University of Reading

Energy transfer in the lower trophic pelagic food web of the Celtic Sea ecosystem

PhD in Environmental Sciences

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Abstract

This thesis provides new understanding on the trophic role of Small Pelagic Fish (SPF) within the Celtic Sea ecosystem. SPF facilitate energy transfer, and changes in their community assemblages could impact food web dynamics. Anchovy, sardine, herring, mackerel, horse mackerel, and sprat spend some or all of their life within the Celtic Sea ecosystem and are of commercial and ecological importance. SPF are predominantly planktivorous, transferring energy from lower (e.g., plankton) to higher trophic levels (e.g., seabirds). The Celtic Sea is relatively understudied despite having undergone environmental changes within the last decades (e.g., recent increase in anchovy, and a decline in herring). The trophic interactions of SPF with planktonic communities and the surrounding environment of the Celtic Sea were investigated through i) diet analysis of SPF (stomach sampling campaign); ii) validation, and analysis of temporal/spatial variability of satellite retrieved phytoplankton chlorophyll-a; and iii) ecosystem modelling (Ecopath with Ecosim, EwE) to investigate the effect of SPF dynamics on the wider Celtic Sea food web.

Stomach analyses indicated seasonal variation in SPF diet, although, calanoid copepods were consumed year-round. As these species are predominantly planktivorous, and chlorophyll-a is a proxy for phytoplankton biomass (a key input into ecosystem models), validation of satellite retrieved chlorophyll-a was undertaken for three algorithms, Sentinel-3A OLCI-OC4ME, Sentinel-3A OLCI-NN, and MODIS-Aqua-OCI+OC3, for the region. Satellite outputs were then considered for use in the Celtic Sea ecosystem model (EwE). Diet of SPF from this study and updated biomass for 2013-2021 were used as an input. The EwE model of the Celtic Sea demonstrated potential to address management related questions regarding SPF. Through the improvement and evaluation of ecosystem model inputs (diet studies and satellite validation), and implementation into the current EwE model, this research has highlighted SPF are key in pelagic energy transfer in the Celtic Sea.

Declaration of Original Authorship

I confirm that this is my own work and the use of all material from other sources has been properly and fully acknowledged.

Roweena Patel

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Introduction

Chapter 1 – Introduction

This thesis investigates the role of Small Pelagic Fish (SPF) and lower trophic levels within the Celtic Sea through a marine food web lens. The Celtic Sea supports important commercial mixed fisheries targeting many different benthic, demersal, and pelagic stocks (Hernvann & Gascuel, 2020). The region is home to diverse range of species, including Atlantic herring (*Clupea harengus*), Atlantic mackerel (*Scomber scombrus*), sprat (*Sprattus sprattus*), European anchovy (*Engraulis encrasicolus*), European sardine (*Sardina pilchardus*), and Atlantic horse mackerel (*Trachurus trachurus*). These small pelagic fish are important components of marine ecosystems. They are predominantly planktivorous and as such link lower and higher trophic levels of the marine food web (Cury et al., 2000). The state of their populations, therefore, plays a critical role ecologically, economically, and socially. Thus, understanding the underlying mechanisms driving their stocks and population dynamics is vital.

In recent decades there have been many environmental changes that have affected marine ecosystems and ecosystem dynamics (Ottersen et al., 2004; Pauly et al., 1998; Votier et al., 2004). Methods such as ecosystem modelling have provided an insight to how these changes may impact ecosystem structure and function, thus its resilience. This, in turn can be used as a tool to inform marine management and spatial planning. Commercial species such as cod (*Gadus morhua*), often have longer time series, stock assessments, diet studies, and fishing mortality values, as such they provide better input data to models than those that are not commercially exploited. Therefore, to advance models representing the changes which have, and may occur in the future, in the ecosystem, localised input data for these data limited species needs to improve. SPF are an example of a functional group (species that can be aggregated by their ecology), that can be data limited within ecosystem or food web modelling (Więcaszek et al., 2015; Temple et al., 2017).

This body of work focuses on the Celtic Sea, southwest of the United Kingdom, and area that is relatively understudied compared to others such as the North Sea, particularly with regards to understanding SPF.

1.1 The Celtic Sea

The study area is defined as the Celtic Sea and Western Approaches (Figure 1.1) located in the shelf-seas of the Northeast Atlantic to the Southwest of the United Kingdom. Two seasonal front systems develop during spring and determine the main oceanographic features in the area: the Celtic Sea Front (separating the Celtic Sea from the Irish Sea) and the Ushant Front, which develops from the coast of Brittany and extends to the western English Channel, dividing the Celtic Sea from the English Channel (OSPAR, 2000). These fronts result in gradients and patchiness of plankton distribution in this area, due to generating vertically mixed and stratified conditions of the water column (Johns, 2006). The two main phytoplankton bloom events in the Celtic Sea take place during spring and autumn (September-October; Pingree et al., 1976).

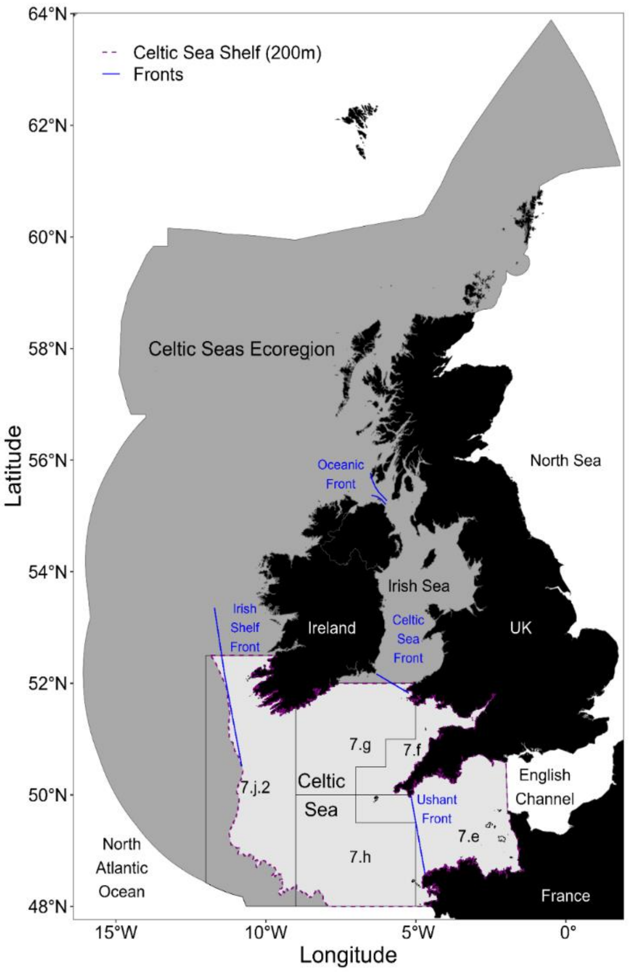

Figure 1.1 - The Celtic Sea (shaded light grey area) and Celtic Seas ecoregion (shaded dark grey area). Purple line = shelf area shallower than 200 m depth matching ICES (International Council for the Exploration of the Seas) divisions (polygons) 7.e – h and 7.j.2 (light grey), blue lines = fronts.

1.2 Phytoplankton in the Celtic Sea

The composition of the phytoplankton community has changed in the Celtic Sea area since the 1980s (Bedford et al., 2020; ICES, 2008; Widdicombe et al., 2010). It was traditionally dominated by diatoms (Figure 1.2b), but more recently these have been decreasing (Bedford et al., 2020; Widdicombe et al., 2010), while coccolithophorids and the dinoflagellate *Prorocentrum minimum,*have been increasing (Widdicombe et al., 2010). Diatoms are dominant in high nutrient regions, with high rates of productivity, and form the base of the copepod-fish food webs. Conversely, dino- and micro-flagellates are lower in productivity and are found in stratified waters, and considered trophic dead ends (Verity & Smetacek, 1996). Regions with higher productivity are usually found within frontal zones (Pingree et al., 1975). Throughout the year, there are three main phases of phytoplankton production, the spring bloom in April at the surface, the deep chlorophyll maxima in May-September, and the autumn surface bloom from September – October (Pingree et al., 1976). The autumn bloom happens through the breaking down of vertical stratification, which releases nutrients found below the thermocline during the summer (Pingree et al., 1976). This is at the end of the annual phytoplankton growing season and represents an important time of year to autumn spawning planktivorous species (e.g., *Clupea harengus* – Atlantic Herring). This bloom is crucial to the survival of planktivorous larvae during the autumn and winter months (Coombs et al., 2010; Cushing, 1990), with the first few days being most critical for development as it is when they require enough suitable prey to ensure their survival (Houde, 2008). In the last few decades, the autumn bloom has become bigger in magnitude than the spring bloom, in terms of chlorophyll concentration (Smyth et al., 2010). Interannual shifts in the phytoplankton community during the autumn bloom season have been associated with the concentration of silicates (Capuzzo et al., 2022). This highlights how environmental conditions play a key role in phytoplankton community composition. It is important therefore, that we begin to understand these environmental changes seasonally and annually and the potential implications to trophic levels such as zooplankton and planktivorous pelagic fish.

Chlorophyll-a (pigment within phytoplankton) can be used as a proxy for phytoplankton biomass which can be used as an indicator for environmental changes (Gohin et al., 2008; Harvey et al., 2019; Pasztaleniec & Poniewozik, 2010). Satellite remote sensing provides an opportunity to monitor chlorophyll-a at high temporal and spatial resolutions, however, to ensure this is comparable with observations they must first be validated for the region of interest.

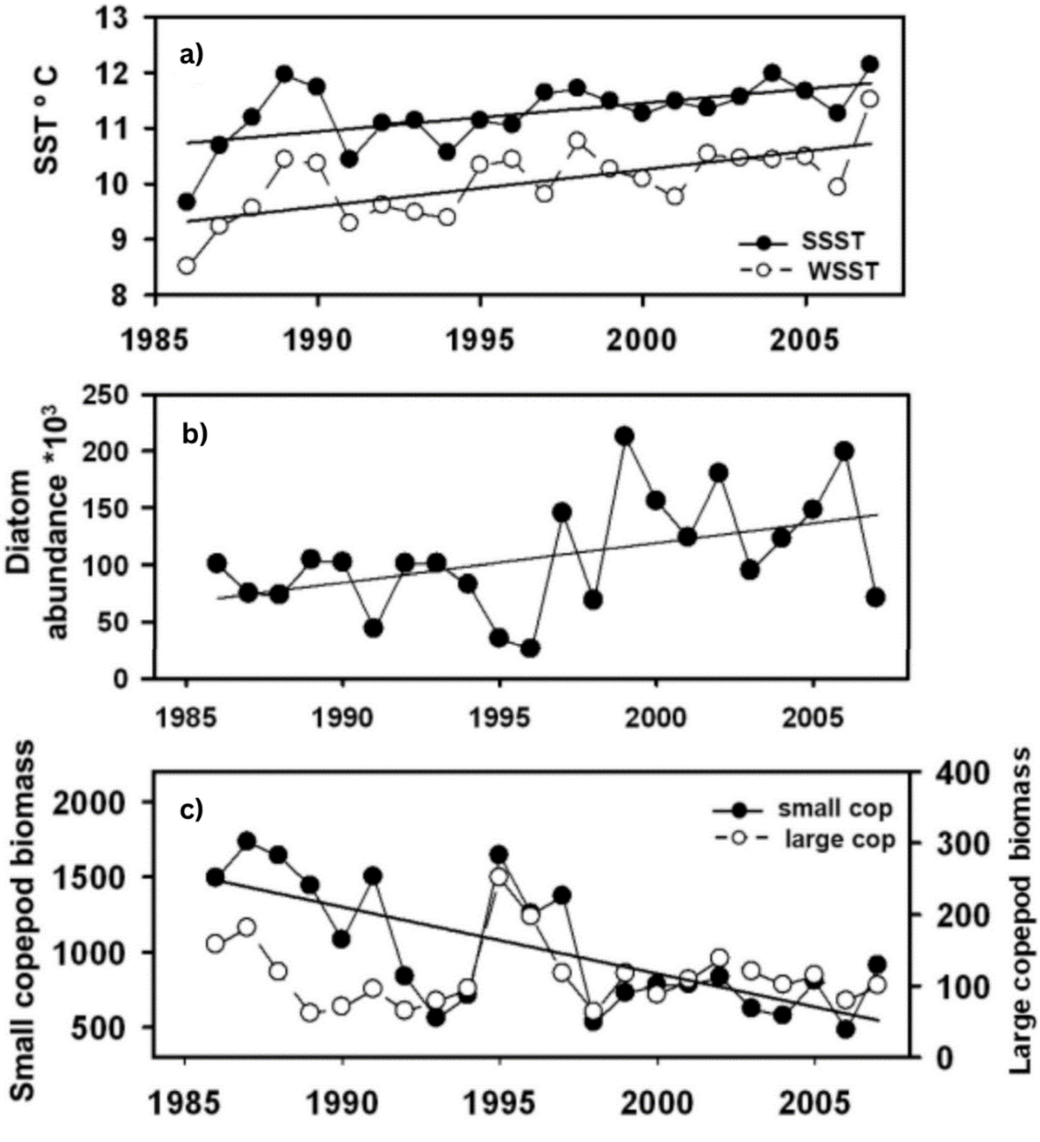

Figure 1.2 - Time series of a) Sea Surface Temperature (ºC) (b); Diatom abundance (c); small and large copepods biomass (mg wet weight) in the Celtic Sea. Adapted from Lauria, (2012).

1.3 Zooplankton in the Celtic Sea

The mesozooplanktonic community of the Celtic Sea is primarily dominated by copepods (Scott et al., 2023, references therein), with only nine to ten taxa contributing to 95% of the plankton community (Scott et al., 2023). Season and year were identified as significant factors of community changes (Scott et al., 2023). Copepods are present throughout the year in the Celtic Sea, with different species present at various times. Calanoid copepods have an initial peak in April-May, with a secondary peak in September-October, depending on specific species, and are usually found around the Ushant front and south of Ireland (Johns, 2006; Kennington & Rowlands, 2006). The frontal regions are associated with seasonal stratification, which may result in elevated copepod abundance (Kennington & Rowlands, 2006; Scott et al., 2023). Cyclopoid copepods are also present throughout the region, with a lower overall abundance than calanoid copepods, and peak in October (Eloire et al., 2010). Since 1985, there has been an overall decrease in small and large copepod (Figure 1.2c; Lauria, 2012), as revealed by data collected by the Continuous Plankton Recorder (CPR). CPR has used 'ships of opportunity' to collect a planktonic time series since 1958. The dominant copepod taxa in the region are considered to be Calanus, with *C. helgolandicus,* a warm water affinity species increasing since 1980s and *C. finmarchicus,* a cold-water affinity species, which has decreased since the 1980s (Planque & Fromentin, 1996). Studies have indicated that significant changes of zooplankton spatial patterns over the last 40 years is potentially related to climate change (Pitois & Fox, 2006). Bedford et al., (2020), used CPR data in conjunction with environmental variables to reveal a negative correlation between sea surface temperature (SST) and small copepods. As such, climate driven variables can influence the zooplanktonic community, which may cause trophic cascades, impact zooplanktonic consumers (SPF), and indirectly affect predators of SPF.

1.4 Small pelagic fish, food webs and the Celtic Sea

The mid trophic level (planktivorous species) of marine food webs frequently consist of a few abundant, most commonly pelagic, schooling fish species (Durant et al., 2009). These species are key components of the ecosystem in terms of energy flows as they channel energy and nutrients from lower trophic levels (plankton) to apex predators (marine mammals). They themselves often fluctuate in abundance, leading to a control of the ecosystem (regulating primary and secondary producers and their predators; Cury et al., 2000; Fauchald et al., 2011). Small pelagic fish species are mid trophic level species, of small or intermediate size and include sardine, anchovy, sprat, herring. They predominantly consume zooplankton, but also phytoplankton (e.g., sardine; Patel et al., 2023; Garrido et al., 2008), and can transform plankton productivity into available food for higher trophic levels (Alder et al., 2008; Bakun et al., 2010; Cury et al., 2000). As these species all feed on plankton, they may compete for food, which could lead to complex interactions. SPF are a primary food source for a wide range of marine predators, for example mammals (Pauly, 1998; Thompson et al., 1995), seabirds (Crawford et al., 2007; Daunt et al., 2008; Furness, 2007; Jahncke et al., 2004) and larger fish (Butler et al., 2010; Logan et al., 2011; Magnussen, 2011; Walter & Austin, 2003). They can also be of commercial importance, as they consist of ~25% of the world's wild capture (FAO. et al., 2018), and 90% of SPF caught are used for reduction industries that produce fish meal and fish oil (Alder et al., 2008). In addition, SPF provide indirect economic and biological importance to the ecosystem, through a supporting service, in regulating energy flows, and are prey species to other fisheries (Hannesson et al., 2009). Therefore, they are important to the functioning of marine ecosystems biologically and economically.

