Methion and Díaz López, 2018; Methion, 2019; Chapters 2 and 3). Most of these measures were suggested as a response to one threat to a particular species, and the reduction of fishing effort had never been seen as a priority. However, given the global impact of fishing on the Rías Baixas shelf ecosystem and the cumulative nature of the impacts caused by human activities on cetaceans, efforts to understand the functioning of ecosystems as a whole, the interactions between the different species within them and the impact of human activities, should be prioritised to develop effective conservation measures for both species and ecosystems (Jennings and Rice, 2011). In

this regard, different measures are suggested to improve the conservation of common dolphins, harbour porpoises and bottlenose dolphins in the area.

First, this study shows that exploitation of fish resources is altering the entire Rías Baixas shelf ecosystem in an unsustainable manner and this is already threatening top predator conservation. Therefore, immediate action should be taken to drastically reduce fishing effort in the area. This could be done by developing methods to accurately calculate the real fishing capacity of the fleet and by improving fishing effort monitoring (McCluskey and Lewison, 2008). Second, the study highlights the need to go beyond single stock management strategies in fisheries management. Fisheries play a major role in ecosystem dynamics, directly affecting the exploited stocks, but also indirectly impacting the rest of the species (Pauly et al. 2005). Therefore, future management strategies should focus on prioritising the conservation of the ecosystem and the species within it while ensuring the sustainability of fisheries. Understanding this also implies acknowledging the fact that all affected parties should be involved in the development of any management strategy or conservation measure in order to ensure their effectiveness. Third, the use of ecosystem based approaches, such as the one presented in this study, requires accurate and extensive datasets on the different interacting actors within the ecosystem (Plagányi and Butterwoth, 2004; Heymans et al. 2016). In this regard, efforts should be focused on obtaining regular scientific data on abundance and biomass of the different functional groups within an ecosystem and on obtaining accurate, reliable, and objective fisheries data, to develop comprehensive and effective conservation decisions and management plans. Fourth, as proposed in other studies (e.g. Cámara and Santero-Sánchez, 2019), a combination of compensation schemes and legal enforcement measures should be applied by the different administrations to help fishermen affected by any of the proposed measures and to encourage good practices in fishing activities. Fifth, global measures, such as the expansion of the first two Natura 2000 network sites and the marine area of the National Park to protect larger areas in coastal waters (Methion, 2019; Chapter 2) and waters above the continental shelf, should be considered in order to favour the protection of the ecosystem as a whole. Last, the conservation measures suggested in this study should be considered as an addition to the strategies already in place and to the ones proposed previously.

5.6. *Conclusions*

Although this work is circumscribed to a relatively small area, it provides a framework that could be extended to other impacted regions and species. Additionally, the scientific understanding of ecosystem dynamics has significantly improved due to the development of software packages such as EwE, and these can be used to enhance management and conservation decisions (Coll et al. 2015; Villasante et al. 2016). For instance, the present study is an example of how ecosystem information can be used to work towards cetacean conservation, and it provides a general framework that can be extended to other species, trophic groups or areas. However, extensive scientific data and accurate and reliable fisheries data are not always available, although they are critical to the understanding of ecosystem functioning, assessing the extent of the impact of human activities on the different species and ecosystems, and creating effective conservation and management frameworks. Findings of the study also show that fishing probably poses the most critical threat to common dolphins, bottlenose dolphins and especially harbour porpoises conservation in the Rías Baixas shelf ecosystem. The situation for these three species is critical and urges the different affected parties to find consensual global solutions to improve both ecosystem and species conservation while developing real sustainable fisheries.



Drawing by Núria Giralt

Chapter 6

General discussion

This last chapter discusses the main findings of the different studies in Chapters 2 to 5 and their contribution to the understanding of common dolphins ecology in Galician waters. The discussion looks into the interconnections among the different chapters and highlights the importance of comprehensive studies focussing on the ecology of the species to improve ecosystem and species conservation. In this regard, the chapter relates the information on common dolphins distribution and their ecological role in the ecosystem with the fishing activities in the area. With this information, the main issues of concern regarding common dolphin conservation are highlighted and discussed, and potential mitigation measures are proposed. The chapter also stresses the need to use interdisciplinary and integrative approaches to study common dolphin ecology and outlines the applicability of the approach used in this thesis to study other species and areas.

6.1. *Thesis overview*

Studies focused on the ecology of a species benefit from the combination of different research techniques and approaches to gather as much information as possible on as many aspects as possible. This information is key to obtaining a global picture of the species distribution, habitat use, foraging ecology, as well as of its relationships with the surrounding ecosystem. In a world where human activities are causing serious impacts on marine species and ecosystems (Halpern et al. 2008; Pompa et al. 2011), understanding cetacean ecology is fundamental in order to assess the impact of human activities on them, and can be a very useful tool to promote appropriate measures to ensure their conservation and that of the surrounding ecosystems (Estes et al. 2016). This is of particular interest in Galicia, where several species of cetaceans are affected by the effects of bycatch and presumably by competition for resources caused by widespread and intense coastal fishing activities. In this regard this thesis aimed to look at the ecology of common dolphins by combining different modelling approaches in an ecosystem context. Additionally, this thesis evaluated the impact of coastal fisheries on common dolphins with the ultimate aim of reviewing and suggesting measures and strategies to improve management and conservation of the species.

As described in Chapter 1, Galicia is a very important region for fisheries at both a national and European scale. At the same time the area shows a high cetacean biodiversity. Therefore, the region provides a unique opportunity to use an interdisciplinary approach to study the ecology of common dolphins, and to assess its role in the ecosystem and the effects of fishing activities on the species. Previous work has looked into specific aspects of common dolphins biology, including distribution and habitat use (López et al. 2004; Spyrakos et al. 2011), causes of strandings (López et al. 2002), interaction with specific fisheries (López et al. 2003; Fernandez-Contreras et al. 2010; Goetz et al. 2014), the environmental status of the species (Saavedra et al. 2018), and trophic interactions between common dolphins and fish species (Saavedra, 2017). Despite these efforts, there are still gaps in the knowledge about common dolphins ecology and their role within Galician coastal water ecosystems, which highlights the need to develop integrative approaches.

Therefore, this work builds on the information provided by previous studies and integrates it with the data collected in the area over a four year period (2014 – 2017). This integration creates an interdisciplinary approach that provides baseline information on common dolphins ecology and interactions with fisheries in Galicia, in an ecosystem context. Furthermore, this thesis considers several interconnected aspects in the different chapters, each one adding to the other, to create a more comprehensive understanding of common dolphin ecology and conservation. In addition, the intense data collection effort conducted year round and completing 273 dedicated boat surveys over four years, provides an important data background that strongly supports the different modelling frameworks and enriches them by taking into consideration seasonal variability. The exhaustive data collection supports a series of integrative studies. These start by exploring the spatial distribution of common dolphins. Additional aspects such as overlap with fisheries, trophic interaction within the ecosystem, and competition for resources with fisheries, are progressively added to obtain an overall and comprehensive picture of the ecology of the species and the major issues of concern for its conservation. This approach is used to suggest ways to strengthen and enhance existing measures for common dolphin conservation and improved fisheries management in the area. The different steps of the integrative approach used in this thesis are discussed in the following sections.

6.2. *Common dolphin's distribution and habitat use*

The work presented in this thesis showed that common dolphins can be mostly found in coastal waters above the continental shelf in the Rías Baixas region, especially in waters 100 to 200 metres deep. The findings also outlined that the rias do not provide suitable conditions for the species (Chapters 2 and 3). This is in agreement with previous studies conducted in Galicia (Spyrakos et al. 2011). Two models (ENMs in Chapter 2 and GAMs in Chapter 3) were used to assess the distribution of the species according to a series of environmental and topographic parameters. Despite using different methodologies (presence-only data in Chapter 2 and presence/absence data in Chapter 3), both models showed similar results overall, that were consistent with common dolphins observation at sea. Presence-only studies require larger data sets to achieve higher model accuracy

(Hernandez et al. 2006). Since both models showed similar results, this suggests that the number of records of common dolphins was large enough to generate an accurate presence-only distribution model. This highlights the importance of the exhaustive data collection carried out in this study over a four year period to obtain trustworthy species distribution models.

Among the environmental variables included in the different models, SSS, SST, tide level and bottom slope were found to have an influence on the distribution and habitat use of the species (Chapters 2 and 3). In particular, the models highlighted waters above the continental shelf, which had higher SSS and lower chlorophyll a level, as an optimal habitat for common dolphins. This is in agreement with field observations, during which the species was most frequently seen in pelagic areas, and seemed to avoid the rias, especially their innermost parts. (Chapters 2 and 3). However, rather than directly determining common dolphin distribution and habitat use, environmental and topographic variables more likely influence the distribution of their prey (Selzer and Payne, 1988; Giannoulaki et al. 2017; Chapters 2 and 3). In this regard, common dolphins would probably be attracted to areas where their prey aggregate. For instance, common dolphin diet in the region is mainly composed of pelagic and benthopelagic species that are most commonly found in waters with higher SSS (Abaunza et al. 2008; Miesner and Payne, 2018). With some nuances, these findings are supported by several studies conducted in other regions (Selzer and Payne, 1988; Cañadas and Hammond, 2008; Cañadas et al. 2009; Giannoulaki et al. 2017; Correia et al. 2019). However, there is some variability among regions that may be a consequence of different combinations of topographic and oceanographic phenomena and environmental variables that generate the optimal conditions for prey aggregation.

Understanding the distribution and habitat use of top predators, such as common dolphins is key to studies that aim at elucidating the ecology of the species. In this regard, the findings of Chapters 2 and 3 concerning the factors determining the distribution of this small cetacean provide valuable information in three ways. First, in a descriptive manner, they highlight specific areas that are important for the species, improving local scientific knowledge and allowing for comparison with other regions.

Second, the information provided can be compared with information on fishing effort or the distribution of other human activities to understand the exposure of the species to human impacts. Third, this information can be combined and used to evaluate existing, and promote new conservation measures and management plans, with the ultimate aim of reducing detrimental interactions with human activities and enhancing species conservation.

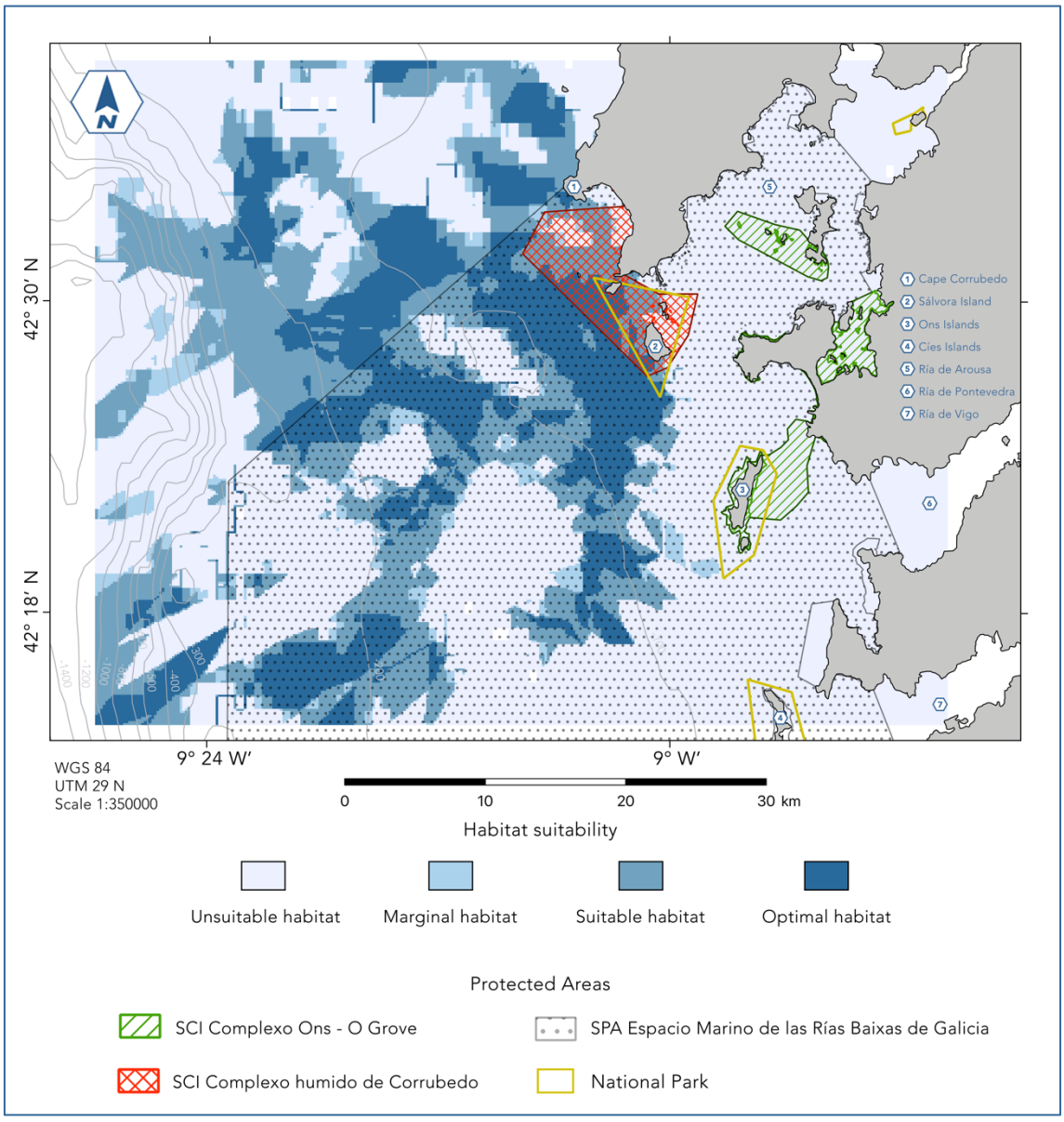


Figure 6.1 *Habitat suitability map showing the spatial overlap between the optimal and suitable habitats for common dolphins and some of the protected areas in the Rías Baixas region. Note the close proximity of the most suitable habitats for the species with the SCI Complexo humido de Corrubedo and the Atlantic Islands National Park area around Sálvora Island.*

In this regard, the habitat suitability study in Chapter 2 showed the most and the least suitable habitats for the species, providing information about its potential distribution. This information was used to assess the degree of overlap between the most suitable habitats for the species and the already existing protected areas (Figure 6.1) (Embling et al. 2010; Methion, 2019). This in turn, can be used to explore the need to extend the boundaries of these areas or the need to change the protection level of the common dolphin within these areas. For instance, the northernmost area of the Atlantic Island National Park around Sálvora Island and the SCI Complexo humido de Corrubedo, include, and are next to, optimal habitats for common dolphins (Figure 6.1). However, none of the protected areas list common dolphins as one of the species of concern within their limits. As these are important areas for this species, this information can be used to support changes in both protected areas. These changes could entail the inclusion of the common dolphin as one of the protected species in the SCI or the expansion of the marine area of both protected sites in order to cover a broader section of the most suitable habitats for the species.

6.3. *Ecosystem structure and role of the common dolphin*

Marine ecosystems are dynamic systems determined by the physical characteristics and the oceanographic processes of the geographic area where they are located, which influence the biotic processes in them (Cury et al. 2008). These, in turn, influence species distribution (Elith and Leathwick, 2009). In this regard, information obtained in Chapters 2 and 3 provided geographical limits for the most suitable habitats for common dolphins (Figure 6.2). This information was used to set the extension of the area that would be used, in a second step, to model the ecosystem dynamics and the ecological role of this cetacean species in continental shelf waters off the Rías Baixas (Chapter 4). This highlighted the importance of integrating information from different sources (dolphin presence data collected in the field and information about spatial distribution and habitat suitability), to build a robust approach to study common dolphins ecology.

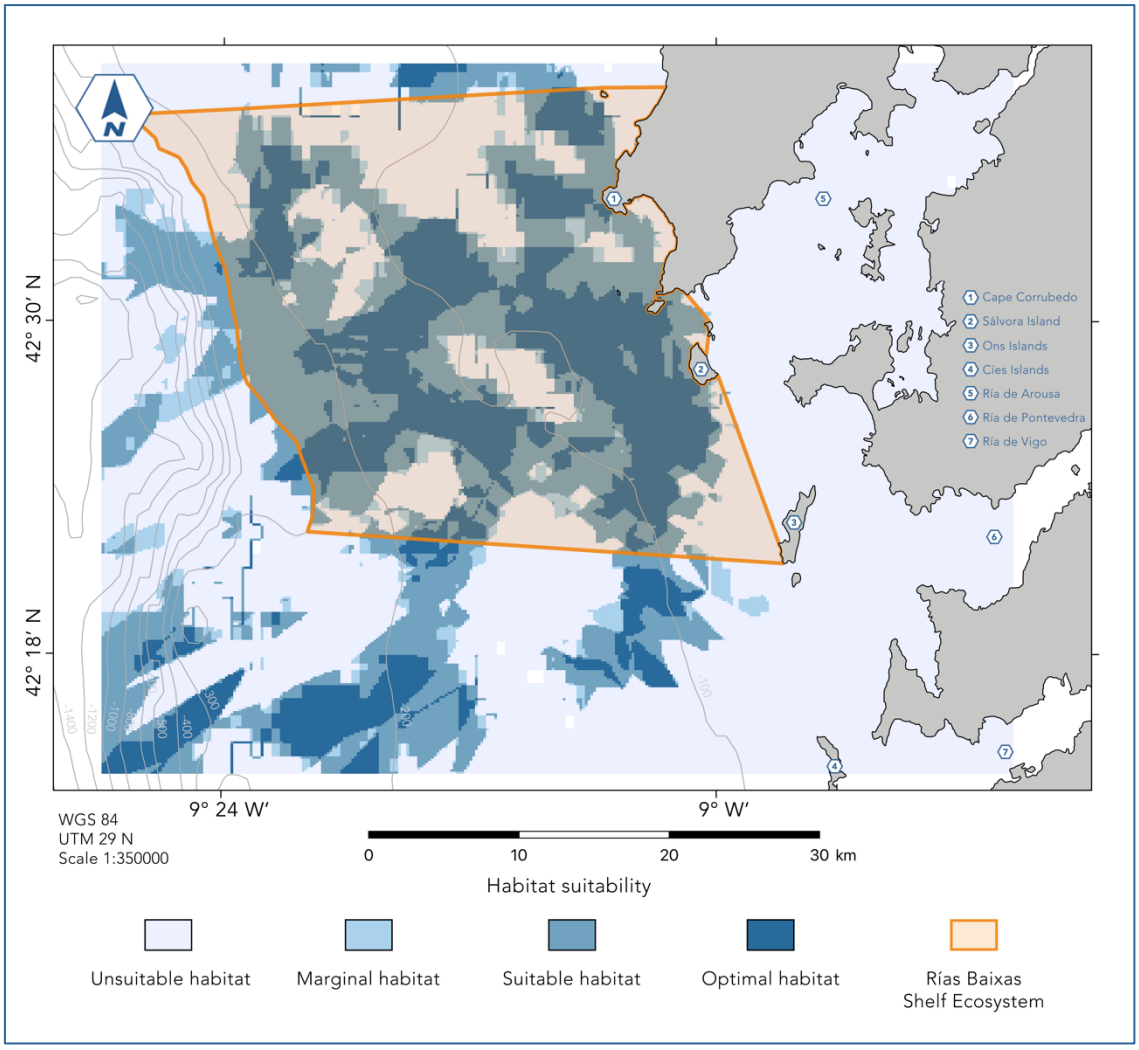


Figure 6.2 *Map showing the overlap between the area chosen to model the Rías Baixas shelf ecosystem and common dolphins optimal and suitable habitats. Protected areas were not included in the figure to avoid overcomplicating the map.*

In this second step, EwE proved a useful tool, not only to create a representation of the trophic dynamics of the Rias Baixas shelf ecosystem, but also to provide new insights to common dolphins ecology in the area. Indeed, the mass-balance model created using EwE showed that this small cetacean is a top predator in an ecosystem with a wasp-waist control, that shares characteristics of both upwelling and estuarine areas worldwide (Chapter 4). Additionally, the system included small pelagic planktivorous fish, blue whiting and zooplankton as main structuring groups, determining the main energy pathways from lower to higher trophic levels and between the pelagic and the non-pelagic environments (Figure 6.3; Chapter 4). These results are in line with previous findings, which highlighted the importance of small pelagic fish in upwelling systems,

where they act as energy-rich species that efficiently transfer energy from phytoplankton to cetaceans (Libralato et al. 2006; Lynam et al. 2017; Spitz et al. 2018). Interestingly, some of these structuring functional groups are essential components of the diet of common dolphins (Santos et al. 2013), and they represent a substantial part of the landed fish biomass in the area (Xunta de Galicia, Conselleria do Mar, 2020a). Hence, these results provide further insights into common dolphin ecology in Galician shelf waters, where they act as top predators, mostly depending on key and structuring functional groups of the ecosystem.

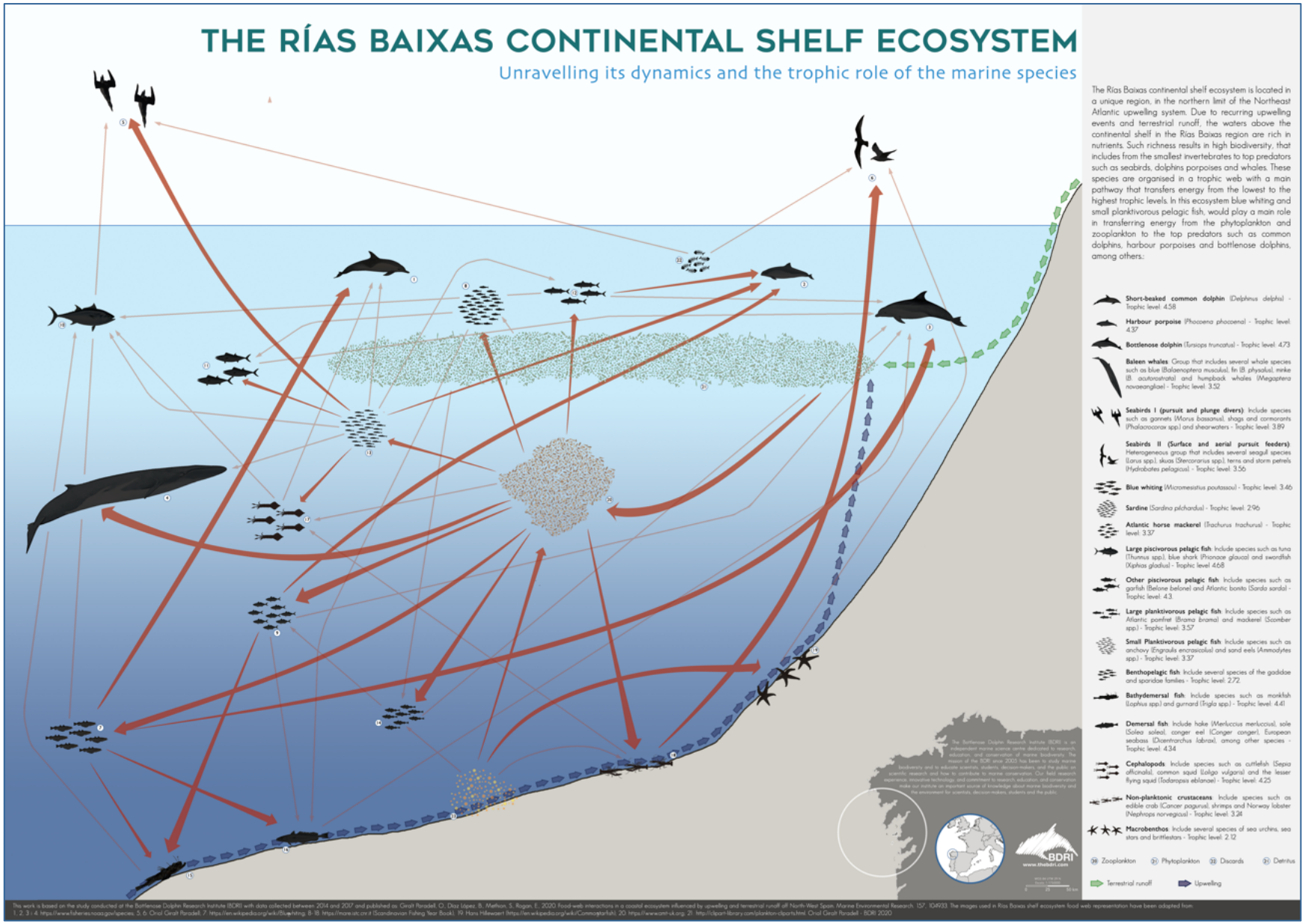

THE RÍAS BAIXAS CONTINENTAL SHELF ECOSYSTEM
Unravelling its dynamics and the trophic role of the marine species
The Rías Baixas continental shelf ecosystem is located in a unique region, in the northern limit of the Northeast Atlantic upwelling system. Due to recurring upwelling events and terrestrial runoff, the waters above the continental shelf in the Rías Baixas region are rich in nutrients. Such richness results in high biodiversity, that includes from the smallest invertebrates to top predators such as seabirds, dolphins porpoises and whales. These species are organised in a trophic web with a main pathway that transfers energy from the lowest to the highest trophic levels. In this ecosystem blue whiting and small planktivorous pelagic fish, would play a main role in transferring energy from the phytoplankton and zooplankton to the top predators such as common dolphins, harbour porpoises and bottlenose dolphins, among others.:
Short-beaked common dolphin (Delphinus delphis) - Trophic level: 4.58
Harbour porpoise (Phocoena phocoena) - Trophic level: 4.37
Bottlenose dolphin (Tursiops truncatus) - Trophic level: 4.73
Baleen whales: Group that includes several whale species such as blue (Balaenoptera musculus), fin (B. physalus), minke (B. acutorostrata) and humpback whales (Megaptera novaeangliae) - Trophic level: 3.52
Seabirds I (pursuit and plunge divers): Include species such as gannets (Morus bassanus), shags and cormorants (Phalacrocorax spp.) and shearwaters - Trophic level: 3.89
Seabirds II (Surface and aerial pursuit feeders): Heterogeneous group that includes several seagull species (Larus spp.), skuas (Stercorarius spp.), terns and storm petrels (Hydrobates pelagicus). - Trophic level: 3.56
Blue whiting (Micromesistius poutassou) - Trophic level: 3.46
Sardine (Sardina pilchardus) - Trophic level: 2.96
Atlantic horse mackerel (Trachurus trachurus) - Trophic level: 3.37
Large piscivorous pelagic fish: Include species such as tuna (Thunnus spp.), blue shark (Prionace glauca) and swordfish (Xiphias gladius) - Trophic level 4.68
Other piscivorous pelagic fish: Include species such as garfish (Belone belone) and Atlantic bonito (Sarda sarda) - Trophic level: 4.3
Large planktivorous pelagic fish: Include species such as Atlantic pomfret (Brama brama) and mackerel (Scomber spp.) - Trophic level: 3.57
Small Planktivorous pelagic fish: Include species such as anchovy (Engraulis encrasicolus) and sand eels (Ammodytes spp.) - Trophic level: 3.37
Benthopelagic fish: Include several species of the gadidae and sparidae families - Trophic level: 2.72
Bathydemersal fish: Include species such as monkfish (Lophius spp.) and gurnard (Trigla spp.) - Trophic level: 4.41
Demersal fish: Include hake (Merluccius merluccius), sole (Solea solea), conger eel (Conger conger), European seabass (Dicentrarchus labrax), among other species - Trophic level: 4.34
Cephalopods: Include species such as cuttlefish (Sepia officinalis), common squid (Loligo vulgaris) and the lesser flying squid (Todaropsis eblanae) - Trophic level: 4.25
Non-planktonic crustaceans: Include species such as edible crab (Cancer pagurus), shrimps and Norway lobster (Nephrops norvegicus) - Trophic level: 3.24
Macrobenthos: Include several species of sea urchins, sea stars and brittlestars - Trophic level: 2.12
Zooplankton
Phytoplankton
Discards
Detritus
Terrestrial runoff
Upwelling
BDRI
www.thebdri.com

Figure 6.3 (previous page) *Visual representation of the structure of the Rías Baixas shelf ecosystem. The figure shows the species interactions, the main transfers of energy (thick arrows) and the secondary transfers of energy (thin arrows) of the Rías Baixas shelf ecosystem.*

Another aspect to consider when studying the ecology of a species are human activities, such as fishing. Human activities have become important actors in ecosystems, directly and indirectly altering trophic dynamics, and should therefore be taken into consideration (Odum, 1975). In this regard, and as seen in other areas (Shannon et al. 2003; Coll et al. 2009a), the EwE model suggested that the Rias Baixas shelf ecosystem was subjected to intense fishing pressure, especially those species with a trophic level greater than III, such as blue whiting (Chapters 4 and 5). Indeed, these were also a fundamental component of the diet of common dolphins (Santos et al. 2013). Therefore, intense fishing pressure on these groups (≥ trophic level 3) could lead to direct and indirect competition for resources with this small cetacean.

A further aspect that could impact common dolphins ecology is related to the importance of small pelagic fish in the Rías Baixas shelf ecosystem. Populations of these fish species are highly affected by shifts in primary production (Pérez et al. 2010; Garrido et al. 2017; Cabrero et al. 2019). In Galician coastal waters, primary production primarily depends on terrestrial runoff and upwelling events (Torres et al. 2003). Despite some controversy about its extent, several studies agree that climate change is likely to affect both upwelling and rainfall regimes in Galicia (Pérez et al. 2010; Casabella et al. 2014; Lorenzo and Alvarez, 2020), which could consequently alter the primary production in the area (Bakun et al. 2015). As a result, and as predicted in other areas, these changes could lead to a reduction in small pelagic fish populations, which require very specific water temperature, upwelling intensity and primary production (Brochier et al. 2013; Bakun et al. 2015). These changes could be propagated through the food web, ultimately affecting common dolphins (Bakun et al. 2015).

In summary, the mass balance model of the Rías Baixas shelf ecosystem provided valuable insights into common dolphin ecology in several ways. First, the model placed the species in an ecosystem context, describing the characteristics that determine the system and that ultimately influence the species living in it. Second, the study identified

the role of common dolphins within the ecosystem and the trophic relationships with the other functional groups. Third, it implied that climate change and fisheries could indirectly cause detrimental impacts on common dolphins, by altering the abundance of their prey. Last, the study took information covering different aspects such as common dolphins diet (Santos et al. 2013), distribution and habitat suitability (Chapters 2 and 3), and fishing activities (Surís-Regueiro and Santiago; 2011; Vázquez-Rowe et al. 2011; Xunta de Galicia, Conselleria do Mar, 2020a,b). This information was combined in an integrative approach to obtain a more comprehensive understanding of the ecological role of common dolphins. Furthermore, this approach highlighted common ground between the distribution and the trophic models, as both showed an eventual vulnerability of common dolphins to fisheries that was further explored.

6.4. *Common dolphins and fisheries*

Interactions between cetaceans and fisheries can occur at several levels and, as seen in Chapter 1, they can have either a direct or an indirect effect (Plagányi and Butterworth, 2009). For operational effects to occur, some premises, such as spatial and temporal overlap between dolphins and fishing operations must be fulfilled (Kaschner et al. 2001; Brown et al. 2015). Ecological effects often entail competition for the same resources or competition for different resources mediated through ecosystem dynamics (Northridge, 2009). Due to the diverse nature of these interactions, studies that approach them from different angles are needed to fully understand their full extent. In this regard, findings of this thesis suggest that both types of interactions are occurring in Galician continental shelf waters. Indeed, the Rías Baixas shelf ecosystem model indicates that the ecosystem is subject to an intense fishing pressure on fish species in trophic levels III or higher (Chapters 4 and 5). This information suggests that indirect and/or direct competition for resources between common dolphins and fisheries is occurring. Furthermore, as will be discussed below, spatial overlap between operating fishing boats and common dolphins occurs in the area, providing an opportunity for direct interactions to take place (Chapter 3).