SPF, such as European anchovy and Atlantic herring, are short-lived (2-3 years), and fast growing, and often have high levels of natural mortality, as such depend on recruitment for their stock size. The high variability in recruitment of SPF is driven by a range of abiotic and biotic factors, this includes but not limited to temperature (Bakun, 2006; Lloret et al., 2004), spawning conditions (availability and substrate quality; Kanstinger et al., 2018), cannibalism (Corten, 2013), predation (Richardson et al., 2011; Tsou & Collie, 2001), prey, availability and phenology (Martino & Houde, 2010; Wilson et al., 2018), and starvation (Leggett & Deblois, 1994). The early stages of growth, are critical for survival and are dependent on sufficient suitable prey (Houde, 2008). As these species are planktivorous, they are potentially affected by variations in environmental processes governing plankton abundance. Knowledge of SPF diet may therefore contribute to a better understanding of the influence changing prey availability can exert on abundance of these species. SPF are important facilitators of energy transfer in marine ecosystems, and the Celtic Sea is no exception. The Celtic Sea (Figure 1.1) is home to many SPF, both cold water affinity and warm water affinity species. The region is a transition zone and as such provides environmental conditions for many types of fish species. Key pelagic fish that spend some or all of their life in the region include Atlantic herring (*Clupea harengus)*, Atlantic mackerel (*Scomber scombrus*), sprat (*Sprattus sprattus*), European anchovy (*Engraulis encrasicolus*), European sardine (*Sardina pilchardus*), and Atlantic horse mackerel (*Trachurus trachurus*). Sprat, sardine, and herring can be found all year round, including during spawning season, where they occupy shallower waters as nursery grounds. Atlantic mackerel (hereby known as mackerel) and horse mackerel, spawn on the shelf edge, after which their larvae drift to more coastal waters (Jansen et al., 2015). Anchovies overwinter in the region possibly to evade the colder North Sea waters (Huret et al., 2020). There have been changes in the abundances of these species in recent years (Figure 1.3). Anchovy abundance has increased northwards since the mid-1990s, possibly due to improved recruitment success of remnant local spawning populations (Huret et al., 2020; Petitgas et al., 2012). Studies on the trophic ecology of European anchovy have previously been performed in the Bay of Biscay, Mediterranean Sea, Baltic Sea or North Sea (e.g., Plounevez & Champalbert, 2000; Raab et al., 2011, 2012; Tudela & Palomera, 1997). Therefore, studying the effect of the increase of anchovy to the Celtic Sea ecosystem, in terms of niche or dietary overlap with other SPF in the region, provides a key opportunity to understand potential competition.

Spawning stock biomass (SSB) of the other five species have also altered within the Celtic and adjacent seas (Figure 1.3). Horse mackerel severely declined in the North Atlantic in the early 1980s

(Figure 1.3b; Hawkins et al., 2003; Lockwood & Shepherd, 1984), these were originally bycatch from the mackerel fishery., Therefore horse mackerel potentially profited from the vacant niche left by mackerel from which they became a new target species for pelagic fleets (Eaton, 1983). When horse mackerel declined from early 2000s, boarfish (*Capros aper*) became the main pelagic target species in the Celtic Sea (Hernvann & Gascuel, 2020). Herring, which has been assessed annually since 1958, has more recently seen a decline (post-2010) in the Celtic Sea (Figure 1.3b) leading to a fishery closure to help the stock recover (ICES, 2020). More recently, sprat and sardine have been assessed, with ICES advice for these species being available since 2013 due to a new survey in the area providing an acoustic survey index (ICES, 2022). This revealed sardine SSB has increased (Figure 1.3a), coinciding with a recent surge of autumn spawning activity in the English Channel and climatic variability (Alheit & Hagen, 1997; Coombs et al., 2010). Therefore, with the recent increase of certain SPF species (anchovy and sardine) and decline in others (herring) it is important to understand how this might contribute to ecosystem functioning. Consequently, Chapter 3 will use stomach content analyses to improve knowledge of trophic interactions and ecosystem functioning of small pelagic fish in the Celtic Sea.

One other way the changes in the Celtic Sea ecosystem has been assessed in recent years is through the development of ecosystem models (Hernvann et al., 2020; Lauria et al., 2012). However not all observed changes are reflected within these models. For example, the recent changes in anchovy stocks (increase) are not highlighted in the model analysis due to limited data availability and/or restricted time frames of the model runs (i.e., anchovy were not present within the ecosystem during the time frame of the model runs). Therefore, it is important that these models reflect changes occurring with the ecosystem incorporating the best available data.

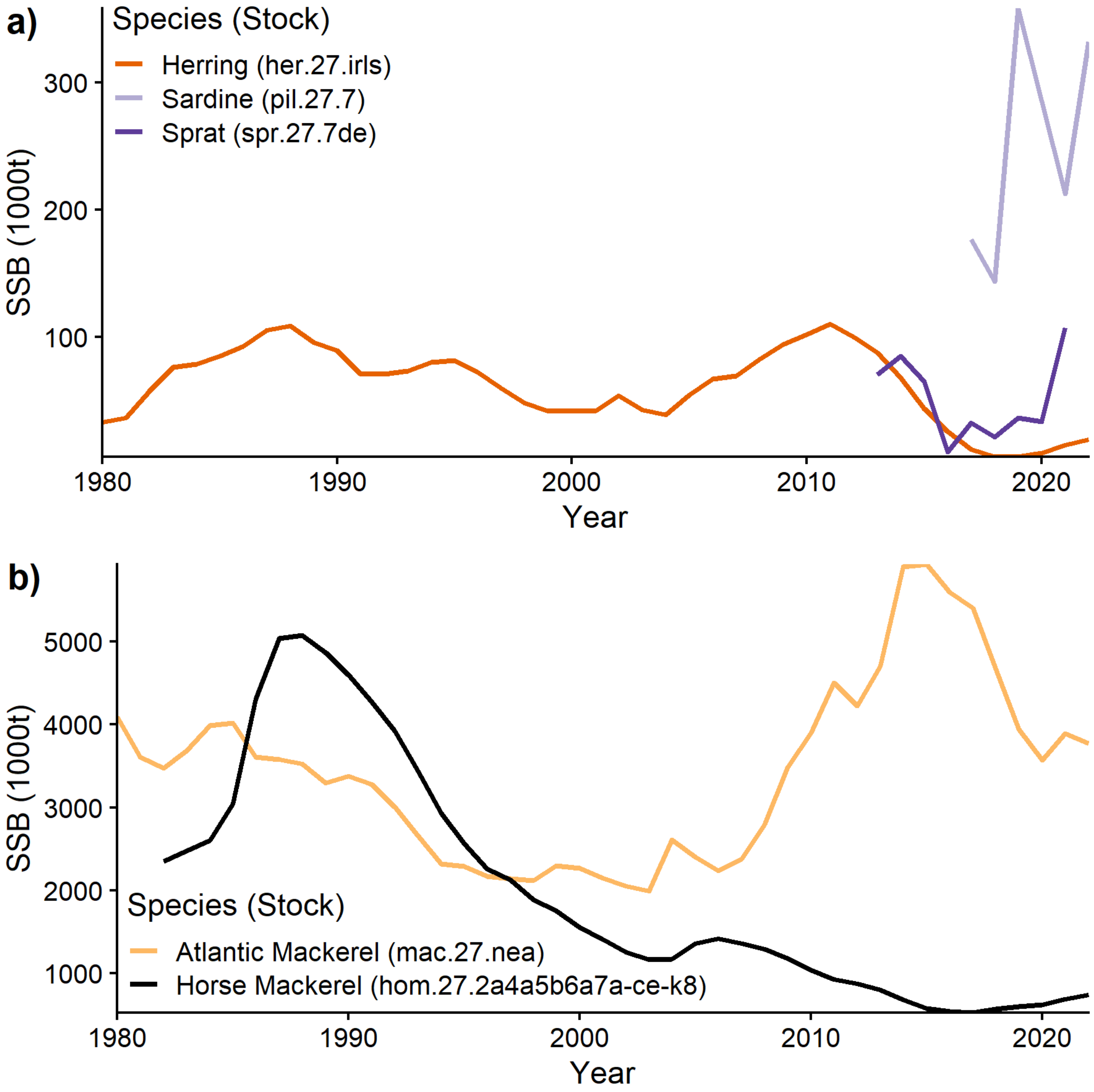

Figure 1.3 - Time series of spawning stock biomass (SSB) in 1000 tonnes, of five pelagic stocks in the Celtic Seas ecoregion. a) Represents herring (*Clupea harengus*) stock from Irish Sea, Celtic Sea, and southwest of Ireland. Sardine (*Sardinia pilchardus*) from Southern Celtic Seas. Sprat (*Sprattus sprattus*) from English Channel. b) Represents Atlantic mackerel (*Scomber scrombus*) from the Northeast Atlantic and adjacent waters. Horse mackerel (*Trachurus trachurus*) from the Northeast Atlantic. Data was downloaded from https://www.ices.dk/data/assessment-tools/Pages/stock-assessment-graphs.aspx Celtic Seas ecoregion assessment year 2022.

1.5 Aims and Objectives

The aim of this research is to evaluate the role of small pelagic fish (SPF) in the Celtic Sea and develop an ecosystem (food web) model to understand the temporal dynamics of SPFs in the Celtic Sea. To meet this aim, the following objectives were undertaken:

1. Conduct a stomach sampling of SPFs, namely, anchovy, sardine, horse mackerel, and sprat in the Celtic Sea and supplement the sampling data with historical fish-stomach data from DAPSTOM, to understand seasonally and ontogenetic diet shifts, and construct a combined diet matrix. Outputs will be used as an input to an ecosystem model.
2. Validate Sentinel 3A- OLCI derived chlorophyll-a with *in situ* measurements from the PELTIC surveys and generate information about phytoplankton groups, e.g. employing a phytoplankton size class algorithm, as potential input into an SPF ecosystem (food web) model of the Celtic Sea.
3. Adapt and update a pre-existing Ecopath with Ecosim model of the Celtic Sea (Hernvann et al., 2020) with newly collated diet data (Objective 1), and new biomass inputs from the PELTIC surveys for SPF. To understand the role of SPF within the Celtic Sea ecosystem and improve predictions of future ecosystem changes.

1.6 Outline of next chapters

The key literature for this thesis and how it relates to the research aims and objectives will be reviewed within **Chapter 2**.

The trophic interactions between lower trophic levels (phytoplankton and zooplankton) and planktivorous fish, SPF, of Celtic Sea food web will be studied by analysing fish stomach content (**Chapter 3**) and by evaluating and validating chlorophyll-a maps from satellite retrievals (**Chapter 4**). These will then be inputted in an ecosystem model to understand the role small pelagic fish on the wider food web of the Celtic Sea (**Chapter 5**).

More specifically**, Chapter 3** will assess the diet of six small pelagic fish in the Celtic Seas ecoregion: Atlantic herring (*Clupea harengus*), Atlantic mackerel (*Scomber scombrus*), sprat (*Sprattus sprattus*), European anchovy (*Engraulis encrasicolus*), European sardine (*Sardina pilchardus*), and Atlantic horse mackerel (*Trachurus trachurus*), using a combination of historical data (DAPSTOM) and data collected onboard PELTIC Survey 2019, A multispecies approach will be applied to investigate feeding strategies (i.e., generalist vs specialist) and potential interspecific competition.

Following this, **Chapter 4** will validate the satellite retrievals of chlorophyll-*a* from Sentinel-3A and MODIS-AQUA in the Celtic Sea with *in situ* measurements. Performance metrics outlined in Pahlevan et al., (2020) will be computed for October 2016, 2017, and 2019 at different time windows (i.e., satellite overpass time to *in situ* data collection time) on three different algorithms. This study aims to contribute to our understanding of the performance of satellite-based chlorophyll-a estimates in the Celtic Sea.

In **Chapter 5** the trophic structure of the Celtic Sea ecosystem, and specifically the role of small pelagic fish, will be investigated through the application of an ecosystem-based mass-balance model Ecopath. The results from Chapter 2 & 3 will be considered as an input to update the model by Hernvann et al., (2020), alongside updated biomass data from PELTIC survey for small pelagic fish. A tropho-dynamic model will be applied, employing outputs from the global earth system model, CMIP6, to optimise the model for SPF, to address management questions. This will provide support for resource management of small pelagic fish in the Celtic Sea.

In **Chapter 6** the main results of the three study chapters in the thesis will be discussed and placed into a broader research context, drawing on the published literature within the field. Finally, any remaining gaps in current knowledge will be identified and recommendations will be made for future studies.

2

Literature Review

Chapter 2 – Literature Review

2.1 Food webs and trophic energy transfer

Food webs, defined by predator prey interactions, determine how a marine ecosystem functions, responds to pressures (internally and externally), and can correspond to ecosystem resilience (Libralato et al., 2014). These predator-prey interactions facilitate the flow of energy, mass, and nutrients through a system (Krebs, 2009; Smith & Smith, 2009), with each organism present occupying a specific position within a food web (trophic level). For example, with respect to the primary resources, a primary producer such as phytoplankton would have a trophic level of 1, those that solely consume primary producers would have a trophic level of 2 (primary consumer) and so on (Figure 2.1). Trophic levels can be represented fractionally (fractional trophic levels) as predators can consume prey at different trophic positions within the food web. It is through this consumption that energy is transferred from basal production by net primary production to apex predators (Figure 2.1). Net primary production is the rate at which primary producers fix organic carbon via photosynthesis minus cell respiration and is classed as input energy into the food web that cascades up to top predators (Trites et al., 1997). The net efficiency of photosynthesis by primary producers in the marine ecosystems is considered to be 3-6% (Miyamoto, 1997), and <10% of energy of that capture is transferred between consecutive trophic levels (i.e., > 2) up to apex predators (Lindeman, 1942; Figure 2.1), termed trophic transfer efficiency.

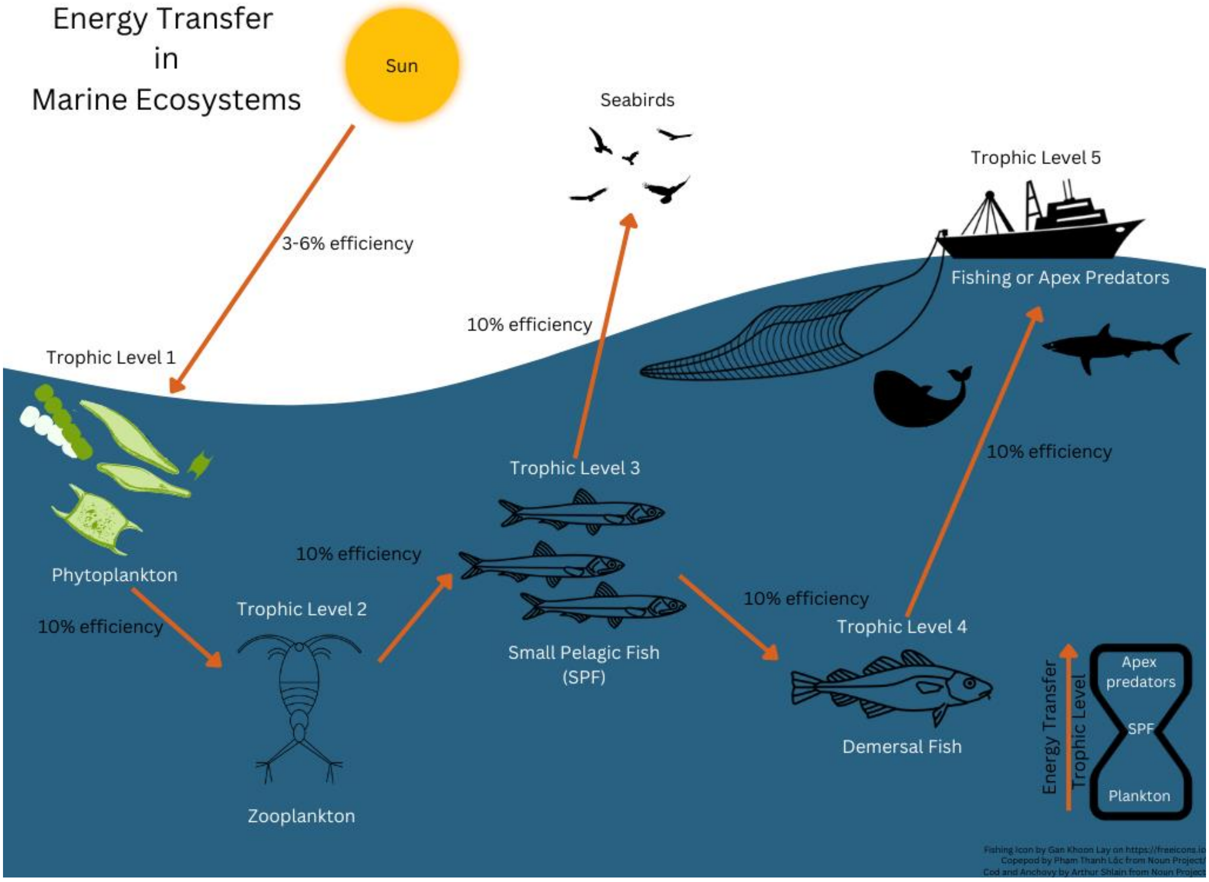

Figure 2.1 - Example of trophic transfer in a marine ecosystem. Figure generated in Canva. Zooplankton (copepod), demersal fish (cod), and small pelagic fish (anchovy) icons from the Noun Project. Fishing icon from freeicons.io.