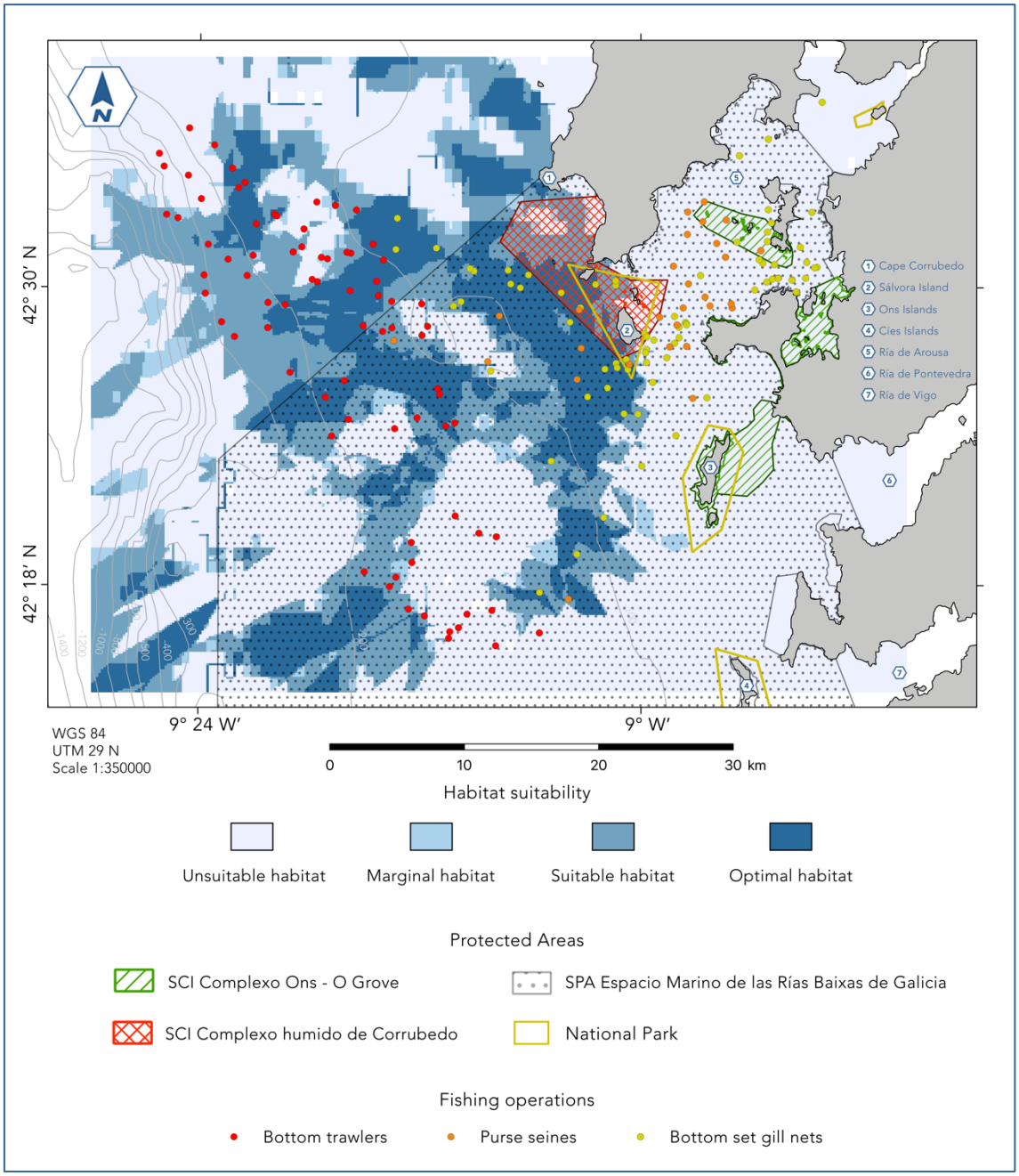


Figure 6.4 *Spatial overlap between common dolphins optimal habitats (Chapter 1), fishing operations and protected areas in the Rías Baixas continental shelf between 2014 and 2017.*

While spatial overlap does not always lead to operational interactions between common dolphins and fisheries, it is a prerequisite for its existence (Matthiopoulos et al. 2008). Therefore, the coexistence of different types of fishing vessels and techniques with common dolphin presence was explored in Chapter 3. The study showed that whereas co-occurrence of common dolphins and bottom-set gill nets and purse seines was not frequent, this small cetacean was regularly recorded in areas where bottom trawlers were

operating. This contrasts with findings in other regions (Breen et al. 2017), but it is in line with other studies conducted in Galicia (Fernandez-Contreras et al. 2010; Goetz et al. 2014). However, the addition of information on the distribution and habitat use of the species, provided a more detailed view (Figure 6.4), and complementary information to that provided by the studies focused on common dolphins bycatch. On the one hand, it confirmed the occurrence of spatial overlap between bottom trawler operations and common dolphins. On the other hand, it showed that bottom set gill nets were used in areas above the continental shelf that were considered optimal habitats for the species. These findings confirmed that the area meets the prerequisite of spatial overlap, which could lead to direct interactions between common dolphins and fisheries, especially trawl fisheries, as reported previously (Fernandez-Contreras et al. 2010; Goetz et al. 2014). Additionally, they suggested that these interactions could be detrimental for this small cetacean, as shown by other studies in Galicia (López et al. 2003; Fernandez-Contreras et al. 2010; Goetz et al. 2014) and in other regions (Morizur et al. 1999; Rossman, 2010; De Boer, 2012; Mannocci et al. 2012; Thompson et al. 2013). In these areas bycatch is considered the main threat to the species conservation (López et al. 2002; Peltier et al. 2016; Murphy et al. 2019).

Results of Chapters 2 and 3 confirmed that the area offers the opportunity for direct interactions between common dolphins and fisheries to occur. Additionally, Chapters 4 and 5 provided new insights on the ecological effects caused by fishing operations on this small cetacean. Previous studies reported that dolphins and fisheries take similar amounts of fish from the ecosystem in the area, and suggested that competition for resources could be taking place (Santos et al. 2014). The trophic mass-balance model of the Rías Baixas shelf ecosystem (Chapters 4 and 5) showed that fisheries were mainly targeting fish species of trophic level III or higher, which included fundamental components of common dolphin diet, such as blue whiting, horse mackerel, hake, mackerel and cephalopods (Santos et al. 2013; Marçalo et al. 2018). In addition, regional catch statistics in Ribeira harbour, the most important harbour in terms of landings in the area, showed that these species comprised approximately 93% of the landed biomass in 2017 (Xunta de Galicia, Consellería do Mar, 2020a). Furthermore, the mass-balance model showed that coastal fisheries exerted a negative impact on most of these fish and

cephalopods groups and on common dolphins (Figure 6.5), providing further evidence that ecological effects of fisheries on this small cetacean do occur in Galicia (Ulanowicz and Puccia, 1990).

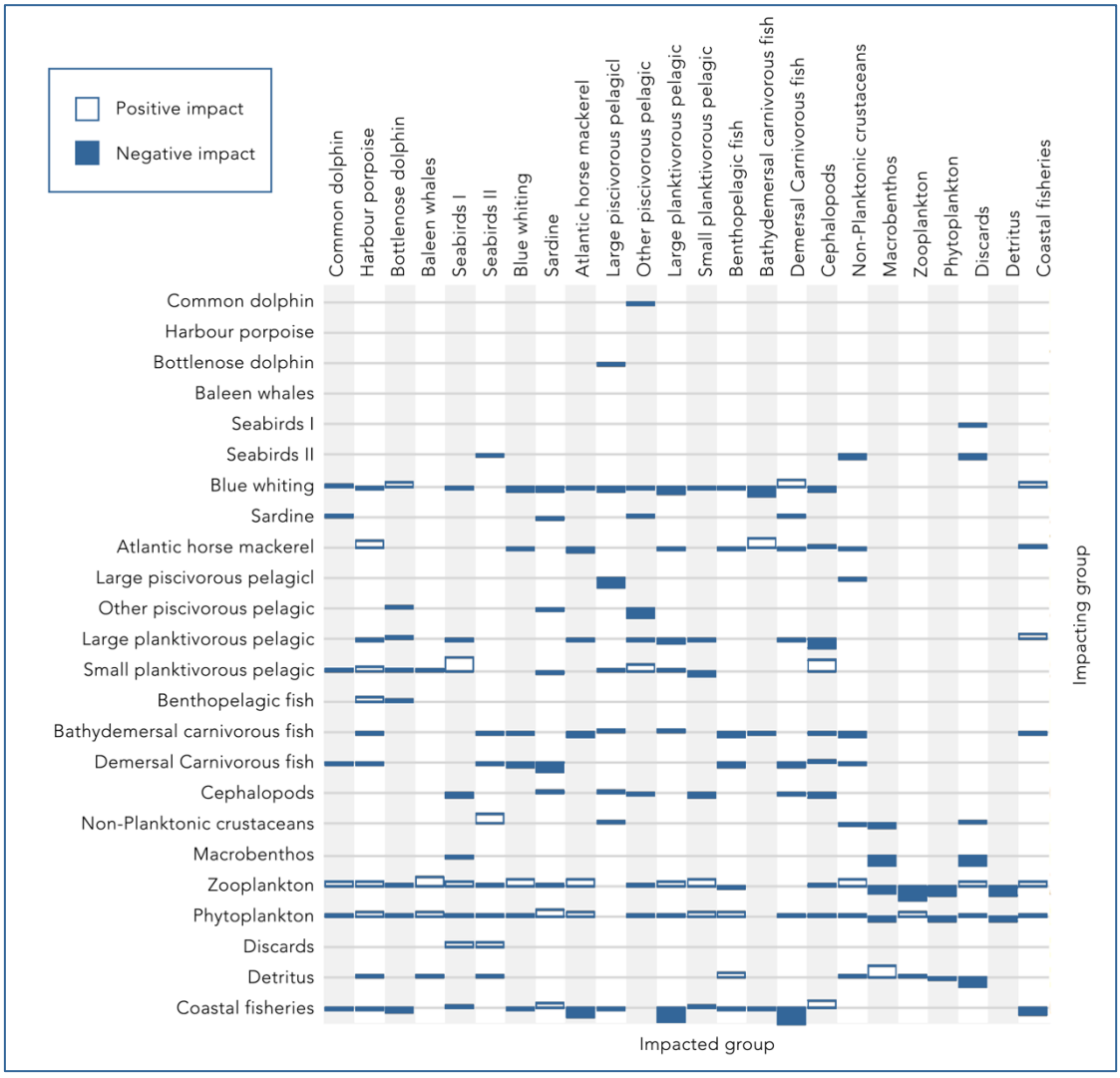


Figure 6.5 *The mixed trophic impact analysis of the 2017 Rías Baixas shelf ecosystem model shows the degree of impact of the different functional groups (rows) on all the functional group (columns). Blue rectangles show a negative impact and white rectangles show a positive impact.*

Building on previous studies in the area (López et al. 2002, 2003; Fernandez-Contreras et al. 2010; Goetz et al. 2014; Santos et al. 2014; Saavedra et al. 2018), and on findings of chapters 2, 3 and 4, 30-year forward projecting dynamic simulations were built in Chapter 5. These were used to analyse the potential ecological effects of fisheries on the Rías Baixas shelf ecosystem in nine possible scenarios under different fishing efforts. Findings of Chapter 5 suggest that ecological effects of coastal fisheries on common

dolphins, and other cetaceans such as harbour porpoises and bottlenose dolphins, do exist in Galicia. In this regard, fisheries and cetaceans would compete for the same resources and this could lead to a tendency towards less varied diets if fishing effort is increased. This competition could lead to a reduction in dolphin biomass, especially in scenarios with very high fishing effort. Similar consequences have been suggested in other areas such as the Bay of Biscay (Lassalle et al. 2012), the Mediterranean Sea (Piroddi et al. 2010), and in an extreme case, overfishing has been documented to be the cause of the disappearance of a common dolphins population in Greece (Bearzi et al. 2008). Previous studies highlighted bycatch as the most important threat that common dolphins are facing (López et al. 2003; Goetz et al. 2014; Peltier et al. 2019). Findings of this thesis however, stress that ecological effects of fisheries on common dolphins pose a severe threat at a population level, which has gone unnoticed so far.

As discussed earlier, human activities are becoming part of the ecosystem dynamics and therefore can and will influence the ecology of the species living in them (Odum, 1975). In addition, the cumulative nature of human impacts on marine ecosystems makes them likely to affect several aspects of the ecology of marine species at once (Halpern et al. 2015). In this regard, this thesis combines information from different approaches that analyse various characteristics of common dolphins, their relationships with the surrounding ecosystem and the effect of anthropogenic activities such as fisheries. Moreover, it generates an integrative framework to better understand common dolphin ecology and how anthropogenic activities, in particular fisheries, are affecting it and provides crucial information to be used in future conservation and management plans.

6.5. *Implications for conservation*

Marine ecosystems, especially those located in coastal regions, are affected by several human activities, which are altering them in unprecedented ways (Vitousek et al. 1997). As a consequence, marine species have to face the direct and indirect impacts of these activities, which often have cumulative effects on marine ecosystems and organisms (Davidson et al. 2012; Halpern et al. 2015). Studying the ecology of a species can also provide insights into the degree to which an ecosystem is impacted and highlights the conservation needs of both species and ecosystems. For instance, as top predators,

cetaceans are extremely sensitive to changes in the ecosystem dynamics (Moore, 2008) and to direct, indirect and cumulative effects caused by human activities (Davidson et al. 2012; Maxwell et al. 2013). Therefore, integrative approaches, such as the one presented in this thesis are crucial when working towards the conservation of marine species and ecosystems.

6.5.1.Identifying the major issues of concern

The present thesis applies different methodologies to study several aspects related to the ecology and conservation of common dolphins. All chapters build on current knowledge of the species in Galician waters and expand it in different ways: (1) generating valuable information that can be used as a reference to work towards the conservation of the species in the area in the future; (2) integrating the results of this thesis with findings from previous studies to obtain a more comprehensive understanding of the impacts of human activities on common dolphins; (3) and applying methodologies that can be exported and applied to other areas and species. Each chapter of the thesis tackles a particular aspect of the ecology of common dolphins and suggests measures to improve the conservation of the species.

Background information on the distribution of a species and the potential human impacts are key to understanding the conservation needs of that species. SDMs provide valuable information on species distribution and can help identify conservation problems, define objectives, and ultimately suggest management actions to improve the species conservation (Embling et al. 2010; Robinson et al. 2011; Guisan et al. 2013; Dransfield et al. 2014). In this regard, the ENM in Chapter 2 highlighted the areas West from Sálvora Island, especially the waters between the coast and the 200 m bathymetry line, as the most suitable areas for the species. However, this information alone is not sufficient to determine if conservation measures are needed, or what areas should be prioritised.

The outputs of SDMs can be used to better understand the effectiveness of already existing protection measures, the real extent of human activities, and their potential impacts on the species in the most suitable habitats for them. To do so, they can be examined in the context of the occurrence of human activities or the location of

protected sites (Marshall et al. 2014; Moradi et al. 2019). In this regard, the integration of the findings from Chapter 2 and 3 highlighted the spatial and temporal overlap between the most suitable habitats for common dolphins, trawlers and, to a lesser extent, bottom set gillnets (Figure 6.4). This information supported previous studies that reported interactions with pair-trawlers and bycatch as being one of the most serious problems for the species in the area (López et al. 2003; Fernandez-Contreras et al. 2010). More importantly, the integration of information highlighted the areas where conservation efforts should be prioritised.

Building on the information on spatial distribution provided by the ENM, Chapters 4 and 5 focussed on understanding the ecological role of common dolphins within the Rías Baixas shelf ecosystem, their interactions with other species and the effect of fisheries. Indeed, ecosystem models such as EwE have already been used to evaluate the consequences of human activities, mainly fisheries, on ecosystems in general (Coll and Libralto, 2012), and on cetaceans in particular (Díaz López et al. 2008; Piroddi et al. 2010, 2011; Lassalle et al. 2012;). The extension of the modelled area in the Rías Baixas shelf ecosystem was determined by identifying the most suitable habitats for the species as a method to provide further information regarding the conservation priorities found in Chapters 2 and 3. Results highlighted that the main concern for common dolphins conservation was the intense fishing pressure to which the ecosystem is subjected.

Each chapter contributed valuable information in a specific way in which fisheries are threatening common dolphins conservation in Galicia. However, the integration of the findings provided a much more comprehensive understanding of how and to what extent fishing activities are affecting this small cetacean. In doing so, they also helped identify the source of the issue, set objectives and prioritise conservation measures and management actions. Identifying the main issues of concern and providing scientific evidence for them are fundamental first steps towards developing effective conservation measures (Margules and Pressey, 2000; Sutherland et al. 2004). In this regard, results of this thesis highlighted that fishing activities pose the main threat to common dolphins in the area, affecting different aspects of their ecology in a cumulative manner. First, the spatial and temporal overlap with bottom trawlers increases common dolphins

susceptibility to bycatch, which has traditionally been considered the major threat for common dolphins in the area (López et al. 2003; Fernandez-Contreras, 2010; Goetz et al. 2014). Second, unsustainable fisheries exploitation leads to direct and indirect competition for fish resources with common dolphins, which could have major implications in the future. These impacts have a dual effect over time on common dolphins, as operational effects may pose an immediate threat, and ecological effects may compromise the species in the future.

6.5.2.Suggesting effective conservation measures

Once the main threats are identified, the next step involves suggesting effective measures to improve the conservation of the species. So far, previous studies have made specific recommendations, such as operational changes, spatial rearrangement of fishing activities and even the potential use of acoustic deterrent devices (López et al. 2003; Fernandez-Contreras et al. 2010; Goetz et al. 2014). All these recommendations were focussed on mitigating the impact of bycatch on common dolphins. Although incidental capture is a major issue of concern for the species in the area, the present thesis provides evidence that competition for resources poses an added and long-lasting threat to common dolphins conservation. Therefore, a dual approach is suggested here to minimise all the impacts of fisheries on the species.

Measures to reduce bycatch

A first group of measures would be aimed at reducing the bycatch in the Rías Baixas region and they should work towards a unique goal of achieving zero bycatch (Dolman et al. 2016). Indeed, incidental capture monitoring has been a priority at a European scale in order to achieve Good Environmental Status (GES) for cetaceans under the Marine Strategy Framework Directive (MSFD) (Santos and Pierce, 2015; Dolman et al. 2016). To do so, and in line with previous studies in the area (López et al. 2003; Fernandez-Contreras et al. 2010; Goetz et al. 2014), higher priority should be set at mitigating the impact caused by bottom trawl fisheries, because common dolphins show a higher vulnerability to them (Chapter 3). Therefore, efforts should focus on restricting the use of this fishing technique to waters deeper than 300 metres. This could be complemented with a ban of setting fishing gear when dolphins are present, a frequent

strategy already used by fishermen (Goetz et al. 2014), although this might be more difficult to put in place.

Measures to reduce competition for resources

The MSFD urges European Union Member States to ensure that "all elements of the marine food webs, to the extent that they are known, occur at normal abundance and diversity levels capable of ensuring the long-term abundance of the species and the retention of their full reproductive capacity" (Dolman et al. 2016). In this regard, Spain considers the reduction of overfishing as one of the three main objectives to achieve GES for marine species. However, most efforts have been set at evaluating and mitigating bycatch (Santos and Pierce, 2015). Overfishing has caused and is causing severe ecosystem alterations and it has been linked to long term changes in top predator abundances (Pauly et al. 1998; Jackson et al. 2001; Bearzi et al. 2006). In addition, despite some recovering fish stocks, still many of the European stocks are exploited in an unsustainable manner (Froese et al. 2018). Additionally, IUU fishing, currently estimated at 40% in North-West Spain (Villasante et al. 2015), escapes any type of control. Despite the negative effects of overfishing in marine ecosystems and species, only a few studies have tried to evaluate the extent of its impact on cetaceans and marine top predators.

Most studies that analyse the effects of fisheries on cetaceans focus on the operational effects, highlighting the degree of impact of different fisheries (López et al. 2003; Fernandez-Contreras et al. 2010; Goetz et al. 2014). The approach used here, provides valuable information about the ecological effects of fisheries on common dolphins. These are less apparent and more difficult to monitor, but certainly cause a more lasting impact on the species and the ecosystem in the long term. Indeed, findings of this thesis highlight excessive fishing effort as the main issue of concern for common dolphins and other cetaceans such as harbour porpoises or bottlenose dolphins in the Rías Baixas region, as it leads to competition for resources (Chapter 5). Therefore, a second group of measures should be focussed on setting management priorities at drastically reducing fishing effort and adopting multispecies management strategies that prioritise ecosystem conservation. To do so, a combination of different approaches is suggested.

First, methods to report fishing capacity and effort of commercial fisheries fail to assess their real extent (Eigaard et al. 2014). This contributes to unsustainable exploitation of fishing resources. For instance, according to official statistics, fishing effort has been declining since the start of the century but landings show an opposite trend (Figure A2.1). Although some authors have linked this increase in landed biomass to better data collection used in official regional statistics (Alonso-Fernández et al. 2019), this could also be linked to inaccurate fishing effort reporting. Therefore, methods that accurately measure the fishing effort should be implemented on all fishing vessels of the fleet, especially on bigger vessels and those using less selective fishing gear (Dolman et al. 2016). Additionally, methods to monitor fishing effort could provide a more comprehensive understanding of its spatial extent and distribution (Shepherd, 2003; Lawrence and Bhalla, 2018). In this regard, although some improvements have been made, still 89% of the EU fishing vessels do not have a Vessel Monitoring System (VMS) to monitor fishing effort (European Court of Auditors, 2017). These mainly include vessels smaller than 15 metres which, in Galicia, represent around 90% of the fishing fleet (Xunta de Galicia, Conselleria do Mar, 2020b). Therefore, the installation of VMS or simpler localisation systems in vessels under 15 metres would lead to a more accurate and transparent control measure of the fishing effort, and should therefore be promoted.

Second, results of this thesis outline the need to go beyond single-stock fisheries management approaches. Although these have been widely used (Prellezo and Curtin, 2015) and their use has meant an improvement in fisheries management, they fail to capture the multispecific nature of ecosystems (Walters et al. 2005). This can lead to management strategies that are not sufficient to ensure ecosystem conservation (Legović et al. 2010). Therefore, as urged by the CFP and the MSFD, fisheries management should be redirected towards adopting an ecosystem approach, which prioritises the protection and conservation of wild habitats and species, while ensuring sustainable exploitation of fishing resources (Jennings and Rice, 2011). This approach would benefit not only exploited marine species, but also other important components of marine ecosystems such as cetaceans, seabirds and other marine top predators.

Last, the spatial redefinition of the already existing protected areas together with an increase in their level of protection are additional measures that could help reduce the impact of fishing in the region. For instance, the protected area of the Atlantic Islands National Park around Sálvora Island and the marine part of the SCI Complexo humido de Corrubedo include and border with some of the most suitable habitats for common dolphins (Figure 6.4). However, this small cetacean is not listed as a protected species in any of these areas. Hence, the inclusion of common dolphins in the list of protected species, and the expansion of these two protected areas to the west, up to the 200 metres bathymetric line (Figure 6.6), could improve common dolphins conservation. Based on the distribution of both fisheries and dolphin, this newly-created area could include two levels of protection. On the one hand, the area between the 100 m and the 200 m bathymetry lines would be designated as a no-take protected area, which is in line with Article 12 of the Habitats Directive. This measure would mainly affect trawling, which is a non-selective and destructive fishing method (Olsgard et al. 2008) and represents the main threat to common dolphin (López et al. 2003; Fernandez-Contreras et al. 2010; Goetz et al. 2014). Therefore, a fishing ban in this area would benefit common dolphins and the whole ecosystem.

On the other hand, fishing operations in the area located between the 100 m bathymetric line and the actual border of the SCI would be restricted to fishing vessels using selective techniques and those employing proven sustainable fishing methodologies. These measures would discourage the use of trawling techniques and encourage the use of more selective, traditional and sustainable fishing techniques, moving fisheries towards a sustainable exploitation of resources (Cámara and Santero-Sánchez, 2019). Although marine protected areas have been proposed to enhance cetacean conservation (Embling et al. 2010; Methion, 2019), and no take areas have proven good measures to improve ecosystem restoration (Sala and Giakoumi, 2018), these should not be regarded as primary solutions to overexploitation in the area but rather complementary actions supporting the aforementioned measures (Beddington et al. 2007).

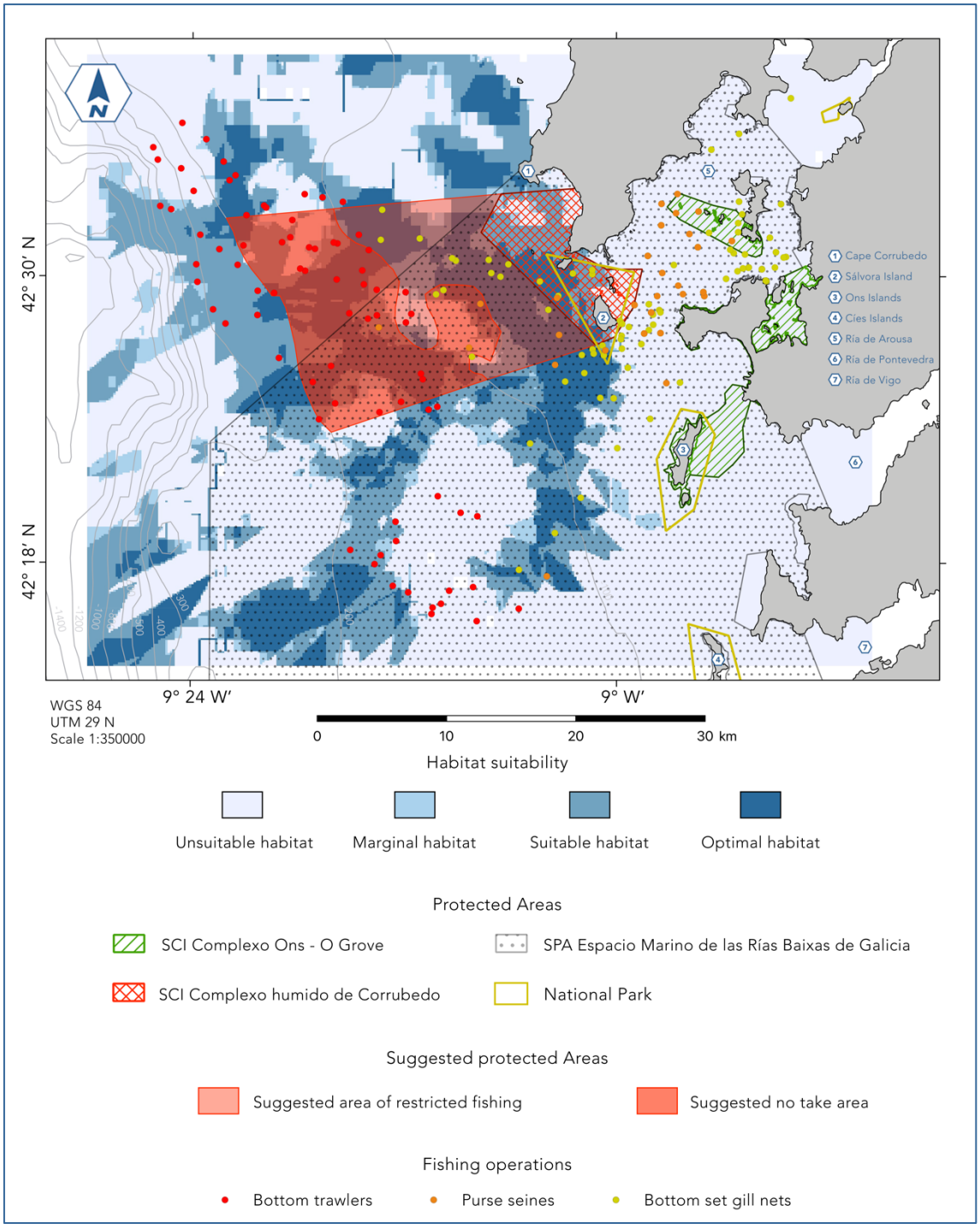


Figure 6.6 *Expansion of the already existing protected areas showing the proposed expansion and the location of the no take protected area and the restricted fishing area.*

Complementary actions

Besides the measures proposed here to mitigate bycatch and competition for resources, additional actions should be considered to improve fisheries management and cetacean and ecosystem conservation. Interaction between marine species and fisheries and the impacts of the latter to the environment have always been a conflicting topic that has confronted, at least, two opposing sectors, fishers and conservationists (Matthiopoulos et al. 2008). However, in order to be effective, measures that aim to promote real sustainable fisheries with the ultimate objective of improving ecosystem and species conservation, should involve all stakeholders in the decision making process (Prellezo and Curtin, 2015; Cámara and Santero-Sánchez, 2019). Often fishers are seen as part of the problem when it comes to ecosystem conservation. However, involving them in being part of the solution would enhance their trust in the process and may favour their willingness to follow and help implement conservation actions. Following up with this idea, scientists and conservationists should develop methods to clearly explain the outcomes of their studies, educate decision-makers and fishers in ecosystem functioning and species ecology, and offer them clear and specific scientific-advice (Osmond et al. 2010).

Any conservation measure should however be supported by a clear legislative framework, which should be specific about their objectives, suggested methods to achieve those objectives, regulations and the penalties laid down for those who don't comply with them (Osmond et al. 2010; Santos and Pierce, 2015). For instance, current legislation on marine protected areas in Spain is rather nonspecific about what fishing activities are allowed in those areas, and the different measures are scattered across regional, national and European legislation (Chapter 2). At an European scale, directives aimed at ensuring biological diversity, such as the MSFD are rather vague in many aspects, which hampers their success (Santos and Pierce, 2015). Therefore, clear and specific legislation is urgently needed to facilitate compliance and create a framework in which enforcement measures could be unequivocally applied where required. Additionally, public authorities and private bodies with management responsibilities should carry out enforcement activities when non-compliances are detected.

Other actions could be aimed at promoting the involvement of the fishing sector in the conservation of marine ecosystems. Traditionally, governments have helped economically unsustainable fisheries through subsidies that, in many occasions, have led to fishing overcapacity (Pitcher, 2001; Sumaila et al. 2016; Zeller and Pauly, 2019). Additionally, they have also been linked to IUU fishing, which is estimated at 40% in North-West Spain (Villasante 2015). Instead of perpetuating this ecologically and economically unsustainable practice, funds could be allocated at promoting compliance with current legislation and development of sustainable and environmental-friendly fishing methods (Sumaila et al. 2016). For instance, eco-label certifications could be given to those fishermen using selective, sustainable fishing methods, complying with current legislation, conforming to landing and effort monitoring and/or taking part in the decision-making processes to improve ecosystem conservation (Dolman et al. 2016; Sumaila et al. 2016). This would (1) help reduce the current excessive fishing effort and capacity, (2) increase the market value of the fish caught, and (3) promote the fishermen's involvement in changing fisheries towards sustainability.

6.6. *Assumptions, limitations and future work*

The present thesis contributes to the scientific knowledge about common dolphin's distribution, habitat use and conservation priorities in the Rías Baixas region and outlines areas where future research is needed. Furthermore, the thesis also provides an integrative approach to studying common dolphins ecology and conservation that can be exported to other species and areas.