Species positioned in the mid trophic levels are key regulators of ecosystem dynamics as they channel energy and nutrients from plankton to top predators (Figure 2.1). One key group of mid-trophic species are pelagic schooling fish or small pelagic fish (SPF), e.g., anchovy and sardines, which dominate many marine ecosystems (Rice, 1995). Overall, food webs determine how the marine ecosystem functions, and thus resilience of the ecosystem itself (Libralato et al., 2014).

The study of trophodynamics (i.e., the dynamics of nutrition and metabolism), first proposed by Lindeman (1942), is fundamental in understanding the flow of energy through an ecosystem. Later studies have strengthened the concept of trophodynamics, paving the way to incorporate food webs to aid ecosystem process understanding (Libralato et al., 2014). Ecologists have debated what controls and regulates marine food webs, for example whether the primary control is ‘top-down’, regulated by predators, or ‘bottom-up’ regulated by resources (Hunter & Price, 1992).

The food web can be controlled by “top-down” processes i.e., by higher trophic levels (e.g., seabirds or marine mammals) or anthropogenic pressures such as fishing. Some food webs are also controlled by intermediary trophic levels through ‘wasp-waist’ control, observed for SPF in upwelling ecosystems (Cury et al., 2003). Another mechanism, is “bottom-up” control, the inverse of top down, where the food web regulation is governed by lower trophic levels e.g., primary production, which could be through changes in temperature (Frederiksen et al., 2006; Ottersen et al., 2004). Higher temperatures can increase metabolic costs of an organism, thereby requiring more energy from lower trophic levels, to maintain their minimal viable size, whilst also reducing the energy that is passed onto higher trophic levels (Arim et al., 2007). Consequently, this can reduce the proportion of basal and apex species, as such reducing the length of the food chain (Arim et al., 2007; Glazier, 2012). Following on from bottom-up control, primary production has been used as a good predictor of translating the potential yield of the world’s ocean (Ryther, 1969). More recently Ware & Thomson (2005), used satellite derived estimates of chlorophyll-a (Chl-a), to analyse the coupling between biomass of primary producers in fisheries production, showing strong bottom-up linkages. Frank et al., (2006), studied the northwest Atlantic, indicating the dependence of fisheries yields on primary production but also the importance of temporal dynamics to quantify top-down and bottom-up control, as this can vary both temporally and spatially. Similarly, satellite remote sensing has been used to show that survival of larval haddock off the shelf of Nova Scotia, Canada depends on the timing of the local spring phytoplankton bloom (Platt et al., 2003). Bottom-up control of fish production has been demonstrated in many ecoregions (Ware, 2000), supporting the general approach of tracing pathways involved in the translation of primary production to fishery yields (Stock et al., 2017)

It is more likely that there is not a single control on the ecosystem but a combination, with the balance being dependent on the ecosystem’s state, diversity, and integrity (Cury et al., 2003; Hunter & Price, 1992). These issues raised by the debate in ecosystem regulation processes are important because marine food webs support the world’s fisheries and understanding the balance of the different controlling mechanisms can help provide insights into the structure and functioning, and potentially resilience, of the ecosystem (Reid et al., 2000).

It has been considered that energy transfer in oligotrophic (poor in nutrients) systems is less efficient than in productive systems (generally considered to be 0.1 or 10% of energy transferred between trophic levels; Jennings et al., 2002). In oligotrophic oceans, primary production (PP) is dominated by picophytoplankton, between 0.2 and 2 μm in size, (Agawin et al., 2000), that are not efficiently captured by copepods, part of the mesozooplankton (between 0.2 to 20mm in size; Irigoien et al., 2014). This may imply there is lower transfer efficiency from primary producer to primary consumers and subsequently higher trophic levels than in more productive systems (Ryther, 1969). There are a lot of uncertainties within trophic transfer efficiencies and estimates of energy transfer can span several orders of magnitude (Bonsall & Hassell, 2007). Therefore, understanding the processes, particularly from lower trophic levels, is key in understanding the functioning and structure of marine ecosystems.

The ecosystem control principles underpin many ecosystem-based models (e.g., Coll et al., 2008; Pauly & Christensen, 1995), which have been used to link PP to fisheries. Multi-trophic level studies of the North Sea have shown there is strong evidence for bottom-up control on the ecosystem (Frederiksen et al., 2006) and within the Celtic Sea, between 1986-2007 the planktonic and herring community were not strongly regulated by top-down control (Lauria et al., 2012). However, these models like many others find collecting baseline data on abundance particularly challenging for non-commercial species that are only caught sporadically (Temple et al., 2018; Więcaszek et al., 2015). Similarly, there is limited to no data on recent species introductions or re-introductions in the area, e.g., anchovy in the Celtic Sea. These species may impact the trophic coupling of the ecosystem. As small pelagic fish pertain to mid-trophic levels, improvements in their baseline data can help disentangle key questions regarding how the Celtic Sea ecosystem is regulated, developing on work on previous work e.g., Lauria et al. (2012) and Hernvann et al., (2020).

2.2 Small pelagic fish in marine food web models

A variety of ecosystem models have been used to understand trophic ecology, such as Ecopath with Ecosim (EwE; Christensen & Walters, 2004), multi-species virtual population analysis (MSVPA; Helgason et al., 1979; Pope, 1979), and stochastic multi-species models (Kinzey & Punt, 2008; Lewy & Vinther, 2004). All of which have been developed to promote ecosystem-based management of fisheries and to understand ecosystem functioning.

EwE is an ecological modelling software built and developed since the 1980s. EwE has three main components: Ecopath (see Figure 2.2 for an example model output), Ecosim and Ecospace. Ecopath is a static snapshot of the system (Christensen et al., 2008), Ecosim is a dynamic simulation module that is used for policy related questions and Ecospace is a spatial-temporal dynamic module used for protected area management (Christensen et al., 2008). The first Ecopath model was created by Polovina, (1984) on French Frigate Shoals, since then Ecosim was developed by Walters et al., (1997) and Ecospace by Walters et al., (1999). Globally, there are over 100 models that have utilised EwE (Colléter et al., 2015), to understand the impacts of fishing on the ecosystem (Adebola & Mutsert, 2019; Coll et al., 2008; Deehr et al., 2014; Heymans & Tomczak, 2016; Johnson, 2006), explore policy options (Chagaris et al., 2015; Dias et al., 2022; Heymans et al., 2009; Montero et al., 2021; Sreekanth et al., 2021; Wang et al., 2012), and simulate ecosystem response to climate change (Ainsworth et al., 2011), amongst many other questions and increasingly to facilitate ecosystem based management. One main drawback of models such as these (EwE, MSVPA and stochastic multi-species models), is the reliance on robust data for local fish diets to estimate accurate predation parameters. Therefore, it is important to ensure that inputs to the models are local and up to date to reflect system investigated.

To date, there have been several ecosystem models developed for the Celtic Sea area, with the majority focussing on using the application Ecopath with Ecosim (Bentorcha et al., 2017; Guénette & Gascuel, 2012; Hernvann et al., 2020; Lauria, 2012; Lauria et al., 2016; Potier, 2021; Figure 2.3). The first EwE model was created in 2009 with each further iteration of the model developed in response to specific research questions (Figure 2.3). The latest model by Potier, (2021), updated the model generated by Hernvann et al., (2020) through the development of specific fishing fleets rather than monospecific fleets as previously assigned, and in doing so provided a more representative overview of the fishing occurring in the Celtic Sea. Hernvann et al., (2020) made major developments from the former model (Moullec et al., 2017). One of the main changes was through the use of a new diet matrix that incorporates stomach content data, stable isotope, and literature data into a Bayesian hierarchical model generated into an R package called ‘EcoDiet’(Hernvann et al., 2022). The inclusion of all these data types ensures the diet matrix provides a representation of the functional group’s diet. Hernvann et al., (2022) used a combination of all three data types and reiterates the importance for updating stomach data to be within the area of interest when using this method. Therefore, it is important that stomach sampling campaigns continue to fill missing data gaps for species, such as SPF within the Celtic Sea. Currently, the models presented in Table 2.2 use either Fishbase diets (Froese & Pauly, 2009), or DAPSTOM (Pinnegar, 2014) for diets of small pelagic fish. However, the SPF stomach samples used are not always collected in the Celtic Sea (e.g., Table 2.2).

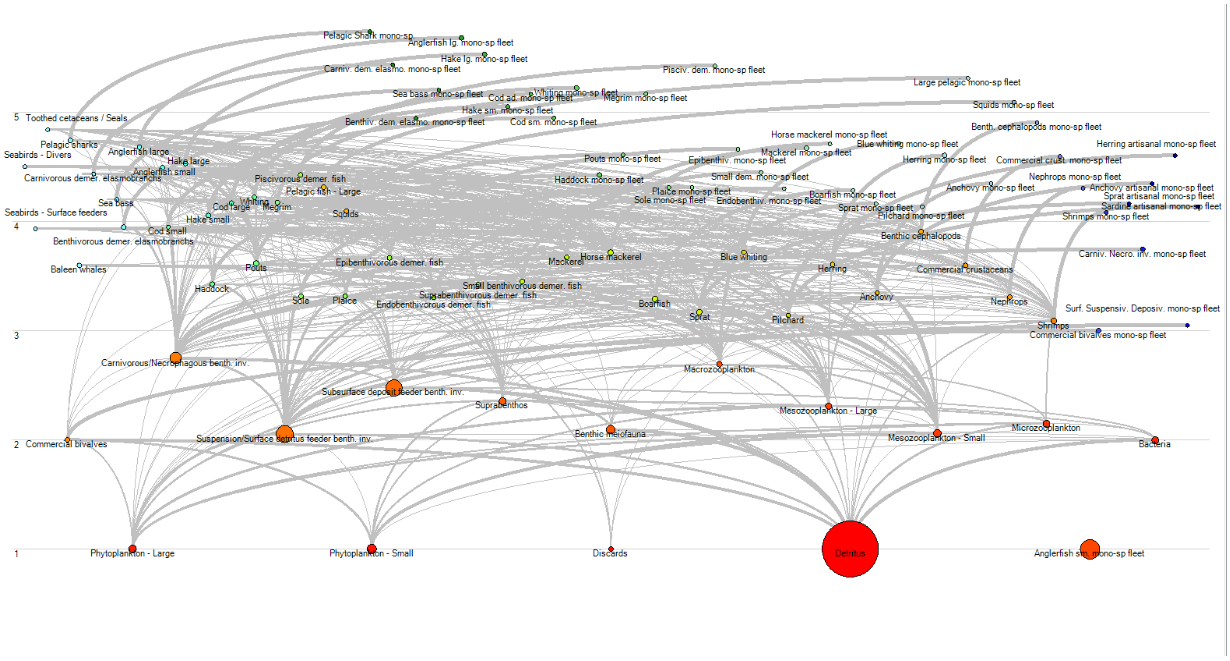

Figure 2.2 – An Example of the Ecopath model of the Celtic Sea ecosystem from Hernvann et al., (2020).

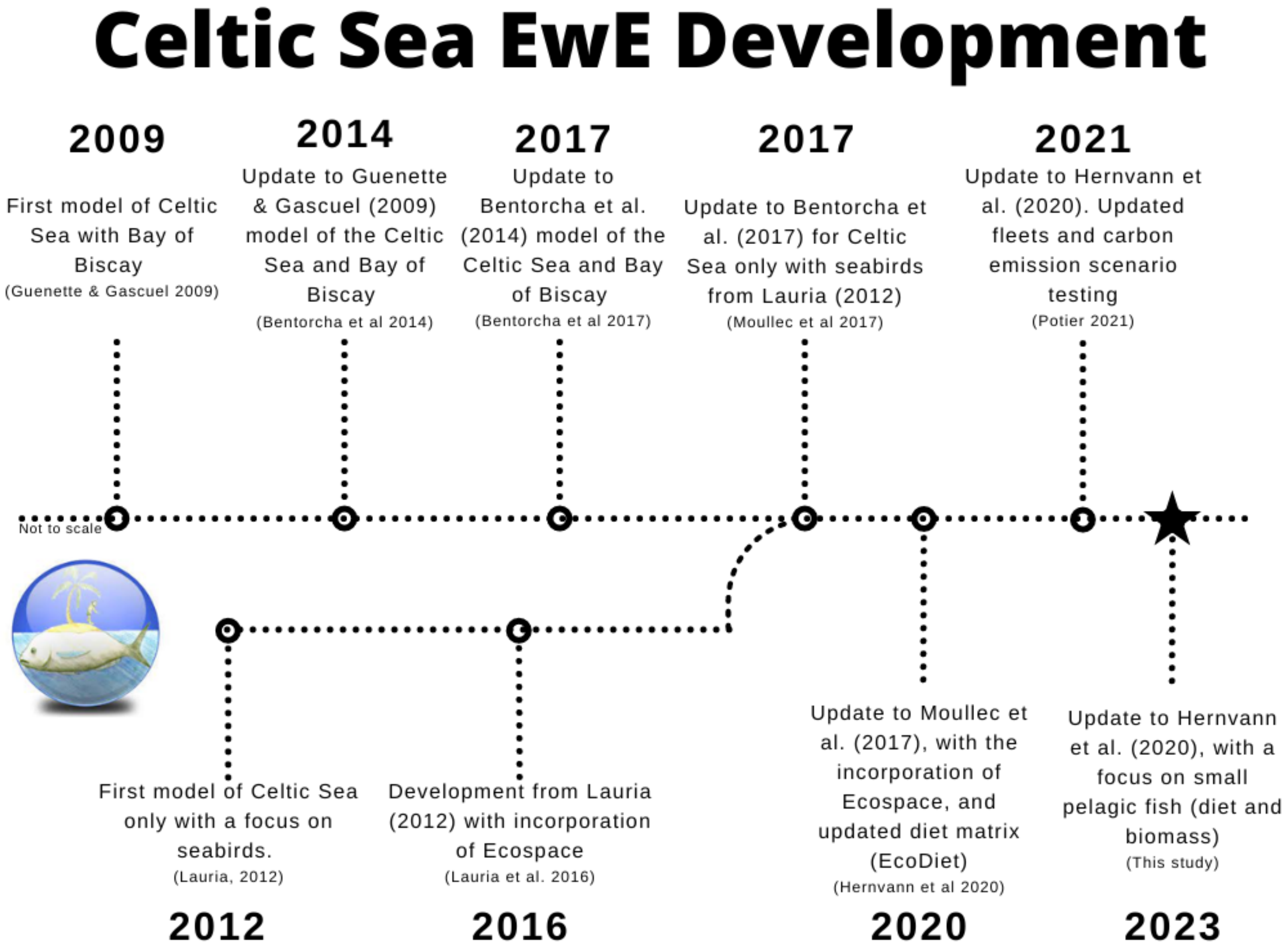

Figure 2.3 - Development of the Celtic Sea ecosystem Ecopath with Ecosim (EwE) model from 2009 - present day.