Different modelling approaches were used to assess the spatial distribution and habitat use of common dolphins, their ecological role in the ecosystem and the main conservation concerns for the species. Models allow the combination of different types of data and information to evaluate specific ecological aspects of ecosystems and species and make predictions about the analysed aspects. However, they are linked to specific assumptions and are susceptible to uncertainty associated with imperfect data collection, the structure of the model itself and the parameters used in it, among other factors (Schuwirth et al. 2019). These assumptions and uncertainty needs to be reported so that they can be accounted for in any management decisions or conservation

measures resulting from the developed models (Guisan et al. 2013; Heymans et al. 2016; Schuwirth et al. 2019).

The outputs of SDMs rely partly on the quantity and quality of the data collected to develop them. In addition, the accurate assessment of a species absence is key in determining its distribution. However, this can be a difficult task, especially when it comes to highly mobile or cryptic species, such as cetaceans (Hirzel et al. 2002). In such cases, presence-only models are considered good and accurate tools to describe and predict a species distribution and habitat use (MacLeod et al. 2008). This was confirmed by the results of Chapter 2, especially the outcomes of the validation methods, which showed that the ENFA was a robust approach. Although authors found that presence-absence models performed better than presence-only models, such as ENFA (Brotons et al. 2004; Segurado and Araújo, 2004), results of Chapters 2 and 3 showed similar environmental factors as main drivers of the species distribution, highlighting similar predictive power.

Since common dolphin movements are highly influenced by the distribution of their prey, and this, in turn is determined by several environmental factors, the following aspects could be considered to improve future studies aiming to assess the distribution of this small cetacean. First, although they are difficult to obtain, data on seasonal movement patterns of the main prey species of common dolphins could be incorporated into the development of SDMs. This would allow a better understanding of cetacean distribution and its response to the movements of its prey. Second, climate change is predicted to influence oceanic dynamics that could ultimately affect fish distribution in the area (Pérez et al. 2010; Casabella et al. 2014; Bakun et al. 2015). Therefore, incorporating information on climate variability into the SDMs would result in models that could better predict the effects of climate change on the distribution of top predators. Finally, this thesis relies on data collected over a four year period. However, environmental changes and shifts in prey distribution may occur over longer time periods. A longer data collection period would better reflect this variability and could therefore provide better predictions about its effects on the distribution and habitat use of common dolphins in the future.

Ecological models, such as EwE, that capture the complex dynamics of trophic interactions within an ecosystem and make future predictions rely on extensive data sets. Indeed, the quality and quantity of the data used to create the model has been outlined as one of the limitations of this approach (Plagányi and Butterworth, 2004). Further constraints have traditionally been associated with the lack of uncertainty estimation around the input parameters, the use of diet composition data from different time periods without accounting for prey species abundance variability over time, and the sensitivity of Ecosim to vulnerability settings, among others (Plagányi and Butterworth, 2004). However, some tools, such as the PREBAL assessment to enhance the balancing process or the implementation of Monte-Carlo routines to assess uncertainty around the input parameters, have been developed to ensure the quality of EwE and tackle the main limitations of the approach (Heymans et al. 2016).

To overcome these constraints, the best available data for the different functional groups for the selected time period was used in this study (Plagányi and Butterworth, 2004). However, scarce data on benthic invertebrates or the lack of regular assessment of top predator biomass and abundance prior to 2014 were considered to limit the EwE model outcomes. Additionally, the aggregation of several fish commercial species into functional groups could have led to the underrepresentation of non-commercial fish species, species interactions and real fisheries catches (Coll et al. 2014; Alexander et al. 2015; Pauly and Zeller, 2016). These limitations should be considered when using the outcomes of these models for managing purposes (Heymans et al. 2016).

Despite these limitations, EwE was considered a useful tool to evaluate the trophic dynamics of the Rías Baixas shelf ecosystem. Furthermore, the results obtained here outline where future research efforts should focus in order to improve ecosystem based management in the area. First, regular and reliable data should be obtained for the different functional groups. This could be done by conducting regular biomass estimate assessments for top predators and by improving landings and bycatch reporting to obtain accurate, reliable and objective information on fisheries catches. Second, the EwE approach could be further developed by dividing some fish functional groups and by creating multi-stanza groups to better capture the species interactions and the

competition for resources between top predators and fisheries. Third, longer time series data would provide a better representation of the temporal fluctuations in species abundance and would allow the temporal variability of environmental factors to be incorporated. This would result in an improvement of the fit of the model to the data. Finally, the inclusion of climate variability in the model, could help explore the effects of climate on the ecosystem, the interactions among the species and the effects of fisheries.

The approach used in this thesis combines spatial and trophic models to have a better understanding of the ecology of common dolphins in the Rías Baixas region, their interaction with fisheries and the main conservation priorities for the species. However, common dolphin distribution in the North-East Atlantic extends beyond the area considered in this thesis (e.g. Murphy et al. 2013). This thesis provides an integrative framework that could be exported to larger areas, such as the continental Galician waters, to better understand the global effect of fisheries on common dolphins in this region, and develop improved management and conservation plans where needed.

Several studies have highlighted the high biodiversity of marine top predators in Galicia (López et al. 2004; Pierce et al. 2010; Díaz López and Methion, 2018, 2019, BDRI, unpublished data), while others have studied thoroughly specific species (Llavona Vallina, 2018; Methion and Díaz López 2018, 2019, Methion, 2019). Additional work has focussed on the impacts of human activities on cetaceans (López et al. 2003; Fernández-Contreras et al. 2010; Goetz et al, 2014, 2015; Hernandez-Gonzalez, 2018). Therefore, results of this thesis can be added to the already existing scientific knowledge on the different cetacean species in Galicia to stress the need to develop adequate conservation and management plans in order to preserve the marine diversity of the area. Moreover, similar approaches could be applied to assess the status of other marine species. In this regard, Chapter 5 outlines the potential detrimental effects of fisheries on harbour porpoises, and stresses the need to develop future projects to further explore these interactions, and improve the scientific knowledge of the conservation status of harbour porpoises in Galicia.

6.7. *Conclusions*

This study is based on data collected over a four year period as part of an ongoing project conducted and funded by a small non-profit organisation, and aimed at understanding the ecology of marine megafauna in Galicia. Despite the limited funding, data collection could be carried out year round for four consecutive years, providing a large, valuable data set, and a strong support for the modelling frameworks.

Findings of this study add to the scientific understanding of common dolphin ecology and their conservation concerns in the Rías Baixas region. In particular, they provide new insights into common dolphin fine scale spatial distribution and habitat use, ecological role in the ecosystem and spatial, temporal and trophic overlap with fisheries. More importantly, they highlight the importance of conducting long-term, year round reliable data collection to create trustworthy modelling frameworks. The interdisciplinary approach used here, proved to be a reliable holistic framework to improve the understanding of common dolphins ecology and the effects of fisheries on the species and the ecosystem. Furthermore, this thesis contributes to common dolphin conservation by expanding the current knowledge on the effects of fisheries on the species and the ecosystem. Previous studies highlighted bycatch as the major issue of concern for common dolphins conservation. However, findings of this study suggest that the detrimental ecological effects of fishing on common dolphins (and other cetaceans) may pose a more severe and long lasting impact on the species, threatening its conservation, and urge for immediate action. A similar framework to the one presented here could be used to improve our understanding of marine top predators and their ecosystems worldwide. This could be then included in the different steps of decision-making processes in marine conservation planning and fisheries management to develop effective measures to protect marine top predators.



Drawing by Núria Giralt

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Appendices

Appendix 1: Supplementary material to Chapter 4

Information and references used for EwE input parameters

In the following tables, information on the methods and references used to gather the EwE input parameters for each functional group is provided.

Table A1.1 *Common dolphin* (*Delphinus delphis*).

Parameter	Value	Unit	Reference
Biomass	0.019	t km^{-2}	Relative abundance calculated from direct observations at sea; Information on average body weight was obtained from López (2003) and Murphy et al. (2009)
P/B	0.089	year^{-1}	Calculated from López (2003), Murphy et al. (2009), Saavedra (2017) and Saavedra et al. (2018).
Q/B	22.99	year^{-1}	Calculated using daily food intake information from Innes et al. (1987).
EE	0	-	Estimated by EwE
P/Q	0.004	year^{-1}	Estimated by EwE
Landings	-	-	Non applicable
Discards	-	-	Non applicable

Table A1.2 *Harbour porpoise (Phocoena phocoena).*

Parameter	Value	Unit	Reference
Biomass	0.001	t km^{-2}	Relative abundance calculated from Díaz López and Methion (2018). Information on average body weight was obtained from Lockyer (2003) and López (2003).
P/B	0.114	year^{-1}	Calculated from López et al. (2002), López (2003), López et al. (2004), McFee et al. (2012), Goetz et al. (2014) and Hammond et al. (2017).
Q/B	28.080	year^{-1}	Calculated using daily food intake information from Innes et al. (1987).
EE	0	-	Estimated by EwE
P/Q	0.004	year^{-1}	Estimated by EwE
Landings	-	-	Non applicable
Discards	-	-	Non applicable

Table A1.3 *Bottlenose dolphin (Tursiops truncatus).*

Parameter	Value	Unit	Reference
Biomass	0.008	t km^{-2}	Relative abundance calculated from direct observations at sea; Information on average body weight was obtained from Mead and Potter (1989), López (2003) and McFee et al. (2012).
P/B	0.053	year^{-1}	Calculated from Mead and Potter (1989), López et al. (2002), López (2003), López et al. (2004), McFee et al. (2012) and Goetz et al. (2014).
Q/B	19.043	year^{-1}	Calculated using daily food intake information from Innes et al. (1987).
EE	0	-	Estimated by EwE
P/Q	0.003	year^{-1}	Estimated by EwE
Landings	-	-	Non applicable
Discards	-	-	Non applicable

Table A1.4 *Baleen whales (Balaenoptera physalus, B. musculus, B. acutorostrata and Megaptera novaeangliae).*

Parameter	Value	Unit	Reference
Biomass	0.061	t km^{-2}	Relative abundance calculated from direct observations at sea (Díaz López and Methion, 2019). Information on average body weight was obtained from Lockyer and Waters (1986).
P/B	0.06	year^{-1}	Calculated from Lockyer and Waters (1986), Morato et al. (2016) and Díaz López and Methion (2019).
Q/B	0.018	year^{-1}	Calculated using daily food intake information from Croll et al. (2006).
EE	0	-	Estimated by EwE
P/Q	0.009	year^{-1}	Estimated by EwE
Landings	-	-	Non applicable
Discards	-	-	Non applicable

Table A1.5 *Seabirds I: Pursuit and plunge divers: Morus bassanus, Phalacrocorax aristotelis, P. carbo, Calonectris diomedea, Puffinus spp. (unidentified shearwaters), P. puffinus, P. mauretanicus, P. gravis, P. griseus). The northern gannet (M. bassanus) was the most abundant species and was thus selected as the representative of the group.*

Parameter	Value	Unit	Reference
Biomass	0.001	t km^{-2}	Relative abundance calculated from direct observations at sea. Information on average body weight was obtained from Wanless and Okill (1994), Dunning Jr. (2007), Liordos and Goutner (2008), Barros et al. (2013) and Reyes-González and González-Solís (2016).
P/B	0.315	year^{-1}	Díaz López et al. 2008.
Q/B	82.794	year^{-1}	Calculated using daily food intake information from Adams et al. (1991).
EE	0	-	Estimated by EwE
P/Q	0.004	year^{-1}	Estimated by EwE
Landings	-	-	Non applicable
Discards	-	-	Non applicable

Table A1.6 *Seabirds II: Surface and aerial pursuit feeders: Larus michahellis, L. melanocephalus, L. marinus, L. fuscus, L.sabini, Sterna sandvicencis, Stercorarius spp. (unidentified skua); S. skua, S. parasiticus, S. pomarinus, Hydrobates pelagicus, Fulmarus glacialis. The yellow-legged gull (L. michahellis) was the most abundant species and thus it was selected as the representative of the group.*

Parameter	Value	Unit	Reference
Biomass	0.001	t km^{-2}	Relative abundance calculated from direct observations at sea. Information on average body weight was obtained from Pons et al. (2004), Dunning Jr. (2007) and Bolton (2008).
P/B	0.251	year^{-1}	Díaz López et al. 2008.
Q/B	182.120	year^{-1}	Calculated using daily food intake information from Munilla (1997).
EE	0	-	Estimated by EwE
P/Q	0.001	year^{-1}	Estimated by EwE
Landings	-	-	Non applicable
Discards	-	-	Non applicable

Table A1.7 *Blue whiting (Micromesistius poutassou).*

Parameter	Value	Unit	Reference
Biomass	-	t km^{-2}	Estimated by EwE
P/B	1.06	year^{-1}	Torres et al. 2013.
Q/B	6.52	year^{-1}	Torres et al. 2013.
EE	0.99	-	Torres et al. 2013.
P/Q	0.163	year^{-1}	Estimated by EwE
Landings	14.079	t km^{-2} year^{-1}	Xunta de Galicia, Consellería do Mar, 2020
Discards	2.379	t km^{-2} year^{-1}	Xunta de Galicia, Consellería do Mar, 2020; Vázquez-Rowe et al. 2011.

Table A1.8 *Sardine (Sardina pilchardus).*

Parameter	Value	Unit	Reference
Biomass	14.089	t km^{-2}	Estimated by EwE
P/B	0.58	year^{-1}	Sánchez and Olaso, 2004.
Q/B	8.8	year^{-1}	Sánchez and Olaso, 2004.
EE	0.61	-	Sánchez and Olaso, 2004.
P/Q	0.066	year^{-1}	Estimated by EwE
Landings	0.54	t km^{-2} year^{-1}	Xunta de Galicia, Consellería do Mar, 2020
Discards	0.091	t km^{-2} year^{-1}	Xunta de Galicia, Consellería do Mar, 2020; Vázquez-Rowe et al. 2011.

Table A1.9 *Atlantic horse mackerel (Trachurus trachurus).*

Parameter	Value	Unit	Reference
Biomass	33.3	t km^{-2}	Estimated by EwE
P/B	0.64	year^{-1}	Torres et al. 2013.
Q/B	6.47	year^{-1}	Torres et al. 2013.
EE	0.8	-	Torres et al. 2013.
P/Q	0.099	year^{-1}	Estimated by EwE
Landings	9.136	t km^{-2} year^{-1}	Xunta de Galicia, Consellería do Mar, 2020
Discards	1.543	t km^{-2} year^{-1}	Xunta de Galicia, Consellería do Mar, 2020; Vázquez-Rowe et al. 2011.

Table A1.10 *Large piscivorous pelagic fish: Prionace glauca, Thunnus alalunga, T. obesus, T. thynnus, Trichiurus lepturus, Xiphias gladius. The big eye tuna (T. obesus) was selected as the representative of the group.*

Parameter	Value	Unit	Reference
Biomass	0.085	t km^{-2}	ICCAT 2018; Xunta de Galicia, Consellería do Mar, 2020
P/B	0.82	year^{-1}	Sánchez and Olaso, 2004.
Q/B	7.8	year^{-1}	Froese and Pauly, 2019.
EE	0.45	-	Estimated by EwE
P/Q	0.105	year^{-1}	Estimated by EwE
Landings	0.004	t km^{-2} year^{-1}	Xunta de Galicia, Consellería do Mar, 2020
Discards	0.0008	t km^{-2} year^{-1}	Xunta de Galicia, Consellería do Mar, 2020; Vázquez-Rowe et al. 2011.

Table A1.11 *Other piscivorous pelagic fish: Auxis rochei, Belone Belone, Katsuwonus pelamis, Sarda sarda. The Atlantic bonito (S. sarda) was selected as the representative of the group.*

Parameter	Value	Unit	Reference
Biomass	0.745	t km^{-2}	ICCAT 2018; Xunta de Galicia, Consellería do Mar, 2020
P/B	0.82	year^{-1}	Sánchez and Olaso, 2004.
Q/B	6.5	year^{-1}	Froese and Pauly, 2019.
EE	0.43	-	Estimated by EwE
P/Q	0.126	year^{-1}	Estimated by EwE
Landings	0.04	t km^{-2} year^{-1}	Xunta de Galicia, Consellería do Mar, 2020
Discards	0.007	t km^{-2} year^{-1}	Xunta de Galicia, Consellería do Mar, 2020; Vázquez-Rowe et al. 2011.

Table A1.12 *Large planktivorous pelagic fish: Brama brama, Scomber colias, S. scombrus, Scomberesox saurus. The Atlantic mackerel (Scomber scombrus) was selected as the representative of the group.*

Parameter	Value	Unit	Reference
Biomass	11.903	t km^{-2}	Estimated by EwE
P/B	1.14	$year^{-1}$	Torres et al. 2013.
Q/B	6.28	$year^{-1}$	Torres et al. 2013.
EE	0.85	-	Torres et al. 2013.
P/Q	0.182	$year^{-1}$	Estimated by EwE
Landings	9.344	t km^{-2} $year^{-1}$	Xunta de Galicia, Consellería do Mar, 2020
Discards	1.579	t km^{-2} $year^{-1}$	Xunta de Galicia, Consellería do Mar, 2020; Vázquez-Rowe et al. 2011.

Table A1.13 *Small planktivorous pelagic fish: Ammodytes spp., Engraulis encrasicolus. The European anchovy (E. encrasicolus) was selected as the representative of the group.*

Parameter	Value	Unit	Reference
Biomass	22.364	t km^{-2}	Estimated by EwE
P/B	1.98	$year^{-1}$	Sánchez and Olaso, 2004.
Q/B	9.13	$year^{-1}$	Sánchez and Olaso, 2004.
EE	0.83	-	Sánchez and Olaso, 2004.
P/Q	0.217	$year^{-1}$	Estimated by EwE
Landings	0.246	t km^{-2} $year^{-1}$	Xunta de Galicia, Consellería do Mar, 2020
Discards	0.042	t km^{-2} $year^{-1}$	Xunta de Galicia, Consellería do Mar, 2020; Vázquez-Rowe et al. 2011.

Table A1.14 *Benthopelagic fish: Argyrosomus regius, Beryx splendens, Boops boops , Lepidopus caudatus, Mugil spp., Pagellus acarne, Pagellus bogaraveo, Pagellus erythrinus, Pagrus pagrus, Phycis phycis, Pollachius pollachius, Trisopterus luscus, Trisopterus minutus, Spondyliosoma cantharus. The genus Trisopterus was selected as the representative of the group.*

Parameter	Value	Unit	Reference
Biomass	5.931	t km^{-2}	Estimated by EwE
P/B	0.68	$year^{-1}$	Outeiro et al. 2018.
Q/B	3.62	$year^{-1}$	Outeiro et al. 2018.
EE	0.71	-	Outeiro et al. 2018.
P/Q	0.188	$year^{-1}$	Estimated by EwE
Landings	1.05	t km^{-2} $year^{-1}$	Xunta de Galicia, Consellería do Mar, 2020
Discards	0.177	t km^{-2} $year^{-1}$	Xunta de Galicia, Consellería do Mar, 2020; Vázquez-Rowe et al. 2011.

Table A1.15 *Bathydemersal piscivorous fish: Beryx decadactylus, Epigonus telescopus, Etmopterus spinax, Helicolenus dactylopterus, Lophius budegassa, L. piscatorius, Trigla spp. The genus Lophius was selected as the representative of the group.*

Parameter	Value	Unit	Reference
Biomass	2.936	t km^{-2}	Estimated by EwE
P/B	1.09	$year^{-1}$	Torres et al. 2013.
Q/B	4.04	$year^{-1}$	Torres et al. 2013.
EE	0.82	-	Torres et al. 2013.
P/Q	0.270	$year^{-1}$	Estimated by EwE
Landings	0.074	t km^{-2} $year^{-1}$	Xunta de Galicia, Consellería do Mar, 2020
Discards	0.013	t km^{-2} $year^{-1}$	Xunta de Galicia, Consellería do Mar, 2020; Vázquez-Rowe et al. 2011.

Table A1.16 *Demersal piscivorous fish: Anguilla spp., Atherina spp., Callionymus lyra, Chelidonichthys lastoviza, Chelidonichthys lucerna, Ciliata mustela, Conger conger, Dicentrarchus labrax, Dicologlossa cuneata, Diplodus sargus, Gaidropsarus mediterraneus, Gobius spp., Lepidorhombus spp., Merluccius merluccius, Microchirus variegatus, Molva dypterygia, Molva molva, Mullus surmuletus, Pegusa lascaris, Platichthys flesus, Pleuronectes platessa, Polyprion americanus, Raja clavata, Scophthalmus maximus, Scophthalmus rhombus, Scorpaena scrofa, Scyliorhinus canicula, Serranus cabrilla, Serranus scriba, Solea solea, Sparus aurata, Trachinus draco, Zeugopterus punctatus. The European hake (Merluccius merluccius) was selected as the representative of the group.*

Parameter	Value	Unit	Reference
Biomass	4.458	t km^{-2}	ICES 2019; Xunta de Galicia, Consellería do Mar, 2020
P/B	0.67	$year^{-1}$	Outeiro et al. 2018.
Q/B	3.81	$year^{-1}$	Outeiro et al. 2018.
EE	0.996	-	Estimated by EwE
P/Q	0.176	$year^{-1}$	Estimated by EwE
Landings	2.098	t km^{-2} $year^{-1}$	Xunta de Galicia, Consellería do Mar, 2020
Discards	0.355	t km^{-2} $year^{-1}$	Xunta de Galicia, Consellería do Mar, 2020; Vázquez-Rowe et al. 2011.

Table A1.17 *Cephalopods: Alloteuthis media, Eledone chirrosa, Illex illecebrosus, Loligo vulgaris, Sepia officinalis, Todaropsis eblanae. The little squid (A. media) was selected as the representative of the group.*

Parameter	Value	Unit	Reference
Biomass	1.794	t km^{-2}	Estimated by EwE
P/B	3.2	$year^{-1}$	Sánchez and Olaso, 2004.
Q/B	7.5	$year^{-1}$	Sánchez and Olaso, 2004.
EE	0.95	-	Sánchez and Olaso, 2004.
P/Q	0.427	$year^{-1}$	Estimated by EwE
Landings	0.232	t km^{-2} $year^{-1}$	Xunta de Galicia, Consellería do Mar, 2020
Discards	-	t km^{-2} $year^{-1}$	Non applicable

Table A1.18 *Non-Planktonic crustaceans: Alpheus glaber, Bathynectes maravigna, Cancer pagurus, Chloroctus crassicornis, Dichepandalus bonnieri, Galathea spp., Goneplax rhomboids, Inachus leptocirus, Liocarcinus depurator, Macropipus tuberculatus, Macropodia tenuirostris, Monodaeus couchii, Munida intermedia, Munida sarsi, Nephrops norvegicus, Paguridae, Pantophilus spinosus, Parapeneus longirrostris, Pasiphaea sivado, Plesionika heterocarpus, Plesionika martia, Polybius henslowii, Polycheles typhlops, Processa spp., Solenocera membranacea. The species Polybius henslowii was selected as the representative of the group.*

Parameter	Value	Unit	Reference
Biomass	10.221	t km^{-2}	Fariña et al. 1997.
P/B	2.35	$year^{-1}$	Outeiro et al. 2018.
Q/B	6.33	$year^{-1}$	Outeiro et al. 2018.
EE	0.95	-	Estimated by EwE
P/Q	0.371	$year^{-1}$	Estimated by EwE
Landings	0.105	t km^{-2} $year^{-1}$	Xunta de Galicia, Consellería do Mar, 2020
Discards	-	t km^{-2} $year^{-1}$	Non applicable

Table A1.19 *Macrobenthos: Amphiuridae, Anseropoda placenta, Astropecten irregularis, Brissopsis lyrifera, Echinocardium cordatum, Echinus acutus, Luidia ciliaris, Luidia sarsi, Marthasterias glacialis, Spatangus purpureus, Strichastrella rosea.*

Parameter	Value	Unit	Reference
Biomass	7.845	t km^{-2}	Sánchez and Olaso, 2004.
P/B	2.5	$year^{-1}$	Sánchez and Olaso, 2004.
Q/B	6.5	$year^{-1}$	Sánchez and Olaso, 2004.
EE	0.236	-	Estimated by EwE
P/Q	0.385	$year^{-1}$	Estimated by EwE
Landings	-	t km^{-2} $year^{-1}$	Non applicable
Discards	-	t km^{-2} $year^{-1}$	Non applicable

Table A1.20 *Zooplankton.*

Parameter	Value	Unit	Reference
Biomass	86.435	t km^{-2}	Estimated by EwE
P/B	39.08	$year^{-1}$	Sánchez and Olaso, 2004.
Q/B	80	$year^{-1}$	Sánchez and Olaso, 2004.
EE	0.8	-	Outeiro et al. 2008
P/Q	0.4885	$year^{-1}$	Estimated by EwE
Landings	-	t km^{-2} $year^{-1}$	Non applicable
Discards	-	t km^{-2} $year^{-1}$	Non applicable

Table A1.21 *Phytoplankton.*

Parameter	Value	Unit	Reference
Biomass	31.061	t km^{-2}	Estimated by EwE
P/B	158.04	$year^{-1}$	Torres et al. 2013.
Q/B	-	$year^{-1}$	Non applicable
EE	0.83	-	Coll et al. 2006.
P/Q	-	$year^{-1}$	Non applicable
Landings	-	t km^{-2} $year^{-1}$	Non applicable
Discards	-	t km^{-2} $year^{-1}$	Non applicable

Table A1.22 *Discards.*

Parameter	Value	Unit	Reference
Biomass	7.608	t km^{-2}	Vázquez-Rowe et al. 2011.
P/B	-	year^{-1}	Non applicable
Q/B	-	year^{-1}	Non applicable
EE	-	-	Non applicable
P/Q	-	year^{-1}	Non applicable
Landings	-	t km^{-2} year^{-1}	Non applicable
Discards	-	t km^{-2} year^{-1}	Non applicable

Table A1.23 *Detritus.*

Parameter	Value	Unit	Reference
Biomass	70.00	t km^{-2}	Torres et al. 2013.
P/B	-	year^{-1}	Non applicable
Q/B	-	year^{-1}	Non applicable
EE	-	-	Non applicable
P/Q	-	year^{-1}	Non applicable
Landings	-	t km^{-2} year^{-1}	Non applicable
Discards	-	t km^{-2} year^{-1}	Non applicable

Table A1.24 *Information on total landings per each functional group in tonnes (Catches) and its conversion to total biomass caught per km2 (Biomass) and total biomass of discards per km2 (Discards). Biomass and Discards values were entered in the model. Discards were calculated using a conversion factor of 16.9, obtained from bycatch estimates in the area, that show that 16.9% of the fish caught in the area is discarded (Vázquez-Rowe et al. 2011).*

Group	Catches (t)	Biomass (t km-2)	Discards (t km-2)
Blue whiting	13,137.63	14.08	2.38
Sardine	503.86	0.54	0.09
Atlantic horse mackerel	8,524.67	9.14	1.54
Large piscivorous pelagic (*Thunnus obesus*)	4.31	0.01	0
Other piscivorous pelagic (*Sarda sarda*)	37.52	0.04	0.01
Large planktivorous pelagic (*Scomber scombrus*)	8,719.33	9.34	1.58
Small planktivorous pelagic (*Engraulis encrasicolus*)	229.37	0.25	0.04
Benthopelagic fish (*Trisopterus* spp.)	979.9	1.05	0.18
Bathydemersal piscivorous (*Lophius* spp.)	122.5	0.13	0.02
Demersal piscivorous (*Merluccius merluccius*)	1,904.35	2.04	0.35
Total	**34,163.44**	**36.61**	**6.19**

Information and references about the studies used to assess the diets of the different functional groups.

The studies used to gather information about the diet of the different groups are shown here detailing the method used and the area where the study was carried out.

Table A1.25 *Shows the type and the precedence of the data used to assess the diet of the functional groups.*

Functional group	Method	Area	Reference
Common dolphin	Stomach content	Galicia	Santos et al. 2014
Harbour porpoise	Stomach content	Galicia	Santos, 1998
Bottlenose dolphin	Stomach content	Galicia	Santos et al. 2007
Baleen whales	-	Several	Pauly et al. 1998
Seabirds I	Pellets	Scotland and Ireland	Lewis et al. 2003; Strauss et al. 2012
Seabirds II	Pellets	Galicia	Munilla, 1997; Alonso et al. 2015
Blue whiting	Stomach content	Portugal	Cabral et al. 2002
Sardine	Model	Cantabrian Sea	Sánchez and Olaso, 2004
Atlantic horse mackerel	Stomach content	Portugal	Cabral et al. 2002
Large piscivorous pelagic fish	Stomach content	Brasil	Vaske-Júnior et al. 2012
Other piscivorous pelagic fish	Stomach content	Tyrrenian Sea	Campo et al. 2006
Large planktivorous pelagic fish	Stomach content	Portugal	Cabral et al. 2002
Small planktivorous pelagic fish	Stomach content	Western Mediterranean Sea	Costalago et al. 2014
Benthopelagic fish	Stomach content	Tyrrenian Sea	Biagi et al. 1992
Bathydemersal piscivorous fish	Stomach content	Portugal	Teixeira et al. 2010
Demersal piscivorous fish	Stomach content	Portugal	Cabral et al. 2002
Cephalopods	Stomach content	Western Mediterranean Sea	Rosas-Luis and Sánchez, 2015
Non-planktonic Crustaceans	Stomach content	Galicia	Signa et al. 2008
Macrobenthos	Model	Cantabrian Sea	Sánchez and Olaso, 2004
Zooplankton	Model	Cantabrian Sea	Sánchez and Olaso, 2004

Consumption table.

Detailed information on the consumption of the different functional groups is shown in the table below. Functional groups area classified in two domains, pelagic and non-pelagic and consumption between and within domains is explored.