In the case of the pre-existing EwE models, SPF have not always been considered as single functional groups; this could be due to lack of data, such as biomass and/or diet data, required as inputs to the steady state model, Ecopath, or changes in the ecosystem. For example, anchovy had been included in the functional group ‘Medium Pelagic Fish’ within the latest Celtic Sea model. Prior to that, the first Ecopath model, generated in 1985, had not considered this species as it was absent in the region. In 2013, a new pelagic survey mapped and quantified anchovy in the Celtic Sea (Doray et al., 2021). Anchovy biomass has increased in the region and has gradually expanded its distribution. Thus, anchovy should be considered as a separate functional group within the model to reflect the change that has occurred. Biomass data for SPF from 2013 has been collected annually through the Cefas' PELTIC survey, and as such can be used as an input to the model. Further, improvements to the pre-existing model (Hernvann et al., 2020) can be made by the inclusion of newly available biomass data from Cefas' Peltic surveys and localised stomach content analyses of SPF.

Table 2.1 Ecopath with Ecosim developments for the Celtic Sea, the key questions the model aimed to answer, and understanding how small pelagic fish (SPF), anchovy, herring, sardine, Atlantic horse mackerel, mackerel, and sprat are represented within the model. CS = Celtic Sea, BoB = Bay of Biscay.

Reference	**Area**	**Aim**	**Model component used**	**Built on previous model?**	**How have SPF been addressed?**		
					Functional Groups	**Diet Data**	**Biomass Data**
Guenette & Gasuel (2009)	CS & BoB	Impact of fishing on this ecosystem using an Ecosim model and considering fisheries, changes in productivity and trophic relationships	Ecopath; Ecosim; EcoTroph	NA	All six SPF included but noted that anchovy was found in BoB only.	Fishbase	ICES where available or estimated by model
Lauria et al. (2012)	CS	Describe the trophic linkages in the Celtic Sea ecosystem, focusing on the functional role of apex predators (seabirds)	Ecopath; Ecosim	NA	Grouped sardine, sprat, herring, anchovy together	DAPSTOM	ICES where available or estimated by model
Bentorcha et al. (2014)	CS & BoB	The impact of fishing on the food web over the last three decades 1980-2012	Ecopath; Ecosim; EcoTroph	Updated from Guenette & Gascuel (2009) modified for 1980 and updated for 2012. Abundance series from the reports of ICES stock	All six SPF included but noted that anchovy was found in BoB only.	Fishbase	ICES where available or estimated by model

				assessment working groups, are used for the adjustment of a Ecosim model			
Lauria et al. (2016)	CS	Update to Lauria (2012) to include new functional groups, update temporal dynamics and fully parameterises a spatial version of the model	Ecopath; Ecosim; Ecospace	Update to Lauria (2012)	All six SPF included but sardine, sprat and anchovy grouped together in Clupeid group	DAPSTOM	ICES where available or estimated by model
Bentorcha et al. (2017)	CS & BoB	The impact of fishing on the food web over the last three decades 1980-2012	Ecopath; Ecosim; EcoTroph	Updated from Bentorcha (2014)	All six SPF included but noted that anchovy was found in BoB only.	Fishbase	ICES where available or estimated by model
Moullec et al. (2017)	CS	(i) analyse the trophic functioning of the Celtic Sea and the Bay of Biscay, (ii) investigate ecosystem changes over the 1980–2013 period and, (iii) explore the response to management measures at the food web scale.	Ecopath; Ecosim; EcoTroph	Updated from Bentorcha et al. (2017) by splitting Celtic Sea and Bay of Biscay into separate ecosystems from 1980 - 2013.	No specific anchovy group, incorporated into Medium pelagic fish functional group	Fishbase – See Table 2.2	ICES where available or estimated by model

Hernvann et al. (2020)	CS	Interdependent impacts of fishing and climate change on the structure and functioning in the Celtic Sea. Represent the effects of the environment on the distribution and productivity of functional groups, from phytoplankton to top predators from 1985 - 2016.	Ecopath; Ecosim; Ecospace	Updated from Moullec et al. (2017) by developing a spatio-temporal explicit model using Ecospace, by incorporating biogeochemical model output (NEMO-ERSEM) and species distribution models. Generated a new Ecopath model for 1985 and 2016.	No specific anchovy group, incorporated into medium pelagic fish functional group	Same as Moullec et al. 2017 + SIA data + literature review + EcoDiet R Package	ICES or EVHOE where available or estimated by model
Potier (2021)	CS	What are the ecosystem effects of each of the Celtic Sea fleets and their interactions via food webs in the context of climate change? And vice versa: how is climate change (CC), through its ecosystem effects, likely to affect each of the Celtic Sea fleets	Ecopath; Ecosim; Ecospace	Updated from Hernvann et al. (2020) the 1985 Ecopath model to include multispecific definition of fleets. The Fs simulated by Hernvann et al. 2020 over the period 1985-2016 are used as forcing time series in the new built model.	Same as Hernvann et al. (2020)	Same as Hernvann et al. (2020)	Same as Hernvann et al. (2020)
This study	CS	Describe the trophic linkages in the Celtic Sea ecosystem, focusing on the functional role of pelagic fish (e.g., anchovy) from 2013	Ecopath; Ecosim	Updated from Hernvann et al. (2020) to focus on SPF.	Removed the medium pelagic group. New group defined for anchovy. All SPF are species separate functional groups	Patel et al. (2023) - DAPSTOM + PELTIC 2019 + EcoDiet R Package	PELTIC + ICES + EVHOE

Table 2.2 - Location of small pelagic fish diet samples used in Moullec et al. (2017).

Common Name	Species	Reference	Source	Locations
Mackerel	*Scomber scombrus*	-	Fishbase	general
Horse mackerel	*Trachurus trachurus*	Smith-Vaniz, (1986)	Fishbase	general
Herring	*Clupea harengus*	Rice, (1963)	Fishbase	Isle of Man Irish Sea
Sardine	*Sardina pilchardus*	Bode et al., (2004); Whitehead, (1985)	Fishbase	general
Sprat	*Sprattus sprattus*	Oven et al., (1995)	Fishbase	Black Sea
Anchovy	*Engraulis encrasicolus*	Plounevez & Champalbert, (2000)	Reference	Bay of Biscay spring spawning

2.3 Development in diet studies to understand trophic relationships

Diet studies (e.g., stomach content analyses) can be utilised to overcome uncertainties in trophic transfer efficiencies, predator-prey interactions, and evaluation of fractional trophic levels within an ecosystem (Pauly & Christensen, 2000; Pauly & Sa-a, 2000). The outcome of diet studies are utilised as key inputs to ecosystem models, thus required at a regional scale, due to variation of predators and prey at larger scales.

Over the past 70 years there have been many methods and developments within diet studies (e.g., Buckland et al., 2017; Hynes, 1950), the majority of which analysed stomach contents. However, there is still not a consensus on best practice. Amundsen & Sánchez-Hernández, (2019) recommended methods based on three main types of objectives, primarily related to quantification:

- Relative diet composition
- Prey selectivity
- Food consumption rate

The first of these (relative diet composition), is the focus of this review and is the objective, of many feeding studies. It provides information on trophic ecology and basic feeding traits, as well as diet shifts (seasonally and ontogenetically). Specific metrics of relative diet composition are consistently calculated throughout the literature (as described in Buckland et al., 2017):

- Frequency of occurrence (presence/absence) - the proportions of individuals containing a particular prey.

- Numerical (count) – Number of items of a prey group as a proportion of the total number of prey items.
- Volumetric points – Visual estimate of relative volumes by assigning a number from 0-10 for a particular prey group.
- Volumetric grid – Area of each prey type when the prey is squashed to uniform depth.
- Volumetric displacements- Volume of water displaced by each prey type.
- Gravimetric weight – Wet or dry weight of each prey type.

Each of these metrics has limitations, for example, numerical count and frequency of occurrence often lack the size-based aspect of the prey item, i.e., the presence of one fish is equivalent to one phytoplankton. Therefore, volumetric or gravimetric methods were considered, with many studies adopting the time-consuming gravimetric weight metric (e.g., Cortés, 1999; Stergiou & Karpouzi, 2001). Amundsen & Sánchez-Hernández, (2019) found little difference between the gravimetric and the volumetric points metric results and therefore recommended the more time efficient volumetric points method, over the gravimetric method. In general, stomach content analyses (SCA) are subject to bias and limitations due to differential digestion rates, degradation of identification structures, snapshot information, uncertain representation of whole population and undetected secondary ingestions (Amundsen & Sánchez-Hernández, 2019).

To combat these limitations, there are several techniques that are being used to complement SCA, such as faecal or regurgitates analyses, behavioural observations, or molecular techniques such as SIA, fatty acids, and DNA methods. Numerous studies have used a combination of SCA and stomach isotope analyses (SIA), for example for small pelagic fish in the Mediterranean Sea (Bachiller et al., 2021), and in bottlenose dolphins (*Tursiops truncates;* Giménez et al., 2017). SIA has emerged as a suitable approach to reconstruct diet and trophic levels through mass-balance mixing models. SIA provides integrated information on the diet of predators over a longer time periods than SCA. This method also has its caveats and biases, however, using stable isotopes to assess the diet of a generalist and opportunistic predators can be challenging due to the broad spectrum of preys consumed. Potential prey species may have a similar isotopic value, resulting in loss of taxonomic resolution when using a mixing model. One major limitations of SIA is the inability to obtain information on the size of prey, an important factor in developing size based trophic models. Other methods such as eDNA, can identify easily digestible organisms such as jellyfish. However, this technique only provides a presence-absence of prey in the diet.

In summary, whilst there is not a standardised method to conduct stomach analyses, using technological advancements such as eDNA and SIA can complement existing visual and gravimetric methods. These methods are complementary as they each resolve a limitation of another method. However, it is important that the chosen method is designed to be compatible with earlier studies, as this can enable the generation of longer diet composition time series of the species of interest. Therefore, as a minimum, the volumetric point method would provide both a more efficient and compatible dataset, should there be economical, time or resource constraints preventing a multi-method approach.

2.4 Small pelagic fish diet studies in the Celtic Sea and limitations

Many diet studies in the Celtic Sea have focused on commercially important demersal and large pelagic species, for example, European hake (*Merluccius merluccius*), European haddock (*Melanogrammus aeglefinus)*, Atlantic cod (*Gadus morhua)*, whiting (*Merlangius merlangus)*, megrim (*Lepidorhombus whiffiagonis),* pollack *(Pollachius pollachius)*, European plaice (*Pleuronectes platessa)*, common sole (*Solea) solea,* black-bellied angler (*Lophius budegassa)*, blue whiting (*Micromesistius poutassou),* and saithe *(Pollachius virens)* (du Buit, 1982, 1992, 1995, 1996; Mahe et al., 2007; Pinnegar et al., 2003; Rault et al., 2017). To our knowledge, there have been limited diet studies of SPF in the Celtic Sea region (Hillgruber & Kloppmann, 2001; Lamb et al., 2019; Pinnegar et al., 2015). Lamb et al., (2019) used molecular techniques to understand jellyfish consumption by mackerel, sprat, and sardine, as jellyfish are easily digested. Their study showed that mackerel consumed jellyfish relatively frequently compared to sprat and sardine (Lamb et al., 2019). More traditional techniques (i.e., through microscopy) in the Celtic Sea demonstrated that mackerel larvae relied mostly on copepod nauplii and eggs when first feeding and later shifted towards cannibalistic piscivory during the next stages of growth (Hillgruber & Kloppmann, 2001). Pinnegar et al., (2015), analysed mackerel data from DAPSTOM (a public database of fish diet composition) in the Celtic Sea, showing copepods were the main prey of their diet. As far as we are aware there have limited recent studies using traditional stomach sampling techniques of SPF in the Celtic Sea. Therefore, Chapter 3 –will investigate the diet composition of SPF in the Celtic Sea and explore the effects of seasonality on their diet, as Scott et al., (2023) indicated that season is a significant factor in zooplanktonic community, and therefore may influence SPF diet.

2.5 Satellite remote sensing as input to models

Satellite remote sensing has provided a large scale, cost-effective solution to observing the oceans. However, in order to use these retrievals (derived from algorithms) at global or regional scales, for example for use in ecosystem modelling (e.g., satellite derived primary production or phytoplankton size classes), they must first be validated by comparison with *in situ* measurements.

Since the deployment of the NASA satellite Coastal Zone Color Scanner (CZCS) in 1978, the first instrument devoted to the measurement of ocean colour, numerous environment variables can be detected from space e.g., Sea Surface Temperature (SST), Chlorophyll concentration (Chl-a) (Chassot et al., 2011). After CZCS, there have been several operational satellites with sensors dedicated to ocean colour e.g., MODIS-Aqua (National Aeronautics and Space Administration - NASA), MERIS (European Space Agency - ESA), Sentinel 3 – OLCI (ESA). The most common remote sensing variables used are SST and Chl-a, followed by surface salinity, windspeed, sea surface height and chlorophyll derived primary productivity (Williamson et al., 2019, Chassot et al., 2011). Some of the newest satellites e.g., Sentinel 3, have higher resolution, and are able to provide continuous ocean colour monitoring, whilst older satellites are to be decommissioned. For Sentinel 3, validation is still ongoing and in optically complex waters (i.e., multiple different water constituents, such as coastal waters) regional validation is required before satellite products can be utilised

(Toming et al., 2017). Retrieval algorithms are sensor specific, and so requires optimisation and validation before use, as all sensor deployments are slightly different.

Empirical models of PP are usually based on Chl-a, which is often geographically specific, and have been studied extensively. Ryther & Yentsch, (1957) pioneered the approach, using a simple regression between log Chl-a and PP and since then a number of studies have improved and developed upon this (Campbell & O'Reilly, 1988; Eppley, 1972). More recently, models have included other parameters such as chlorophyll specific carbon fixation in the water column, sea surface daily photosynthetically available radiation (PAR), the euphotic depth and chlorophyll concentration at the surface from a satellite sensor (Behrenfeld & Falkowski, 1997). Semi-analytical approaches have also been developed (Platt & Sathyendranath, 1988, 1993), utilising satellite remote sensing derived Chl-a. The difference between these two approaches is the complexity of the semi analytical approach (Platt & Sathyendrath, 1993), that requires the evaluation of many photosynthetic parameters at various illuminations. End users use satellite derived carbon and chlorophyll for various different applications.

Over the last few decades, there have been many strides in refining the algorithm from satellite derived Chl-a to PP (Behrenfeld & Falkowski, 1997; Longhurst et al., 1995). Satellite derived PP has been used in food web analysis to understand how primary productivity impacts fisheries yields. Chassot et al., (2011), and Friedland et al., (2012), linked phytoplankton productivity from SeaWiFS to catch yields, with adjustment to the trophic level of the catch. This adjustment meant that the length of the food web can be taken into consideration. Friedland et al., (2012) updated Chassot et al., (2010)'s model by adding mesozooplankton productivity and particle fluxes into the equation as a ratio between secondary production and primary production.

Despite there being strong relationships between phytoplankton production (primary production) and fish catches (Ware & Thomson, 2005), the relationships between these two trophic levels are not always simple (Stock et al., 2017), in part, as catches are not necessarily representative of biomass.

Stock et al., (2017) model supported Ryther’s hypothesis that PP and trophodynamics processes must act cooperatively to generate observed catch gradients. The model used global fish catch data (Sea Around Us - Pauly et al., 2020) and plankton food web fluxes from an earth system model (ESM2.6 - utilising satellites Chl-a retrievals from SeaWIFS), to conceptualise the flow of energy in marine ecosystems.

In the development of food web models, satellite remote sensing variables e.g., chlorophyll-a are beginning to be utilised. Chlorophyll-a can be derived through the use of maximum band ratios or neural networks e.g., standard products from European Space Agency (ESA). Vertically Generalised Production Model (VGPM – Behrenfeld & Falkowski, 1997), utilises satellite retrievals collected by MODIS-Aqua and SeaWiFS to generate primary production. Previous EwE models in the Celtic Sea used a time series of PP as a forcing variable of the productivity of phytoplankton groups (Hernvann et al., 2020). However, MODIS-Aqua is due to be decommissioned, therefore, to continue to use products such as VGPM newer satellites are required. Newer satellites, such as the Sentinel 3 mission from the European Space Agency, are of higher spatial resolution (300m compared to MODIS – 1km), with retrievals still undergoing validation. Currently the satellite retrievals for Sentinel 3-OLCI have not been validated within the Celtic Sea. The use of satellite derived variables requires validation for each region as they may be affected by environmental specificities (Toming et al., 2017). Therefore, Chapter 4 will investigate the performance metrics of S3A-OLCI chlorophyll-a retrievals with *in situ* data collected onboard Cefas’ PELTIC survey in the Celtic Sea.