Table A1.26 *Consumption of the different groups classified in pelagic (PL) and non-pelagic (NPL) domains.*

Prey \ Predator	D	1	2	3	4	5	6	7	8	9	10
Domain (D)		PL	PL	PL	PL	PL	PL	NPL	PL	NPL	PL
1. Common dolphin	PL	0	0	0	0	0	0	0	0	0	0
2. Harbour porpoise	PL	0	0	0	0	0	0	0	0	0	0
3. Bottlenose dolphin	PL	0	0	0	0	0	0	0	0	0	0
4. Baleen whales	PL	0	0	0	0	0	0	0	0	0	0
5. Seabirds I	PL	0	0	0	0	0	0	0	0	0	0
6. Seabirds II	PL	0	0	0	0	0	0	0	0	0	0
7. Blue whiting	NPL	0.14	0	0.05	0	0	0.01	2.24	0	0	0
8. Sardine	PL	0.05	0	0	0	0	0.01	0	0	0	0
9. Atlantic horse mackerel	NPL	0.03	0.01	0	0	0	0.01	0	0	0	0
10. Large piscivorous pelagic fish	PL	0	0	0.01	0	0	0	0	0	0	0.02
11. Other piscivorous pelagic fish	PL	0.02	0	0.02	0	0	0	0	0	0	0.02
12. Large planktivorous pelagic fish	PL	0.05	0	0.02	0	0	0	0	0	0	0.17
13. Small planktivorous pelagic fish	PL	0.05	0.01	0	0.06	0.07	0	8.96	0	0	0.06
14. Benthopelagic fish	NPL	0.02	0.01	0.01	0	0	0	0	0	0	0.04
15. Bathydemersal piscivorous fish	NPL	0.03	0	0	0	0	0	2.24	0	0	0.07
16. Demersal piscivorous fish	NPL	0.03	0	0.01	0	0	0	0	0	0	0.01
17. Cephalopods	PL	0.03	0	0.01	0	0	0	2.24	0	0	0.14
18. Non-planktonic Crustaceans	NPL	0	0	0	0	0	0.11	0	0	0	0.1
19. Macrobenthos	NPL	0	0	0	0	0	0.04	0	0	0	0
20. Zooplankton	PL	0	0	0	0.33	0	0	208.26	86.79	215.46	0.03
21. Phytoplankton	PL	0	0	0	0	0	0	0	37.2	0	0
22. Discards	NPL	0	0	0	0	0.02	0.05	0	0	0	0
23. Detritus	NPL	0	0	0	0	0	0	0	0	0	0
Sum		0.45	0.03	0.13	0.39	0.09	0.23	223.94	123.98	215.46	0.66
Total PL		0.2	0.01	0.06	0.39	0.07	0.01	219.46	123.98	215.46	0.44
% PL		44.44	33.33	46.15	100	77.78	4.34	98	100	100	66.67
Total NPL		0.25	0.02	0.07	0	0.02	0.22	4.48	0	0	0.22
% NPL		55.56	66.67	53.85	0	22.22	95.66	2	0	0	33.33

Table A1.26 *continued.*

Prey \ Predator	11	12	13	14	15	16	17	18	19	20	23
Domain (D)	PL	PL	PL	NPL	NPL	NPL	PL	NPL	NPL	PL	NPL
1. Common dolphin	0	0	0	0	0	0	0	0	0	0	0.09
2. Harbour porpoise	0	0	0	0	0	0	0	0	0	0	0.01
3. Bottlenose dolphin	0	0	0	0	0	0	0	0	0	0	0.03
4. Baleen whales	0	0	0	0	0	0	0	0	0	0	0.08
5. Seabirds I	0	0	0	0	0	0	0	0	0	0	0.01
6. Seabirds II	0	0	0	0	0	0	0	0	0	0	0.01
7. Blue whiting	0	0	0	0	5.46	11.14	0	0	0	0	45.15
8. Sardine	1.16	0	0	0	0	2.56	0	0	0	0	27.98
9. Atlantic horse mackerel	0.01	0	0	0	5.22	0.73	0	0	0	0	47.35
10. Large piscivorous pelagic fish	0	0	0	0	0	0	0	0	0	0	0.17
11. Other piscivorous pelagic fish	0.15	0	0	0	0	0	0	0	0	0	1.32
12. Large planktivorous pelagic fish	0	0	0	0	0	0	0	0	0	0	16.99
13. Small planktivorous pelagic fish	3.52	11.81	0	0	0	1.09	10.83	0	0	0	48.36
14. Benthopelagic fish	0	0	0	0	0.59	0.92	0	0	0	0	5.46
15. Bathydemersal piscivorous fish	0	0	0	0	0	0.19	0	0	0	0	2.95
16. Demersal piscivorous fish	0	0	0	0	0	0	0.4	0	0	0	3.41
17. Cephalopods	0	1.94	0	0	0.47	0.19	0.19	0	0	0	2.98
18. Non-planktonic Crustaceans	0	0	0	0	0.12	0.08	0	0	0	0	36.43
19. Macrobenthos	0	0	0	0	0	0	0.22	1.81	2.55	0	25.19
20. Zooplankton	0	61	204.18	11.32	0	0.08	1.82	57.32	2.55	1,853.17	2058.54
21. Phytoplankton	0	0	0	5.86	0	0	0	0	0	4,031.34	834.52
22. Discards	0	0	0	0	0	0	0	0	0.15	0	0
23. Detritus	0	0	0	4.29	0	0	0	5.56	45.74	1,030.31	0
Sum	4.84	74.75	204.18	21.47	11.86	16.98	13.46	64.69	50.99	6,914.82	3,157.04
Total PL	4.83	74.75	204.18	17.18	0.47	3.92	12.84	57.32	2.55	5,884.51	2,991.09
% PL	99.79	100.00	100.00	80.02	3.96	23.09	95.39	88.61	5.00	85.10	94.74
Total NPL	0.01	0	0	4.29	11.39	13.06	0.62	7.37	48.44	1,030.31	165.94
% NPL	0.21	0.00	0.00	19.98	96.04	76.91	4.61	11.39	95.00	14.90	5.26

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Appendix 2: Supplementary material to Chapter 5

Fishing effort and landings

Information on fishing effort and landings for Ribeira Harbour was gathered:

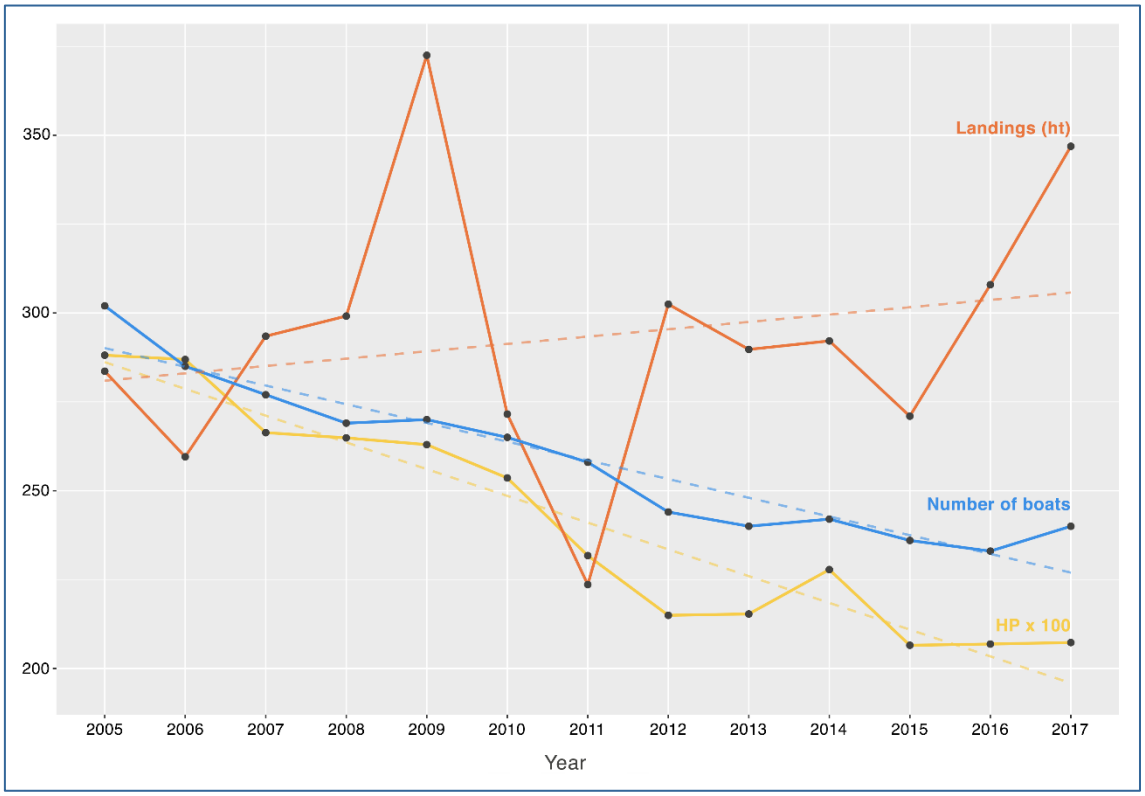


Figure A2.1 *Evolution of the number of fishing boats, their power (horse power divided by 100) and landings (in hectotonnes) registered in Ribeira harbour between 2005 and 2017 (Xunta de Galicia, Consellería do Mar, 2020b). Dashed lines show the trends during the 2005 – 2017 period.*

Information and references used for EwE input parameters

Information on the values of the input parameters for the 2005 Ecopath Sías Baixas shelf ecosystem model are shown in the next tables.

Table A2.1. *Functional groups included in the model detailing the domain they were assigned to, the values of the input parameters and the source for each of the parameters entered in the model. Further information on the sources of the input parameters for the 2017 model (in bold) can be found in Tables A1.1 – A1.23).*

Group	Domain	B	P/B	Q/B	EE	Data source
Common dolphin	Pelagic	0.036	0.05	**23**	-	B + P/B (calculated from López et al. 2004); Q/B assumed to be the same as in the 2017 model; EE estimated by Ecopath
Harbour porpoise	Pelagic	0.001	0.11	**28.08**	-	B + P/B (calculated from Hammond et al. 2013); Q/B assumed to be the same as in the 2017 model; EE estimated by Ecopath
Bottlenose dolphin	Pelagic	**0.076**	**0.05**	**19.08**	-	B + P/B + Q/B assumed to be the same as in the 2017 model (no reliable information found to calculate B); EE estimated by Ecopath
Baleen whales	Pelagic	**0.061**	**0.06**	**6.46**	-	B + P/B + Q/B assumed to be the same as in the 2017 model (no reliable information found to calculate B); EE estimated by Ecopath
Seabirds I, pursuit and plunge divers	Pelagic	**0.001**	**0.32**	**82.79**	-	B + P/B + Q/B assumed to be the same as in the 2017 model (no reliable information found to calculate B); EE estimated by Ecopath
Seabirds II, surface and aerial feeders	Pelagic	**0.001**	**0.25**	**182.12**	-	B + P/B + Q/B assumed to be the same as in the 2017 model (no reliable information found to calculate B); EE estimated by Ecopath
Blue whiting	Non-pelagic	21.030	**1.06**	**6.52**	-	B (ICES, 2019a + Xunta de Galicia, Consellería do Mar, 2020a); P/B and Q/B assumed to be the same as in the 2017 model; EE estimated by Ecopath
Sardine	Pelagic	78.695	**0.58**	**8.8**	-	B (ICES, 2018b + Xunta de Galicia, Consellería do Mar, 2020a); P/B and Q/B assumed to be the same as in the 2017 model; EE estimated by Ecopath
Atlantic horse mackerel	Non-pelagic	18.839	**0.64**	**6.47**	-	B (ICES, 2018c + Xunta de Galicia, Consellería do Mar , 2020a); P/B and Q/B assumed to be the same as in the 2017 model; EE estimated by Ecopath
Large piscivorous pelagic fish	Pelagic	0.105	**0.82**	**7.8**	-	B (ICCAT, 2018 + Xunta de Galicia, Consellería do Mar, 2020a); P/B and Q/B assumed to be the same as in the 2017 model; EE estimated by Ecopath

Table A2.1 Continued

Group	Domain	B	P/B	Q/B	EE	Data source
Other piscivorous pelagic fish	Pelagic	0.115	0.82	6.5	-	B (ICCAT, 2018 + Xunta de Galicia, Consellería do Mar, 2020a); P/B and Q/B assumed to be the same as in the 2017 model; EE estimated by Ecopath
Large planktivorous pelagic fish	Pelagic	9.349	1.14	6.28	-	B (ICES, 2019b + Xunta de Galicia, Consellería do Mar, 2020a); P/B and Q/B assumed to be the same as in the 2017 model; EE estimated by Ecopath
Small planktivorous pelagic fish	Pelagic	5.914	1.98	9.13	-	B (ICES, 2019c + Xunta de Galicia, Consellería do Mar, 2020a); P/B and Q/B assumed to be the same as in the 2017 model; EE estimated by Ecopath
Benthopelagic fish	Non-pelagic	-	0.68	3.62	0.71	P/B + Q/B + EE assumed to be the same as in the 2017 model (no reliable information found to calculate B); B estimated by Ecopath
Bathydemersal piscivorous fish	Non-pelagic	2.474	1.09	4.04	-	B (ICES, 2019d + Xunta de Galicia, Consellería do Mar, 2020a); P/B and Q/B assumed to be the same as in the 2017 model; EE estimated by Ecopath
Demersal piscivorous fish	Non-pelagic	2.020	0.67	3.81	-	B (ICES, 2019e + Xunta de Galicia, Consellería do Mar, 2020a); P/B and Q/B assumed to be the same as in the 2017 model; EE estimated by Ecopath
Cephalopods	Pelagic	-	3.2	7.5	0.92	P/B + Q/B + EE assumed to be the same as in the 2017 model (no reliable information found to calculate B); B estimated by Ecopath
Non-planktonic crustaceans	Non-pelagic	-	2.35	6.33	0.02	P/B + Q/B + EE assumed to be the same as in the 2017 model (no reliable information found to calculate B); B estimated by Ecopath
Macrobenthos	Non-pelagic	-	2.5	6.5	0.24	P/B + Q/B + EE assumed to be the same as in the 2017 model (no reliable information found to calculate B); B estimated by Ecopath
Zooplankton	Pelagic	-	39.08	80	0.8	P/B + Q/B + EE assumed to be the same as in the 2017 model (no reliable information found to calculate B); B estimated by Ecopath
Phytoplankton	Pelagic	-	158.04	0	0.83	P/B + Q/B + EE assumed to be the same as in the 2017 model (no reliable information found to calculate B); B estimated by Ecopath
Discards	Non-pelagic	5.062	-	0	-	B calculated from Xunta de Galicia, Consellería do Mar, 2020a and Vázquez-Rowe et al. 2011
Detritus	Non-pelagic	70.000	-	0	0.34	B + Q/B + EE assumed to be the same as in the 2017 model (no reliable information found to calculate B)

Table A2.2 *Information on total landings, (combining the coastal and artisanal fleets) per each functional group in tonnes (Catches) and its conversion to total biomass caught per km^2 (Biomass) and total biomass of discards per km^2 (Discards). Biomass and Discards values were entered in the model. Discards were calculated using a conversion factor of 16.9, obtained from bycatch estimates in the area, that show that 16.9% of the fish caught in the area is discarded (Vázquez-Rowe et al. 2011).*

Group	Catches (t)	Biomass (t km-2)	Discards (t km-2)
Blue whiting	9,603.96	10.29	1.74
Sardine	3,974.2	4.26	0.72
Atlantic horse mackerel	5,909.33	6.33	1.07
Large piscivorous pelagic fish	5.3	0.01	0
Other piscivorous pelagic fish	5.79	0.01	0
Large planktivorous pelagic fish	6,147.93	6.59	1.11
Small planktivorous pelagic fish	26.03	0.03	0.01
Benthopelagic fish	305.88	0.33	0.06
Bathydemersal piscivorous fish	267.9	0.29	0.05
Demersal piscivorous fish	1,702.03	1.82	4.76
Total	**27,948.35**	**29.96**	**1.74**

Table A.2.3 *Indicates the groups for which time series were included (P: Partial) and the sources used to obtain. Fishing mortalities (F) were calculated dividing the total catches (C) by the total biomass (B).*

Functional group	B	C	F	Source
Common dolphin	P	No	No	BDRI, 2018b
Harbour porpoise	P	No	No	BDRI, 2018b
Bottlenose dolphin	No	No	No	-
Baleen whales	No	No	No	-
Seabirds 1: Pursuit and plunge divers	P	No	No	BDRI, 2018a
Seabirds 2: Surface and aerial pursuit feeders	P	No	No	BDRI, 2018a
Blue whiting	Yes	Yes	Yes	**B**: Xunta de Galicia, Consellería do Mar, 2020a + ICES, 2019a **C**: Xunta de Galicia, Consellería do Mar, 2020a
Sardine	Yes	Yes	Yes	**B**: Xunta de Galicia, Consellería do Mar, 2020a + ICES, 2018b **C**: Xunta de Galicia, Consellería do Mar, 2020a
Atlantic horse mackerel	Yes	Yes	Yes	**B**: Xunta de Galicia, Consellería do Mar, 2020a + ICES, 2018c **C**: Xunta de Galicia, Consellería do Mar, 2020a
Large piscivorous pelagic fish	No	Yes	No	**C**: Xunta de Galicia, Consellería do Mar
Other piscivorous pelagic fish	No	Yes	No	**C**: Xunta de Galicia, Consellería do Mar, 2020a
Large planktivorous pelagic fish	Yes	Yes	Yes	**B**: Xunta de Galicia, Consellería do Mar, 2020a + ICES, 2019b **C**: Xunta de Galicia, Consellería do Mar, 2020a
Small planktivorous pelagic fish	Yes	Yes	Yes	**B**: Xunta de Galicia, Consellería do Mar, 2020a + ICES 2019c **C**: Xunta de Galicia, Consellería do Mar, 2020a
Benthopelagic fish	No	Yes	No	**C**: Xunta de Galicia, Consellería do Mar, 2020a
Bathydemersal piscvorous fish	Yes	Yes	Yes	B: Xunta de Galicia, Consellería do Mar, 2020a + ICES, 2019d C: Xunta de Galicia, Consellería do Mar, 2020a
Demersal piscivorus fish	Yes	Yes	Yes	**B**: Xunta de Galicia, Consellería do Mar, 2020a + ICES, 2019e **C**: Xunta de Galicia, Consellería do Mar, 2020a
Cephalopods	No	Yes	No	**C**: Xunta de Galicia, Consellería do Mar, 2020a
Non-Planktonic Crustaceans	No	Yes	No	**C**: Xunta de Galicia, Consellería do Mar, 2020a
Macrobenthos	No	No	No	-
Zooplankton	No	No	No	-
Phytoplankton	No	No	No	-
Discards	No	No	No	-
Detritus	No	No	No	-

Results of the 2005 Rías Baixas shelf ecosystem Ecopath model

The next tables and graphs show some of the results obtained for the Ecopath model created with the Back to the Future approach.

Keystoneness index

Table A2.4 *Shows the keystoneness index (KS), top-down effects (TD), biomass, trophic level (TL) and Impact of each functional group.*

Functional Group	KS	TD	Biomass	TL	Impact
Small planktivorous pelagic fish	-0.0742	2.41%	25.185	3.37	0.874
Zooplankton	-0.155	33.68%	128.32	2.37	1
Phytoplankton	-0.217	13.65%	47.246	1	0.668
Blue whiting	-0.227	44.54%	29.892	3.46	0.622
Atlantic horse mackerel	-0.33	14.98%	27.434	3.37	0.488
Bathydemersal piscivorous fish	-0.342	94.57%	3.269	4.41	0.445
Non-Planktonic Crustaceans	-0.346	24.84%	21.849	3.24	0.463
Demersal piscivorous fish	-0.374	95.02%	4.224	4.34	0.415
Large piscivorous pelagic fish	-0.416	92.91%	0.502	4.68	0.373
Large planktivorous pelagic fish	-0.444	77.34%	9.349	3.57	0.358
Cephalopods	-0.502	84.39%	1.906	4.25	0.307
Bottlenose dolphin	-0.512	74.6%	0.76	4.73	0.299
Other piscivorous pelagic fish	-0.594	89.62%	2.375	4.3	0.249
Benthopelagic fish	-0.64	2.47%	4.868	2.72	0.226
Sardine	-0.715	58.6%	78.695	2.96	0.233
Macrobenthos	-0.981	99.89%	15.14	2.12	0.106
Seabirds 2: Surface and aerial pursuit feeders	-1.001	98.42%	0.001	3.56	0.0969
Common dolphin	-1.421	91.48%	0.036	4.58	0.0369
Seabirds 1: Pursuit and plunge divers	-1.994	99.95%	0.001	3.89	0.00986
Harbour porpoise	-2.605	98.85%	0.001	4.37	0.00241
Baleen whales	-2.774	98.89%	0.061	3.52	0.00163

Results of the PREBAL assessment

The graphs below show the results of the PREBAL assessment (Link et al. 2010), once the balancing was completed. The PREBAL approach was used as guidance through the balancing process.

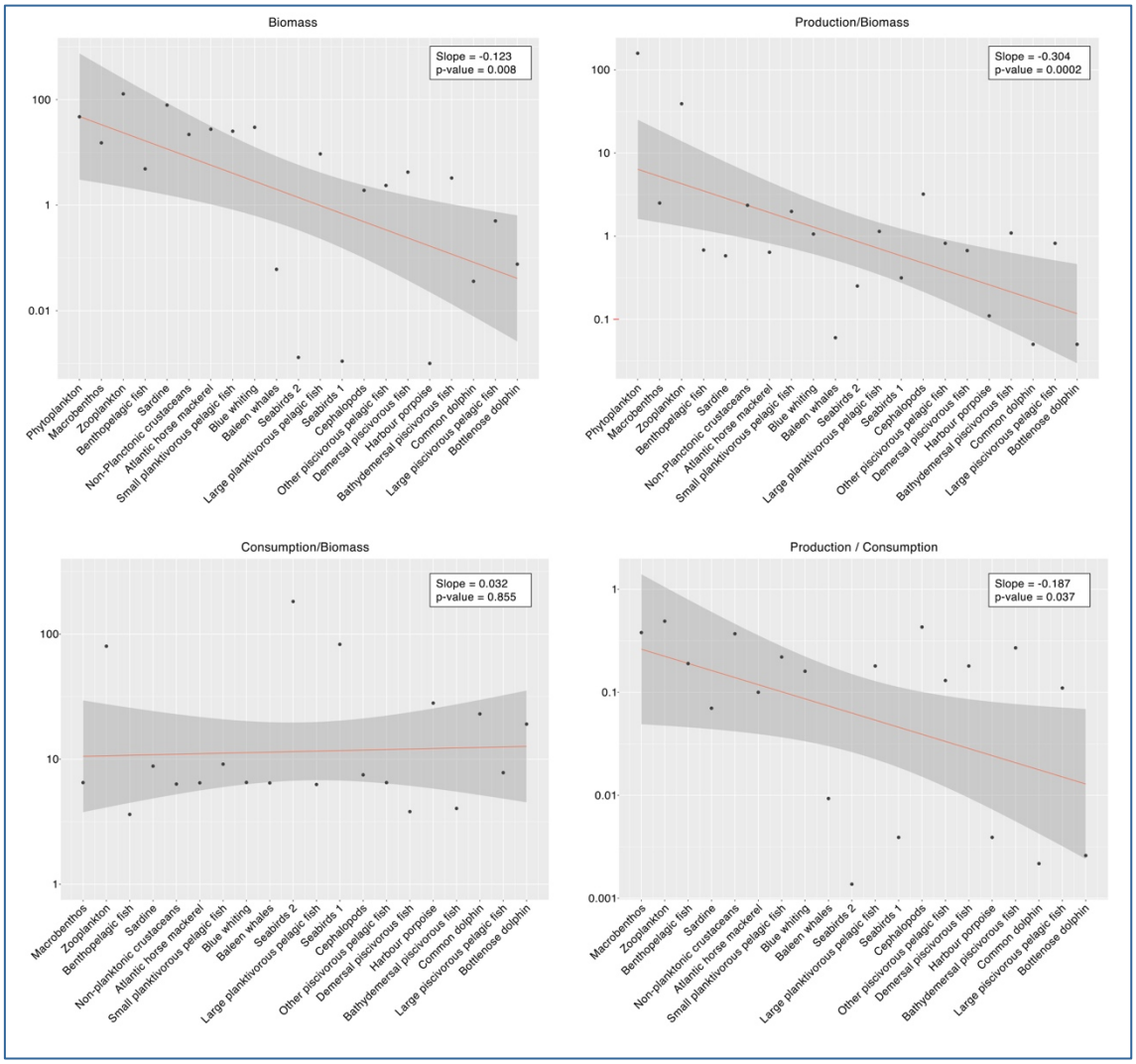


Figure A2.2 *PREBAL outputs for the 2005 Rías Baixas shelf ecosystem model. Functional groups (black dots) are displayed by increasing trophic level from left to right. Orange lines show a linear model fitted into the data with the shaded area showing the 95% confidence interval.*

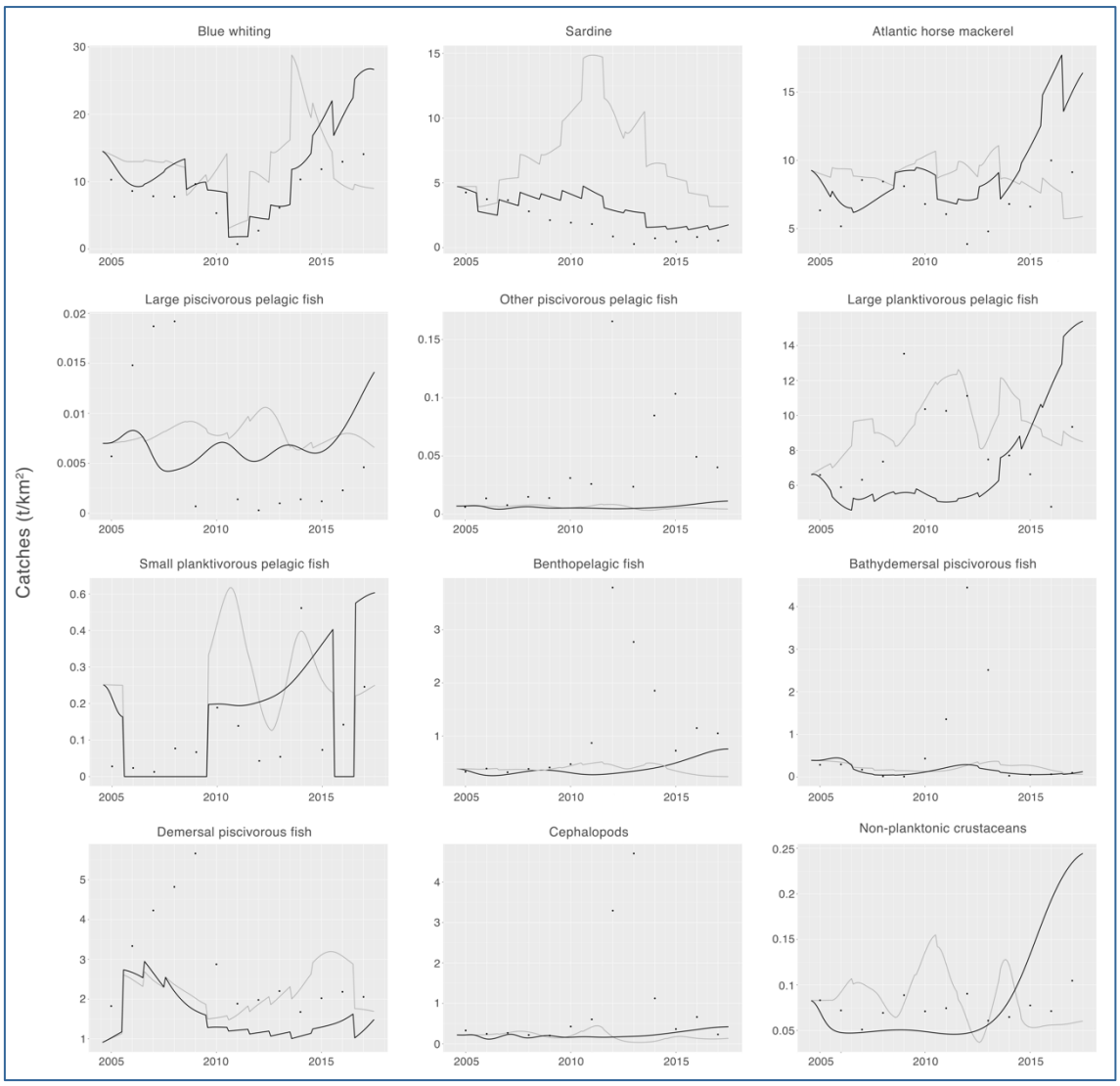


Figure A2.3 *Catches trends obtained for the Ecosim model prior the automated stepwise fitting process (grey line) and the model with the lowest SS and lowest AICc (black line). Black dots show the observed catches.*



Figure A2.4 *Evolution of the contribution of the different functional groups in the common dolphin's diet. The black lines on the graphs above show the common dolphin's relative biomass trends for each scenario.*

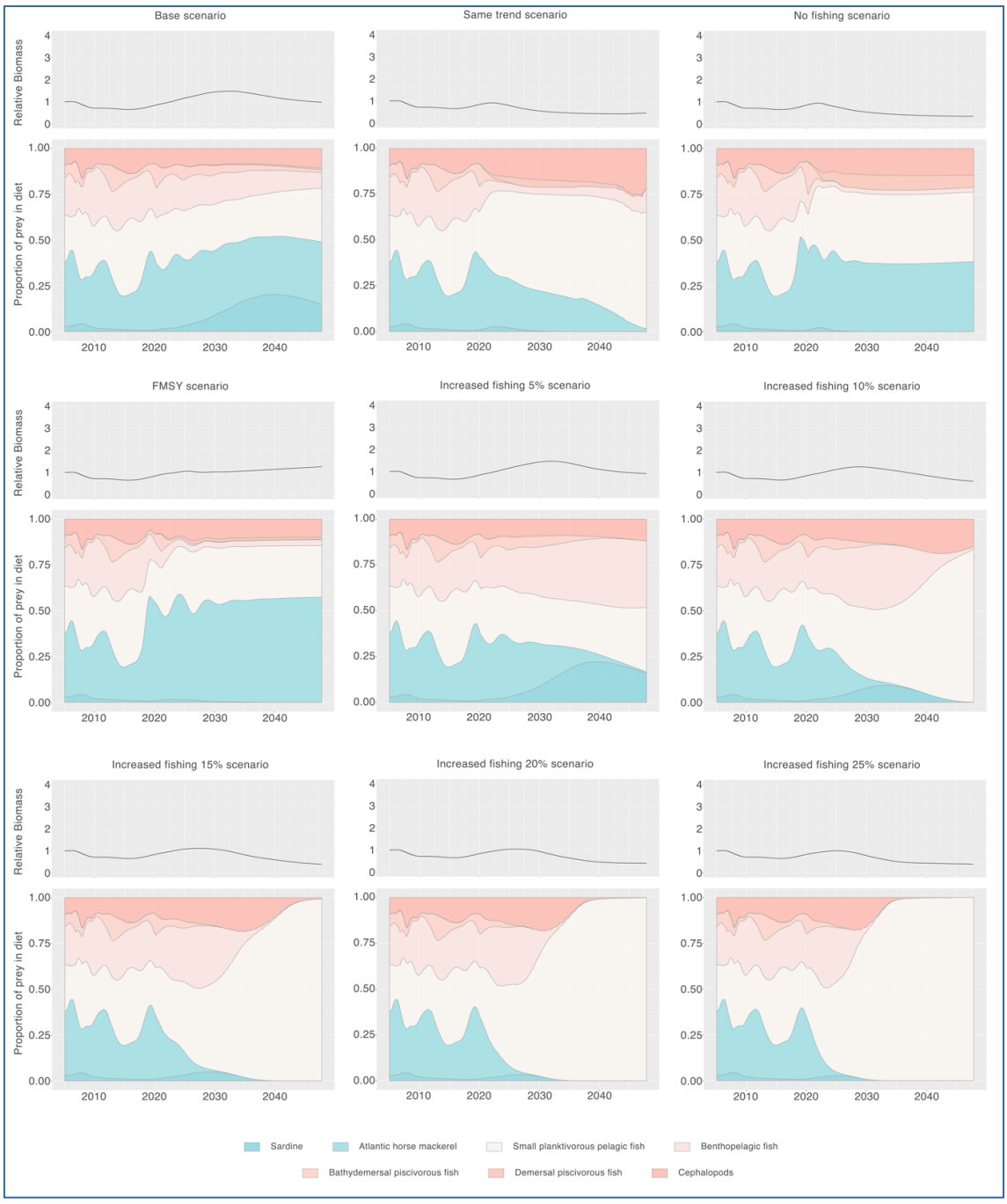


Figure A2.5 *Evolution of the contribution of the different functional groups in the harbour porpoise's diet. The black lines on the graphs above show the harbour porpoise's relative biomass trends for each scenario.*



Figure A2.6 *Evolution of the contribution of the different functional groups in the bottlenose dolphin's diet. The black lines on the graphs above show the bottlenose dolphin's relative biomass trends for each scenario.*

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