For the development of ecosystem-based models, the importance of localised data is paramount for understanding how the ecosystem is regulated (e.g., top-down or bottom-up control). The Celtic Sea ecosystem regulation is still unclear with both indirect and direct top-down and bottom-up controls on the ecosystem (Lauria et al., 2012). Species in the system such as anchovy have increased within the region and are part of mid trophic group called SPF, a key group in energy transfers to apex predators (bottom-up) and they themselves are potentially regulated by predators (top-down). The impact of SPF community change and how this may affect ecosystem regulation in the Celtic Sea is poorly understood. Whilst many previous models in the region have included SPF in their model, the data (biomass and diet) is often limited. This literature review highlights the importance of developing the knowledge base of SPF in the Celtic Sea, by the improving of data representing lower trophic levels. This body of work as stated in the Aims and Objectives, will include novel stomach content analyses using the volumetric method of SPF and validation of newly operational satellites (Sentinel 3) to represent phytoplankton size classes, in order to progress pre-existing models in the Celtic Sea.

3

Seasonality of diet overlap among small pelagic fish in the waters southwest of the UK

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Chapter 3 – Seasonality of diet overlap among small pelagic fish in the waters southwest of the UK

3.1 Introduction

Small pelagic fish (SPF) are important components of marine ecosystems. They are predominantly planktivorous and as such, link lower and higher trophic levels (TLs) (Cury et al., 2000). They support 25% of the world’s total fish landings (in weight), primarily through anchovy, sardine, mackerel, and herring (FAO, 2018). The state of their populations therefore plays a critical role, ecologically, economically, and socially. Thus, understanding the underlying mechanisms driving their stocks and population dynamics is vital. SPF are often short-lived with high recruitment, and so may be a useful indicator species for ecosystem changes, because of their important ecological links between plankton and higher TLs (Bakun, 2006). Furthermore, SPF are affected by changes in environmental conditions (Van Der Lingen et al., 2006), both indirectly, through their planktonic prey, and directly, by interannual variability in recruitment (Lloret et al., 2004; Patti et al., 2020). In addition, biomass changes in SPF could be partially attributed to inter- and intra-specific interactions, e.g., food competition (Bachiller et al., 2021; Utne et al., 2012). The feeding behaviour of these species within the ecosystem influences the stability of marine food webs. Generalist (non-selective) feeders are able to readily switch between prey types depending on availability and can help maintain stability by compensating for oscillations of specific food sources generated by environmental changes, thus supporting energy flows (Beckerman et al., 2006; Dunne et al., 2002; Gravel et al., 2011; Rooney et al., 2006). As SPF are prey for piscivorous fish (Trenkel et al., 2005), marine mammals, and seabirds (Kaschner et al., 2006), food webs with SPF that are generalist (non-selective) feeders are deemed to be more resilient to climatic variability (Beaudoin et al., 2001).

The Celtic Sea, Irish Sea, and English Channel, defined as the Celtic Seas ecoregion (ICES, 2004;Figure 1.1), supports important commercial mixed fisheries targeting many different benthic, demersal, and pelagic stocks. The ecoregion is home to a diverse range of SPF species, including Atlantic herring *Clupea harengus*, Atlantic mackerel *Scomber scombrus*, sprat *Sprattus sprattus*, European anchovy *Engraulis encrasicolus*, European sardine *Sardina pilchardus*, and Atlantic horse mackerel *Trachurus trachurus*. Each of these species is planktivorous for at least part of their lifecycle, and therefore they likely have overlapping diets (Bachiller & Irigoien, 2015; Raab et al., 2012). Sprat, sardine, and herring are found throughout the year in the Celtic Seas ecoregion, including during the spawning season (Bréchon et al., 2013; Wallace & Pleasants, 1972). The larvae and juveniles utilise the relatively shallow waters as nursery grounds. Horse mackerel and mackerel larvae drift from the shelf edge (the main spawning ground) into the coastal waters after hatching (Jansen et al., 2015). Anchovies overwinter within the Celtic Sea region, possibly to escape the colder waters of the North Sea (Huret et al., 2020). Several of these planktivorous species have shown substantial changes in abundance in the region (e.g., Beare et al., 2004; ICES, 2010; Shephard et al., 2014). For example, European anchovy in the area has increased since the mid-1990s (Beare et al., 2004), due to increased recruitment success (Huret et al., 2020; Petitgas et al., 2012). In contrast, some herring populations in the region have been in decline, causing fisheries closures (ICES, 2020). The region is also an important spawning and nursery ground for migratory species, notably Atlantic mackerel, and Atlantic horse mackerel (Ellis et al., 2002; ICES, 2007), which have also exhibited changes in their distribution in the region (van der Kooij et al., 2015). Sardine populations have been shown to fluctuate with climatic variability (Alheit & Hagen, 1997), and a recent increase in autumn spawning activity of sardine in the English Channel has been observed (Coombs et al., 2010). Sprat stock and structure within the Celtic Seas ecoregion is generally unknown. However, since 2013, there has been ICES advice on sprat within the region due to new surveys providing an acoustic survey index (ICES, 2022). In other regions, such as the Baltic Sea, there have been changes in sprat abundance over time (Eero et al., 2012), possibly attributable to many different factors (indirect and direct), including bottom-up processes, e.g. food availability and temperature. As such, it is acknowledged that the changes in SPF populations are partially climate driven (Alheit et al., 2009; Checkley et al., 2009).

Given the possible diet overlap between these planktivorous species, it is likely that the increase of any of these species will have an impact on the food availability for others and may particularly impact specialist feeders. Thus, understanding the dietary overlap between these co-occurring species is crucial, as it will help determine the trophic interactions within the community, and the distribution of other species within the ecosystem (Bachiller et al., 2021; Bachiller & Irigoien, 2015), ultimately affecting fisheries yields. Better understanding of the dietary overlap between SPF is also important for improving fisheries advice. This is because many fish population dynamics models use diet data to understand trophodynamics and feeding ecology to underpin fisheries management, e.g., ATLANTIS (a spatially explicit end-to-end marine ecosystem model with dynamically integrated physics, ecology and socio-economic modules; Audzijonyte et al., 2019; Fulton et al., 2004), Ecopath with Ecosim (Christensen et al., 2014; Pauly et al., 2000), and OSMOSE (Object-oriented Simulator of Marine Ecosystems; (Shin & Cury, 2001). In addition, single species models and individual-based models including fish energy budget can provide spatial and temporal estimates of biomass of certain SPF (e.g., Boyd et al., 2018, 2020). To our knowledge, there have only been a handful of diet studies in the Celtic Seas ecoregion (Denis et al., 2016; Hillgruber & Kloppmann, 2001; Lamb et al., 2019; Pinnegar et al., 2015). Many of the diet studies focused on higher TLs (du Buit, 1982, 1992, 1995, 1996; Mahe et al., 2007; Pinnegar et al., 2002; Rault et al., 2017), and information on SPF is limited. SPF are important facilitators of energy in ecosystems, which respond strongly to bottom-up changes (Peck et al., 2021), such as plankton availability. The planktonic communities in the Celtic Seas ecoregion change seasonally (Eloire et al., 2010; Johns, 2006); therefore, understanding overlapping resources between these SPF at the seasonal scale can help understand the ecological relevance of these species to the ecosystem.

The main aim of this paper is to adopt a multispecies approach to determine the diet composition of 6 main SPF across seasons and investigate their potential inter-specific competition in the Celtic Seas ecoregion. We hypothesise that the SPF species will have generalist feeding behaviours and similar diets within the Celtic Seas ecoregion. To investigate this, we used stomach content analyses from fish samples collected during a multidisciplinary fishery survey (Pelagic ecosystem survey in the western English Channel and Celtic Sea [PELTIC]) in October 2019 (Cefas, 2019; Doray et al., 2021) to complement the historical stomach data archived in a database, DAPSTOM (an integrated Database Portal for fish STOMach Records; Pinnegar, 2014). The compiled dataset was used to (1) simultaneously determine the diets of 6 pelagic species at different life stages (i.e., larvae and non-larvae) across seasons to establish feeding strategies (i.e., generalist vs specialist); and (2) compute a species pairs diet overlap index (Pianka) to understand potential competition between species pairs. By addressing potential trophic interactions of key pelagic species, this study provides insights relevant to fisheries management multispecies assessment and food web modelling (e.g., Bentorcha et al., 2017; Lauria et al., 2012).

3.2 Methodology

3.2.1 Sampling area

The study area includes the western English Channel, Celtic Sea, and Irish Sea, collectively defined here as the Celtic Seas ecoregion (ICES, 2004). The SPF community in this area are generally confined to shelf waters of < 200 m depth (Figure 3.1). Two seasonal front systems develop during spring and determine the main oceanographic features in the area: the Celtic Sea Front (separating the Celtic Sea from the Irish Sea) and the Ushant Front, which develops from the coast of Brittany and extends to the western English Channel (dividing the Celtic Sea from the English Channel) (OSPAR, 2000). These fronts generate spatial heterogeneity in oceanic conditions, including gradient of food distribution for SPF in this area.

3.2.2 Stomach sampling

Stomach contents of 6 main pelagic species (Atlantic herring, Atlantic mackerel, sprat, European anchovy, European sardine, and Atlantic horse mackerel) were examined in this study. The stomach contents included a combination of historical data (DAPSTOM; Pinnegar, 2014) and new samples collected onboard the PELTIC survey. These new samples were collected because the historical data for species such as anchovy were underrepresented within this region in certain seasons.

3.2.2.1 Historical data

The DAPSTOM dataset is a stomach contents database designed and built by Pinnegar, (2014), in response to a 'data-rescue' call from the EU Network of Excellence project EurOcean. The current database (version 5.3) spans from 1893 to 2016, sampled across all seasons. DAPSTOM was filtered for the 6 species of interest and samples taken from the Irish Sea, Celtic Sea, and English Channel. DAPSTOM contains both 'pooled' and individual fish stomach data (where 'pooled' data is a single record for multiple stomachs sampled, more commonly recorded in the earlier surveys). In some circumstances, the actual number of a particular prey item was not recorded; instead, the 'frequency of occurrence' of a particular prey item was collected (i.e., the number of stomachs containing a particular prey item). Therefore, all records are considered as the minimum number of prey items in the stomach, although it is possible that prey items and consumption could be underestimated (Pinnegar, 2014). The number of stomach samples used from DAPSTOM is shown in Table 3.1.

3.2.2.2 PELTIC stomach sampling survey

The PELTIC survey is an annual autumn survey conducted on board the RV 'Cefas Endeavour' and is designed and implemented by the Centre for Environment, Fisheries and Aquaculture Science (Cefas) since 2012 (ICES, 2012). This survey aimed to address gaps in the knowledge about SPF and the surrounding ecosystem to understand the role these species play in the ecosystem, and to help inform sustainable management practices.

Stomach samples used in this study were collected during the survey in 2019 (30 September to 28 October) from the Celtic Sea and western English Channel. Anchovy, sardine, sprat, and horse mackerel were sampled from catches obtained by the 20 × 40 m herring mid-water trawl. The sampling strategy was opportunistic: at each station, a minimum of 3 individuals of the same species were analysed. The total numbers of stomachs sampled of each species are found in Table 3.1(PELTIC values presented in parentheses).

Table 3.1 - Number of stomach samples per season used in the analysis, in the Celtic Sea, Irish Sea, and western English Channel. Numbers not in parentheses: the combined non-empty stomach samples from the PELTIC Survey and DAPSTOM; numbers in parentheses: non-empty stomach samples from PELTIC only. Stomachs with no season assigned and the number of empty stomachs (from a combination of seasons) were not used in further analysis. (−) No data available for the species and season. Individuals classed as larvae were ≤ 4 cm in length, all other individuals were > 4 cm. *Due to low sample numbers these samples are removed from further analyses. Numbers of empty stomachs by season are in Table A 1.

	Season					
Species	**Spring (MAM)**	**Summer (JJA)**	**Autumn (SON)**	**Winter (DJF)**	**Unknown Season**	**Empty Stomachs**
Anchovy	13	-	38 (38)	-	-	9
Herring	97	154	66 (0)	360	-	904
Herring larvae	85	-	1* (0)	2968	26	1459
Horse mackerel	98	-	22 (19)	2*	9	385
Horse mackerel larvae	-	6	7 (4)	-	40	18
Mackerel	1949	259	-	15	-	806
Mackerel larvae	-	27	3* (0)	-	85	75
Sardine	7	106	65 (41)	-	-	37
Sardine larvae	-	24	3* (0)	-	15	345
Sprat	61	1*	79 (25)	487	-	559
Sprat larvae	70	2*	11 (0)	77	-	197

Prior to stomach extraction, each fish was measured (to the nearest 0.5 cm) and weighed (nearest 0.1 g). Stomach extraction and content analysis were carried out on board following recommended methods (Amundsen & Sánchez-Hernández, 2019) and in line with methods used in DAPSTOM. Stomachs were preferably analysed immediately after extraction (or preserved in 90% ethanol for a maximum of 90 d) using a binocular microscope (Olympus SZX16 with the SZX2 base) and a magnification of 0.7−11.5 and ×10 optic lenses. The linear size of prey (mm), if fully intact, was taken. The minimum number of individuals within each prey group was recorded and they were identified to the highest taxonomic resolution. The stomach contents from historical records from the Celtic Seas ecoregion were merged with those from the survey (Table 3.1).

This data was split by meteorological seasons: spring (March−May), summer (June−August), autumn (September−November), and winter (December−February), to explore the possible effects of prey availability. As the life history of the species can influence size and prey (Wilson et al., 2018), the data was split based on fish length, into larvae (≤ 4 cm), and juveniles and adults, which together we call non-larval fish (> 4 cm). This threshold was chosen based on a natural split of around 4 cm of the available fish lengths in the dataset across the different species (Figure A 1). Spatial coverage of stomach samples is shown in Figure 3.1. Due to the inconsistency in data availability, it was not possible to analyse the dataset by specific areas, i.e., Celtic Sea, Irish Sea, and western English Channel (see Appendix - Figure A 2).

For consistency, the prey groupings were standardised based on those available from DAPSTOM and were dependent on the taxonomic resolution during identification. The numerical estimations (percentage contribution of each prey group) were calculated per SPF species by summing the minimum number of each prey group, dividing by the total number of prey, and then dividing by the total number of non-empty stomachs. Any prey group that contributed to < 3% of the overall stomach were removed for ease of interpretation and to identify the major prey groups, as rare or uncommon prey groups for species with small sample size may be overemphasised (Berg, 1979). All further analyses used the calculated proportions. It was assumed that stomachs for all individuals are at 100% and of equal capacity, as DAPSTOM does not have a stomach fullness measure. All analyses and figures were generated in R (version 3.6.3; R Core Team, 2020), and the diet composition network using R package ‘visNetwork’ (Almende et al., 2019).

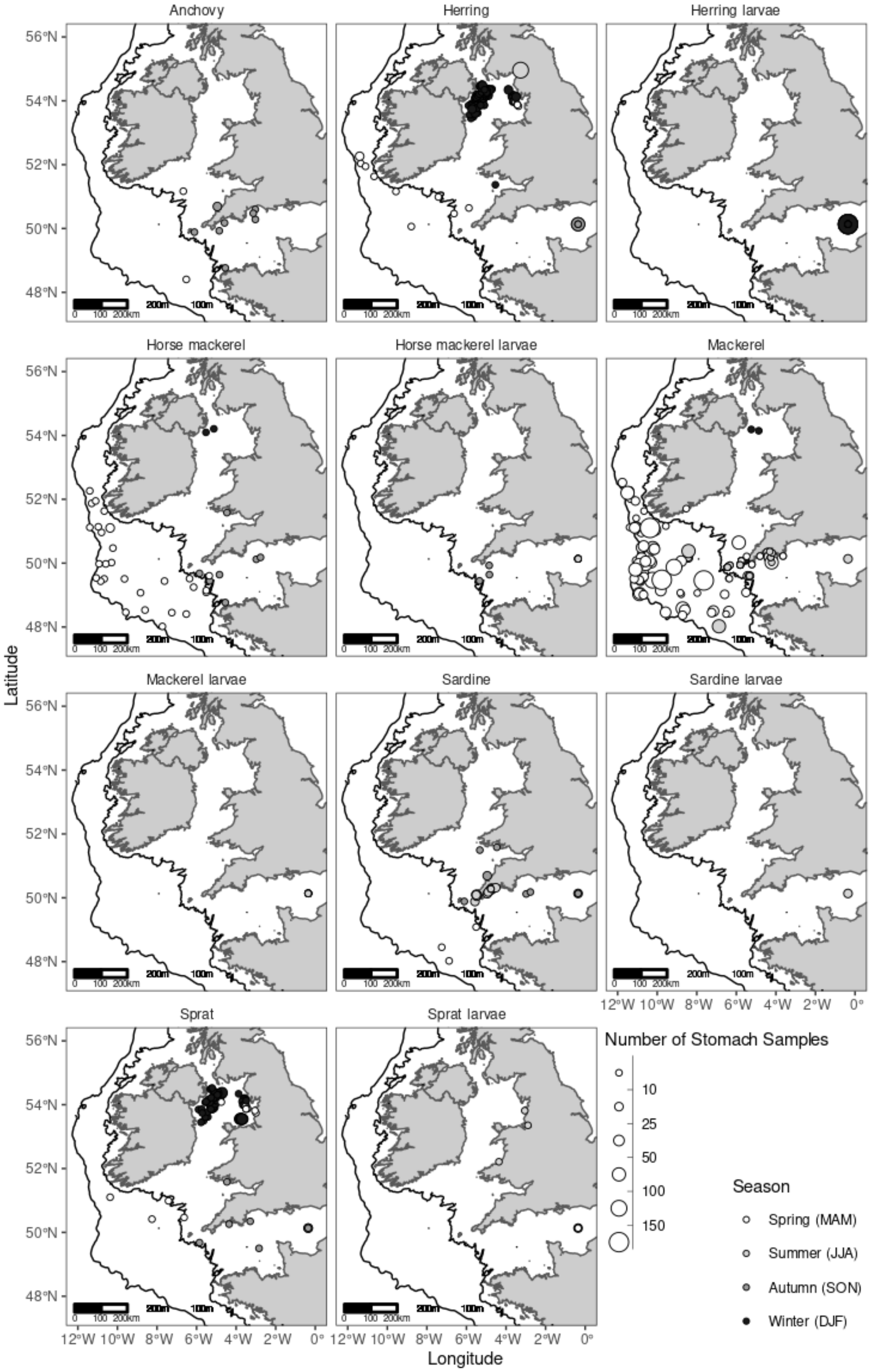


Figure 3.1 - Spatial distribution and number of non-empty stomach samples from DAPSTOM and the PELTIC survey within the Celtic Seas ecoregion for 6 pelagic species (anchovy, herring, horse mackerel, mackerel, sardine, and sprat); larvae defined as < 4 cm. Thick black lines: simplified 100 and 200 m isobaths.

3.2.3 Fractional trophic level

Fractional TL of a species represents the trophic position of the species based on weighted average contribution of prey from different TLs into its diet. Fractional TL for each pelagic species was calculated seasonally from the diet matrix representing the fractions of prey in the diet of the predator and the fractional TLs of the prey species using Equation 3.1 (Cortés, 1999):

$$TL_i = 1 + \left(\sum_{j=1}^{n} DC_{ij} \cdot TL_j \right) \tag{3.1}$$

where TL is the trophic level of predator species i, TL_j is the fractional trophic level of prey group j, DC_{ij} represents the fraction of j in the diet of i, and n is the total number of prey species. For the calculation, prey groups require a trophic level, these were obtained from literature sources (Table A 2).

3.2.4 Strategies of feeding

To understand the feeding strategy (i.e., specialised or generalised) and prey importance by diet (Bacha & Amara, 2009) of the SPF species, prey composition was analysed. We followed the graphical method described in Costello (1990) with the modifications outlined by Amundsen et al., (1996) by using prey numbers (Scharf et al., 2000). The method compares the relative frequency of occurrence (i.e., the percentage of non-empty stomachs that a prey group occurred) with the frequency in numbers (percentage of abundance) as described in Bachiller et al., (2021).

To examine how relative prey size (linear length in mm) differs among fish species across seasons we generated relative frequency histograms of predator/prey size ratios (PPSRs) of prey consumption as described in Bachiller et al., (2013, 2021). The size of prey was taken from measurements on the PELTIC survey or DAPSTOM. For the prey groups where size information was not available, size ranges from literature were used (Table A 3). A high PPSR value represents smaller prey items consumed, while lower PPSR values larger items ingested into the stomach (Scharf et al., 2000).

3.2.5 Diet overlap

From the relative prey proportions generated from stomach data, three different overlap indices were computed for further analyses: Morisita, Schoener (also known as percentage overlap), and Pianka (Krebs, 1999). Although the Morisita index (range 0–1, where 0 = no similarity and 1 = complete similarity) takes into consideration the abundances of the prey groups within the stomachs and is less dependent on sample size (Krebs, 1999; Wolda, 1981), it can overrepresent similarities, with values sometimes exceeding 1 (i.e. >100%) (Chao et al., 2006). On the other hand, the Schoener percentage overlap (Schoener, 1970) is often biased by sample size (Krebs, 1999), and was not considered for our data, which included varying sample size for six species. We therefore focused only on the Pianka overlap index (Pianka, 1973), defined by Equation 3.2, for further analysis.

$$O_{jk} = \frac{\sum_{i}^{n} p_{ij} p_{ik}}{\sqrt{\sum_{i}^{n} p_{ij}^2 \sum_{i}^{n} p_{ik}^2}} \tag{3.2}$$

where O_{jk} = Pianka's measure of niche overlap between species j and species k, p_{ij}=proportion of resource i of the total resources used by species j, p_{ik} = proportion of resource i of the total resources used by species k, and n = total number of resources states. Pianka overlap ranges from 0 (where there are no resources in common) to 1.0 (a complete overlap). The Pianka overlap was calculated using R Core Team (2020; version 3.6.3) and package 'spaa' (Zhang, 2016). The Pianka index was bootstrapped with 1000 iterations to estimate a 95% confidence interval. To compare the spread of the bootstrap, a normalised metric was derived (hereafter termed normalised spread - NS) which was calculated by dividing the spread of the confidence intervals by the average of Pianka index calculated from the diet matrix and multiplied by 100. The lower the normalised spread, the greater the confidence in the range as the sample-to-sample variation is smaller. This provided a defined and normalised value to compare between different samples. The Pianka index was categorised into low (<0.4), medium (0.4-0.7), and high (>0.7) (Keast, 1978; Novakowski et al., 2008). A Principal Component Analysis (PCA; Legendre & Legendre, 1998) was applied to explore the differences and overlap in the species' diet. The PCA was undertaken in R (R Core Team, 2020; version 3.6.3) using the 'factoextra' package (Kassambara & Mundt, 2020).

3.2.6 Diversity indices

Shannon diversity (H') of prey consumed and prey richness (S, defined as the total number of prey groups consumed) indices were calculated to understand whether there was a difference in diversity of prey groups between the stomachs of the SPF species. Shannon diversity index (H') is described in Equation 3.3.

$$H' = -\sum_{i=1}^{S} p_i \ln p_i \tag{3.3}$$

where pi is the proportion of the prey group made up of species *i*. Prey richness (S) is the total number of prey groups consumed.

3.2.7 Statistical analyses

An ANOVA was performed for diet overlap, H', and S between non-larval fish species to understand the differences between species and seasons. Only non-larval species (i.e., > 4 cm) were chosen due to data constraints with the larval species, with many of them only sampled during 1 season. The ANOVA was computed in R (R Core Team, 2020; version 3.6.3).

3.3 Results

3.3.1 Diet composition and feeding strategies across seasons

The diet composition of the SPF in the study area changed across seasons, highlighted by the difference in abundances of prey groups (Figure 3.2). Most of the species consumed calanoid copepods regardless of season. Values of S and H' for all non-larval species differed between seasons, with both indices statistically significant (ANOVA, F = 7.0491, p = 0.0262; ANOVA, F = 18.48, $p = 7.5 \times 10^{-12}$, respectively).

Non-larval sprat consistently consumed copepods in all seasons, particularly calanoid copepods (16− 72%; Figure 3.2). S of prey groups in non-larval sprat across the seasons was low (between 2 and 3); spring had a maximum S equal to 3 and a higher value of H’ (0.786) compared to autumn, which had the lowest H’ (0.44; Figure 3.3). The dominant prey group for non-larval sprat changed between seasons: calanoid copepods (72%) in spring, cyclopoid copepods (84%) in autumn, and teleost eggs (72%) in winter (Figure 3.2). Non-larval sprat also consumed diatoms (16%) and copepod eggs (12%) in spring. The Costello diagram (Figure 3.4) indicated that across all seasons, calanoid copepods was the dominant prey group for non-larval sprat, with > 45% occurrence. The low PPSR values indicated consumption of relatively large prey groups across all seasons (Figure 3.5).

Sprat larvae had greater S in spring and autumn (4), mostly consuming phytoplankton in spring (67%) and winter (86%). However, sprat larvae in autumn ingested an almost equal split between calanoid copepods, diatoms, other phytoplankton, and tintinnids (26, 26, 26, and 23% respectively; Figure 3.2), resulting in a higher value of H’ than in spring (1.38 and 1.00 respectively; Figure 3.3). Sprat larvae diet in winter had a lower H’ (0.41) and S (2) compared to spring and autumn.

Calanoid copepods were consumed in all seasons by non-larval herring (18−95%) and were the dominant prey groups in summer and autumn (Figure 3.2). In autumn and summer, herring almost exclusively consumed calanoid copepods (95% and 81% respectively), with a low S (2), and low H’ (0.18) in autumn Figure 3.3). The highest value of H’ was in winter (1.34) alongside the highest S (4).

There was no dominant prey group in winter (Figure 3.2). During spring, over half of non-larval herring diet was dominated by teleost eggs (54%), with the rest consisting of calanoid copepods (32%) and euphasiids (7%; Figure 3.2). In winter, herring prey group frequencies were <50% (Figure 3.4), compared to summer and autumn, in which calanoid copepods were dominant in the diet.

Similarly, herring larvae had a varied diet in winter, consuming a wider range of prey groups (winter: S = 5; spring: S = 4; Figure 3.3), and a higher H' than in spring (winter: H' = 1.51; spring: H' = 1.23; Figure 3.3). Calanoid copepods were present in spring and winter of herring larvae diet (Figure 3.2), accounting for 51% of the ingested prey in spring, with the remaining 49% equally split between cirripedes, copepod eggs, and bivalves. No data for herring larvae in summer and autumn were available.

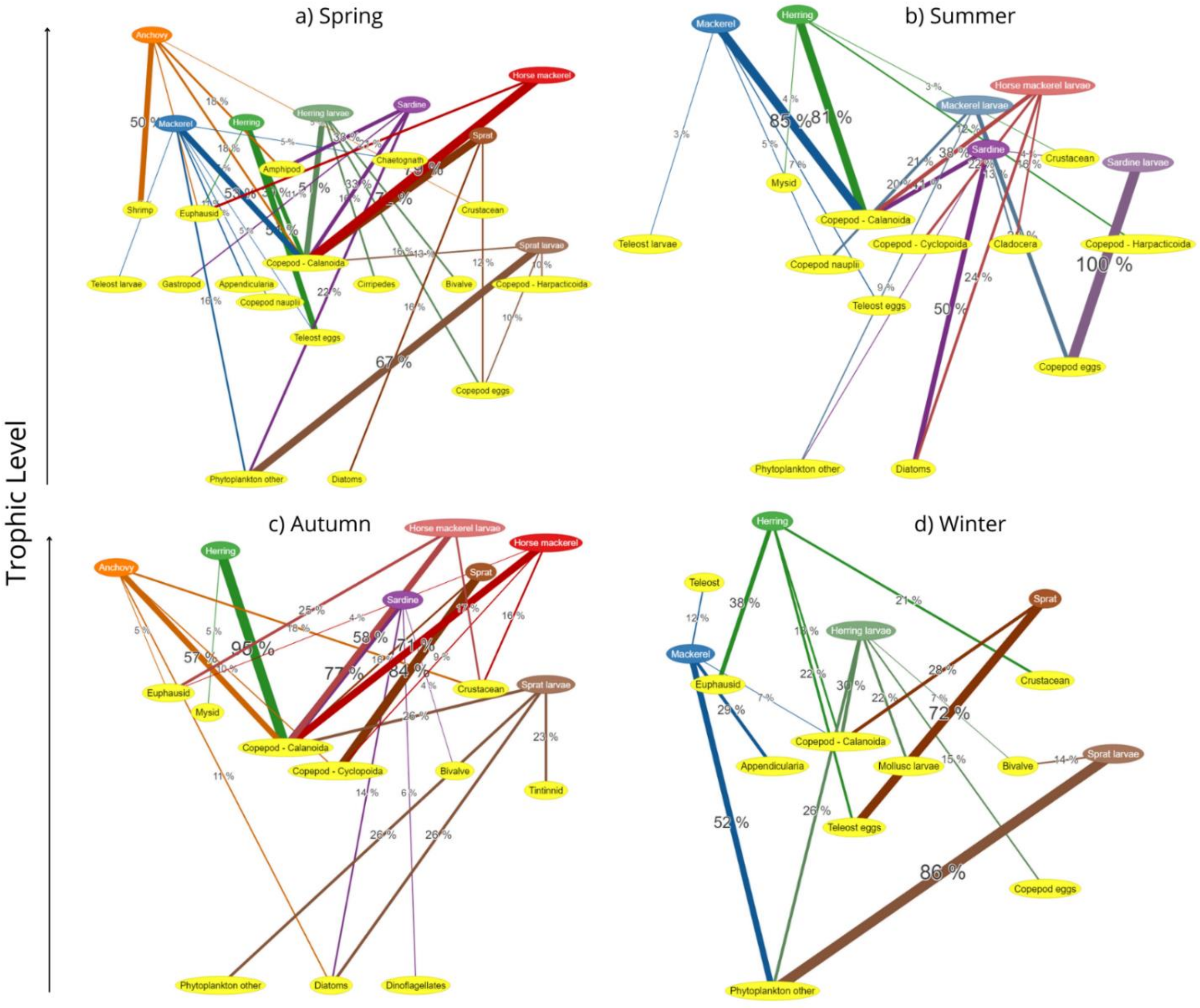


Figure 3.2 - Average proportions of prey groups consumed by 6 pelagic species (anchovy, herring, horse mackerel, mackerel, sardine, and sprat) and overlapping prey types across seasons (a: spring, MAM; b: summer, JJA; c: autumn, SON; d: winter, DJF) in the Celtic Sea, Irish Sea, and English Channel. Yellow nodes: prey groups; non-yellow nodes: predators. Predator species arranged by trophic levels of the species (y-axis) and calculated from the diet composition shown in the network using Eq. (1). Percentage contribution of prey type to a species diet indicated by thickness and numerical value of each edge. Non-larval species are > 4 cm, unless defined as larvae, which are ≤ 4 cm.

Sardines varied their diet across seasons (Figure 3.2), although it was the only species which consistently consumed phytoplankton throughout the year. Throughout the seasons, S did not change (4); however, H' was lowest in autumn (0.77) and highest in spring (1.31). In spring, they consumed mainly calanoid copepods (33%) and amphipods (33%), while in summer, they switched towards a greater phytoplankton based diet (50% diatoms, 5% other phytoplankton, 41% calanoid copepods, and 4% crustaceans). Sardine's diet in autumn was dominated by calanoid copepods (77%; Figure 3.2). Many of the prey groups consumed had a frequency of abundance of < 50% and frequency of occurrence < 60%, with calanoid copepods most dominant in autumn and summer and no group dominant in spring (Figure 3.4). Sardine consumed a wide range of prey sizes from relatively large to small, indicated by both low and high PPSR groups (Figure 3.5). Sardine larvae were only sampled in the summer and only consumed copepod eggs; as such, H' and S were low (S = 1, H' = 0; Figure 3.3).

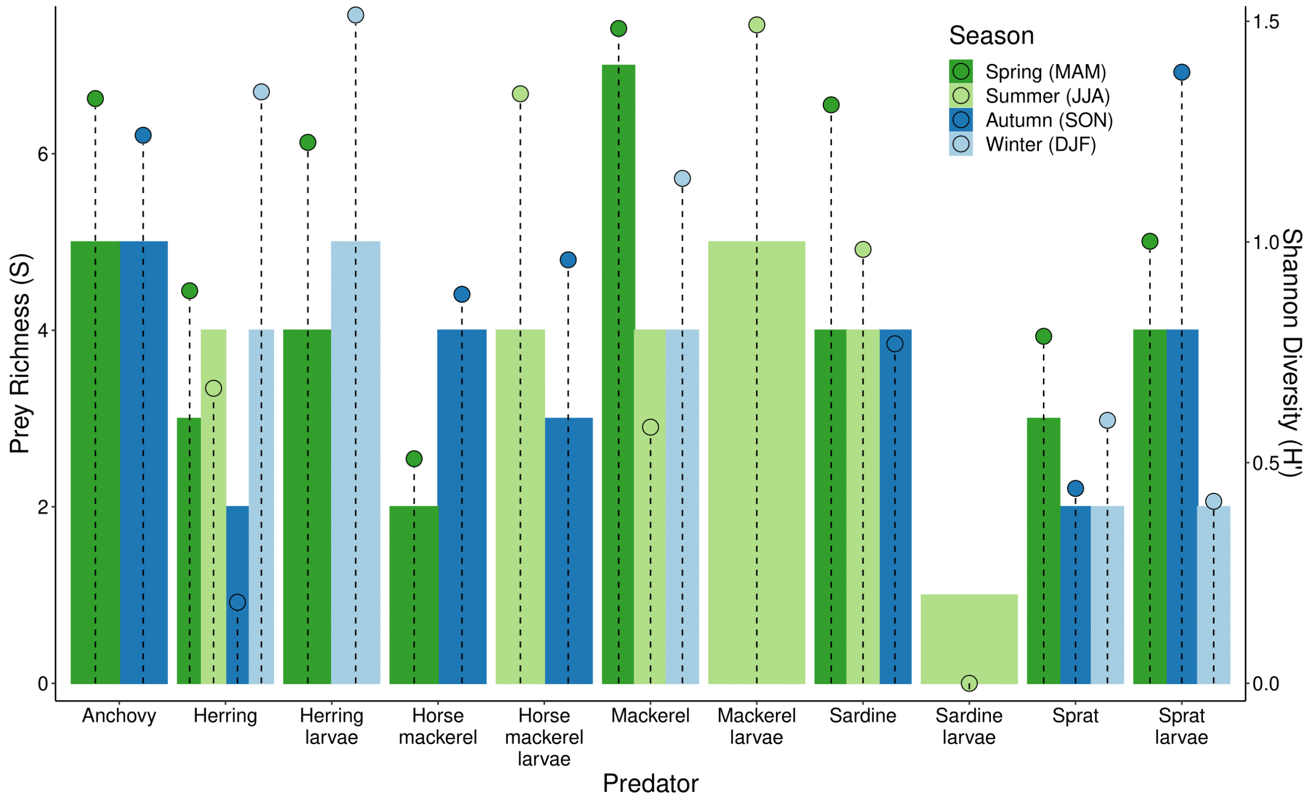


Figure 3.3 - Prey richness (S; data bars; left-hand axis) and Shannon diversity index of prey (H '; data points; right-hand axis) for 6 pelagic species (anchovy, herring, horse mackerel, mackerel, sardine, and sprat) in the Celtic Seas ecoregion. Non-larvae are > 4 cm, unless defined as larvae, which are ≤ 4 cm.

Anchovies had a varying diet across the seasons, although calanoid copepods (18−57%) and crustaceans (5−18%) were part of their diet in all seasons sampled (spring and autumn; Figure 3.2). They had the same S values (5) in spring and autumn, and similar H' values for each season (spring: H' = 1.32; autumn: H' = 1.24; Figure 3.3). In spring, anchovies consumed mostly shrimp (50%), with a mixture of amphipods (18%), copepods (18%), crustaceans (4%), and euphausiids (9%). In autumn, the diet of anchovies showed an increase in calanoid copepods to 57%, and an increase in crustaceans to 23%. Shrimp and calanoid copepods were the dominant prey groups in spring and autumn respectively, at > 50% in frequency and occurrence (Figure 3.4). The size of prey consumed was relatively large in comparison to body length, with mainly low PPSR values in both seasons (Figure 3.5). No anchovy larvae samples were available. The main constituent of horse mackerel diet across all seasons was calanoid copepods (e.g., 79% and 71% of diet in spring and autumn respectively; Figure 3.2). This is also consistent with the Costello diagram (Figure 3.4) in autumn where the frequency and occurrence were > 50%. The remaining diet in spring consisted of euphausiids (21%) and in autumn of a mixture of crustaceans (16%) and cyclopoid copepods (4%).

Horse mackerel diet in autumn had a higher S, H', and a cluster of low frequency and low occurrence prey groups than in spring (autumn: S = 4, H' = 0.88; spring: S = 2, H' = 0.51; Figure 3.3). Overall, the PPSR low values demonstrated that horse mackerel consume relatively large prey groups (Figure 3.5). Horse mackerel larvae had an S of 4 in summer, consuming calanoid copepods (38%), cyclopoid copepods (22%), diatoms (24%), and Cladocera (16%), supported by a higher H' value (summer: H' = 1.33; autumn: H' = 0.95; Figure 3.3). In autumn, horse mackerel larvae had a lower S (3), as they did not consume phytoplankton (diatoms), but, like the non-larval horse mackerel, they consumed a higher amount of calanoid copepods (58%; Figure 3.2).

Mackerel switched diet across seasons, with calanoid copepods as the consistent prey group, e.g., 53% of the diet in spring and 85% in summer (Figure 3.2). Values of S and H' were highest in spring (S = 7, H' = 1.48), decreasing to an S of 4 in summer and winter. Winter had higher H' compared to summer (winter: H' = 1.14; summer: H' = 0.58; Figure 3.3). In winter, non-larval mackerel consumed less calanoid copepods (7%) and more non-diatom phytoplankton (52%) compared to the other seasons. The remaining composition consisted of appendicularians, which increased from 11% in spring to 29% in winter; no appendicularians were consumed in autumn (Figure 3.2). In winter, there was no dominant prey group (Figure 3.4). Mackerel consumed relatively large prey groups for their size, as demonstrated by low PPSR groups; however, alongside sardines, they were the only species to consume a high PPSR group (Figure 3.5).

In summer, there was no dominant prey group for mackerel larvae. They consumed copepod eggs (38%), calanoid copepods (21%), copepod nauplii (20%), Cladocera (13%), and phytoplankton (9%; Figure 3.2). This resulted in a high S (5) and H’ (1.49) (Figure 3.3). Mackerel larvae consumed relatively large prey groups for their size, demonstrated by low PPSR groups (Figure 3.5).

In general, the majority of the prey groups had low frequency of occurrence (Figure 3.4), but there was a wide spread of prey groups in the diet of all 6 species (Figure 3.2). This observation suggests that all 6 SPF exhibit generalist feeding behaviours (Figure 3.4). Notably, both the relative frequency and occurrence of calanoid copepods were high (> 70%) in the diet of herring in summer, in herring larvae in spring, horse mackerel in autumn, horse mackerel larvae in autumn and spring, and sprat in spring.

Regarding PPSR, many of the species (horse mackerel; horse mackerel larvae, mackerel larvae, herring larvae, and anchovy in all seasons) consumed large prey, representing > 50% of diet composition (indicated by low PPSR values). Non-larval sardine in autumn and mackerel in winter were the only predators to consume smaller sized prey groups compared to their body size (indicated by higher PPSR values; Figure 3.5).

Figure 3.4 - Costello diagram for 6 pelagic species (anchovy, herring, horse mackerel, mackerel, sardine, and sprat) in the Celtic Seas ecoregion. Non-larvae are >4 cm, unless defined as larvae, which are ≤4 cm. Amphi: Amphipods; Append.: appendicularians; Calan.: calanoid copepods; Chaeto.: Chae to gnatha; Clado.: Cladocera; Cop. eggs: copepod eggs; Crust.: crustaceans; Cyclo.: cyclopoid copepods; Dino.: dinoflagellates; Euphau.: euphausiids; Fish larv.: fish larvae; Gastro.: gastropods; Harpact.: harpacticoid copepods; Moll.: mollusc; Phyto. Other: phytoplankton other (non-diatoms or dinoflagellates); Tintin.: tintinnids.

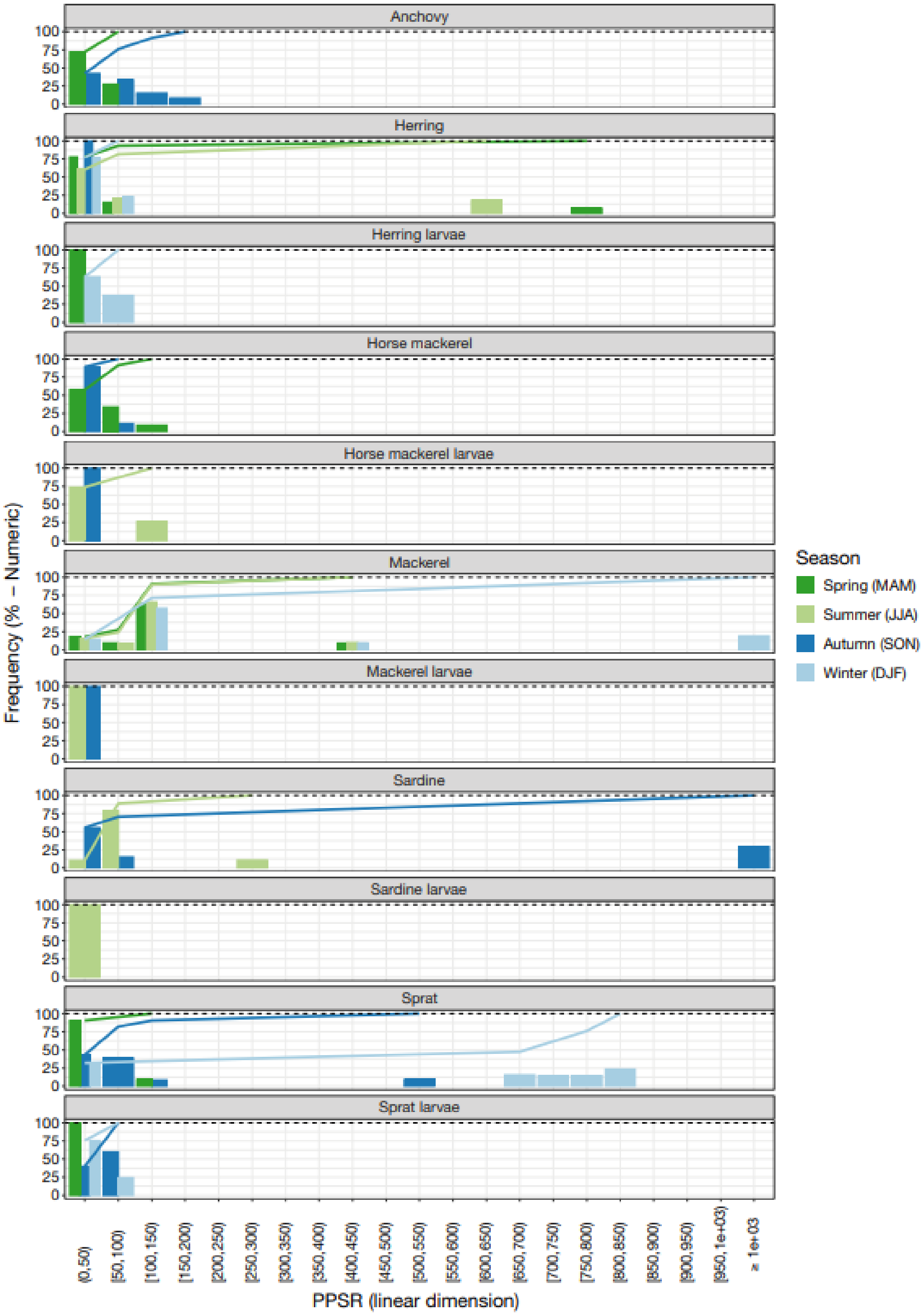


Figure 3.5 - Seasonal variability of prey size using predator:prey size ratio (PPSR; total length predator:total length prey) for 6 pelagic species (anchovy, herring, horse mackerel, mackerel, sardine, and sprat) in the Celtic Seas ecoregion. Non-larval species are >4 cm, unless defined as larvae, which are ≤4 cm. Data lines: cumulative frequency of the predator:prey size ratio groups; dashed lines: 100% frequency.

3.3.2 TLs

TLs for most SPF were variable across seasons, except for horse mackerel (3.27−3.28), which had minimal fluctuations (Table 3.2). Sprat larvae had the lowest TL of 2.16, of all species regardless of season, while anchovy had the highest overall TL of 3.51 in spring (Table 3.2). In autumn, horse mackerel larvae had their highest TL, while for herring it was in winter. However, 1-way ANOVA indicated there were no statistically significant differences in TLs across seasons and across species (ANOVA, F = 0.667, p = 0.587).

Table 3.2 - Trophic levels calculated for each of the 6 species across seasons using Eq. (2.1). 'Average' (this study) and Fishbase (from Froese & Pauly 2009) values are mean ± SE. (−) No available data.

	Season					
Species	**Spring (MAM)**	**Summer (JJA)**	**Autumn (SON)**	**Winter (DJF)**	**Average**	**FishBase**
Herring	3.01	3.22	3.23	3.30	3.19 (±0.06)	3.4 (±0.1 se)
Herring larvae	-	3.06	-	2.76	2.91 (±0.15)	-
Anchovy	3.51		3.14	-	3.32 (±0.18)	3.2 (±0.36 se)
Sardine	3.11	2.65	2.97	-	2.88 (±0.17)	3.1 (±0.1 se)
Sardine larvae	-	2.50	-	-	2.50 (±)	-
Mackerel	3.01	3.18		2.65	2.94 (±0.16)	3.6 (±0.2 se)
Mackerel larvae	-	2.78	-	-	2.78	-
Sprat	2.94	-	3.12	2.92	2.99 (±0.06)	3.0 (±0.07se)
Sprat larvae	2.32	-	2.54	2.16	2.34 (±0.11)	-
Horse mackerel	3.28	-	3.27	-	3.27 (±0.00)	3.5 (±0.0 se)
Horse mackerel larvae	-	2.88	3.35	-	3.11(±0.23)	-

3.3.3 Diet overlap

The PCA (Figure 3.6) showed that non-larval mackerel differed from all other SPF in spring (Figure 3.6a), as they consumed prey groups the other species did not (such as copepod nauplii, Chaetognatha, Appendicularia, and fish larvae). All other SPF were closely located in orthogonal space, and as such, consumed similar prey groups (Figure 3.6a). In spring, high diet overlap was observed between all combinations of mackerel, herring larvae, horse mackerel, and sprat, with the highest overlap between horse mackerel and sprat (Pianka index = 0.932, NS = 107.3; Figure 3.7; Table A 4).

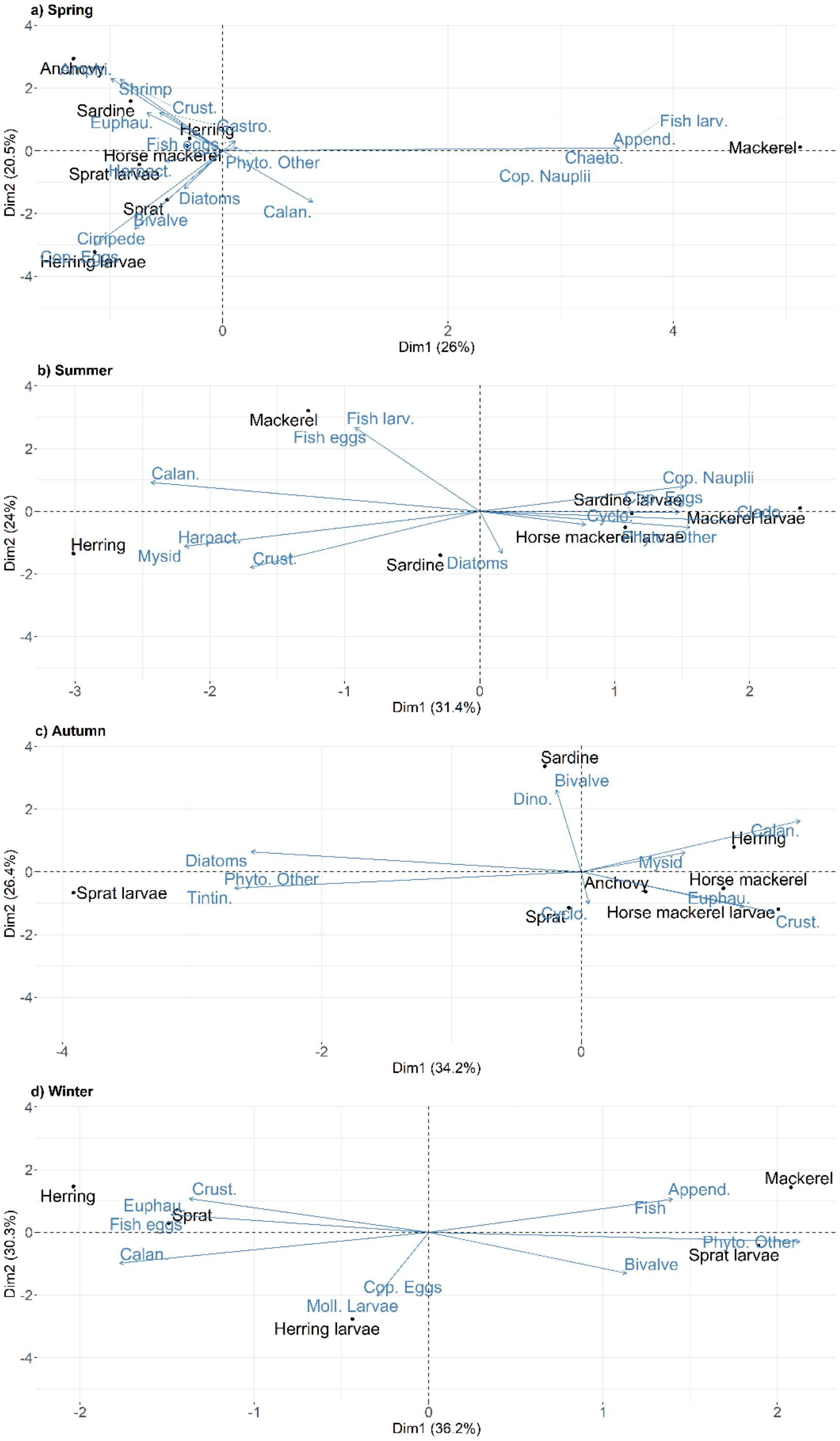


Figure 3.6 - Principal component analysis (PCA) of diet composition for 6 pelagic species (anchovy, herring, horse mackerel, mackerel, sardine, and sprat) for 2 PCA components (Dim1 vs. Dim2) for each meteorological season (a: spring, MAM; b: summer, JJA; c: autumn, SON; d: winter, DJF) in the Celtic Seas ecoregion. Black text: pelagic species; blue text: prey species (variables); blue arrows: direction of the variables as projected into 2D space. Predators are >4 cm, unless defined as larvae, which are ≤4 cm. Prey abbreviations as in Figure 2.4.

Herring larvae had high overlap with mackerel (Pianka = 0.81), sprat (Pianka = 0.89), and horse mackerel (Pianka = 0.85; Figure 3.7). In summer, there was only 1 cluster, formed by sardine larvae, mackerel larvae, and horse mackerel larvae (Figure 3.6b), while sardine, mackerel, and herring were isolated in orthogonal space, in particular, herring driven by calanoid copepods, harpacticoid copepods, and mysids (Figure 3.6b). Sardine larvae had only 1 high overlap, with mackerel larvae (Pianka = 0.76, NS = 43), while mackerel larvae diets had generally low overlaps (< 0.45) with the other SPF considered (Figure 3.7). Herring and mackerel presented the highest diet overlap in summer (Pianka = 0.98, NS = 101.7). In autumn, horse mackerel larvae, sprat, anchovy, horse mackerel, and herring formed a cluster (Figure 3.6c). Sardine and sprat larvae were isolated, driven by dinoflagellates/bivalves and phytoplankton/tintinnids respectively (Figure 3.6c). Autumn was characterized by high diet overlap between anchovy and horse mackerel, and between herring and sardine (Pianka = 0.98, NS = 34.3; Pianka = 0.979, NS = 102.0, respectively; Figure 3.7, Table A 3). In general, anchovy had a high diet overlap with all other species except sprat and sprat larvae. Sprat only had low overlaps (< 0.4) in autumn. In winter, no clear clustering was observed (Figure 3.6d); herring larvae and sprat diets were both driven by copepod Calanoida and teleost eggs. The only high diet overlap in winter was between sprat larvae and mackerel (Pianka index = 0.84, NS = 118.0). Overall, horse mackerel larvae had a high diet overlap with both herring and sardine in both summer and autumn, while the sprat−sprat larvae, herring−sprat larvae, and anchovy−sprat combinations had generally low diet overlaps throughout the seasons.

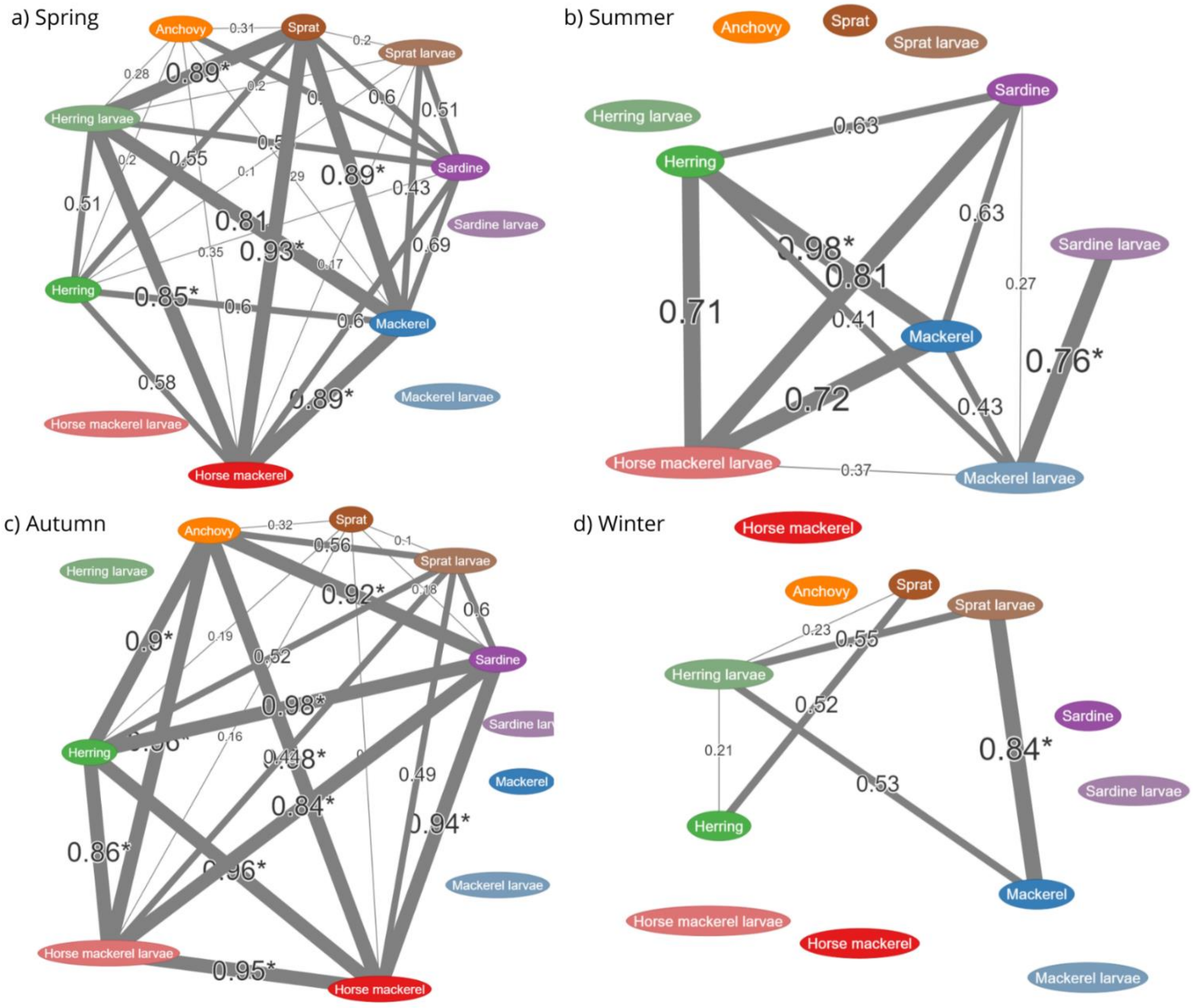


Figure 3.7 - Pairwise dietary overlap (Pianka's index) network of 6 pelagic species (anchovy, herring, horse mackerel, mackerel, sardine, and sprat) across seasons (a: spring, MAM; b: summer, JJA; c: autumn, SON; d: winter, DJF) in the Celtic Seas ecoregion using Eq. (2). Pianka overlap ranges from 0 (where there are no resources in common) to 1.0 (a complete overlap). *Low normalised spread (normalised spread was calculated by dividing the spread of the confidence intervals by the average of the Pianka index multiplied by 100); these values are in Table S5. Predators are > 4 cm, unless defined as larvae, which are ≤ 4 cm. Thickness of lines represent Pianka index value.

There was no statistically significant difference in diet overlap between seasons for all non-larval SPF species (ANOVA, F = 2.48, p = 0.082), indicating that collectively the average of diet overlaps of the predators between different seasons did not change. However, for a few given species, there were significant differences of overlap between seasons (Table 3.3): non-larval anchovy (ANOVA, F = 11.32, p = 0.012), sprat (ANOVA, F = 9.11, p = 0.019), and mackerel (ANOVA, F = 7.09, p = 0.027).

Table 3.3 - ANOVA of Pianka index of all and individual species and the seasons that were compared. *Significant ($p \leq 0.05$).

Species	F value	P value	Seasons
All	2.48	0.0823	Spring/Summer/Autumn/Winter
Anchovy	11.32	0.012*	Spring/Autumn
Herring	1.24	0.349	Spring/Summer/Autumn/Winter
Mackerel	7.10	0.0262*	Spring/Summer/Winter
Horse mackerel	0.41	0.541	Spring/Autumn
Sardine	0.86	0.460	Spring/Summer/Autumn
Sprat	9.12	0.0194*	Spring/Autumn

3.4 Discussion

3.4.1 Diet composition and overlap of juveniles and adults (non-larvae)

This study found that the diet composition of SPF in the Celtic Seas ecoregion changed across seasons. Despite intra-annual variability in prey consumption by most species, calanoid copepods were the most prominent prey for all species, as well as some of the most abundant prey types, in agreement with other studies on similar species (e.g., Bachiller & Irigoien, 2015; Möllmann et al., 2004; Raab et al., 2012). In fact, calanoid copepods are found throughout the year in the study area, with peaks in abundance in April and May, and a secondary peak between October and December, depending on specific calanoid species (Johns, 2006; Kennington & Rowlands, 2006). Calanoid species are most abundant around the Ushant Front area and south of Ireland (Johns, 2006), where non-larval horse mackerel and mackerel were sampled, and west of the Isle of Man (Kennington & Rowlands, 2006), where the majority of non-larval sprat and herring were sampled. These areas are associated with seasonal stratifications that could help result in elevated copepod abundances (Kennington & Rowlands, 2006). This could explain the medium to high overlaps between these 2 species pairs, due to the peak in calanoid copepods in spring. Autumn was the season with the highest diet overlap between the SPF species (particularly the comparison anchovy− horse mackerel) possibly due to the consumption of similar prey groups and similar proportions. However, autumn is the ending of the planktonic growing season, with prey groups such as calanoid copepods lowest from December to March (Johns, 2006). Winter had the smallest diversity of prey groups, likely because of the decrease in diversity in plankton in this season (Giering et al., 2019; Johns, 2006). The majority of both horse mackerel and mackerel were sampled in between the 100 and 200 m isobaths towards the shelf edge (south of Ireland), where calanoid copepods are present and peak during spring (Johns, 2006), which may explain the high overlap between these species.

Horse mackerel's diet was particularly selective towards calanoid copepods, possibly explaining the strong diet overlap between this species and the other SPF. Horse mackerel also preyed upon cyclopoid copepods in autumn, in coincidence with the peak in abundance of this species (Eloire et al., 2010). Observations from the Bay of Biscay and the Belgian part of the North Sea (Bachiller & Irigoien, 2015; Van Ginderdeuren et al., 2013) indicated that horse mackerel can show an opportunistic active predation on larger prey items (e.g. euphausiids) when they are available. As such, the consumption of calanoid copepods in this study may indicate the absence of larger prey item in the planktonic community during feeding.

Similarly, this study found herring consumed a small range of prey groups of generally larger sizes, with calanoid copepods the most common, in addition to euphausiids and mysids, as also observed in the North Sea (Casini et al., 2004; Corten, 2000; Flinkman et al., 1998). Celtic Sea herring are autumn-spawners, and it is thought that during the spawning period, feeding is limited (Hardy, 1924; Muus & Nielsen, 1999); therefore, even if herring consumed almost exclusively calanoid copepods in autumn, they are less likely to be competitors with other species during this season. Furthermore, herring can switch to smaller prey items if larger prey sizes are not available (Gibson & Ezzi, 1992). In this study, herring did not have a dominant prey group during spring and winter but consumed a higher number of teleost eggs, likely as result of insufficient planktonic prey availability (Segers et al., 2007). Teleost eggs also contributed to sprat diet, which have been reported to prey on plaice eggs and cod eggs in the Irish Sea (Ellis & Nash, 1997; Fox et al., 2012; Plirú et al., 2012) and in the Baltic Sea (Nissling, 2004), respectively. Conversely, these species could actively select teleost eggs when available and as such, result in a lower proportion of calanoid copepods in the diet, due to opportunistic predation. This could be addressed with the addition of concurrent plankton biomass data; however, this is outside the scope of this study. Further studies would be required to understand the result in increased predation on fish eggs, as there are potential bottom-up effects on the recruitment of the species predated upon. Overall, herring and horse mackerel displayed more specialist feeding behaviours, and could be vulnerable to changes in the availability of a particular prey.

Mackerel showed a generalist feeding strategy with the largest values for species richness and Shannon diversity in spring, and diverse prey sizes consumed in winter, in agreement with several previous studies (e.g., Bachiller et al., 2016; Debes et al., 2012; Kvaavik et al., 2019; Óskarsson et al., 2016; Utne et al., 2012; references therein). This study has shown the importance of appendicularians in the diet of mackerel in the Celtic Seas ecoregion in spring and winter, which as such may be non-coincidental consumption, as reported in the Norwegian Sea (Bachiller et al., 2016; Langøy et al., 2012; Prokopchuk & Sentyabov, 2006).

Sardine and mackerel were the main consumers of phytoplankton and were the only predators to consume smaller prey items (PPSR results), which is commonly reported for sardine (e.g., Garrido et al., 2008), particularly in nearshore habitats (Emmett et al., 2005). Sardine was the only species that consistently consumed phytoplankton throughout the year, but also consumed larger prey items such as crustaceans, decapods, and copepods, consistent with findings in the Bay of Biscay (Bachiller & Irigoien, 2015). This demonstrates that this species can use both particulate and filter feeding (Garrido et al. 2007; Bachiller et al., 2020; 2021), although filter feeding is the main feeding mode (Garrido et al., 2008). Phytoplankton was also identified as part of sprat diet, although this has rarely been reported in non-larval sprat diet (this study; Falkenhaug & Dalpadado, 2014), while other studies have observed the absence of phytoplankton within the diet (Bernreuther, 2007; Casini et al., 2004; Dickmann et al., 2007; Raab et al., 2012; Voss et al., 2009). It is possible that phytoplankton were ingested, through a shift to filter feeding, to maximize energy intake and availability (Falkenhaug & Dalpadado, 2014; Gibson & Ezzi, 1992). Many SPF (e.g., sardine and herring) can switch between filter (non-selective) and particulate (selective) feeding (e.g., Garrido et al., 2007; Nikolioudakis et al., 2014; Van Der Lingen et al., 2006), which allows the fish to appropriately exploit the planktonic food web (van der Lingen et al., 2009).

Anchovy consumed large prey groups compared to their body size, such as euphausiids in this study (PPSR results), in the North Sea (Raab et al., 2011) and in the Bay of Biscay (Bachiller & Irigoien, 2015). This suggests that anchovy within the study area could use an opportunistic prey selection for larger prey items in spring. However, euphausiids have an initial peak in May and a main peak in October and are found primarily south of Ireland (Johns, 2006). The spring samples are found in areas of high euphausiid abundance, compared to autumn samples located off the Cornish coast; therefore, prey availability could be a contributing factor to feeding strategy. Many of the dietary seasonal changes in this study are likely attributable to prey availability (Pinnegar et al., 2003), and will suit the SPF with generalist feeding behaviours (Beckerman et al., 2006; Dunne et al., 2002; Gravel et al., 2011; Rooney et al., 2006), such as mackerel and anchovy.

3.4.2 Diet composition and overlap of larvae

Copepod eggs were a main component in sardine larvae diet, particularly in summer. During maturation, the larvae shift their diet from copepod eggs to copepodites and then adult copepods, concomitant with larvae size changes (Conway et al., 1994; Morote et al., 2010; Munuera-Fernández & González-Quirós, 2006). In contrast with non-larval sprat, sprat larvae consumed largely phytoplankton, reflecting an ontogenetic shift in diet (Dickmann et al., 2007). As with sprat, herring showed an ontogenetic diet shift, as non-larval herring consumed prey groups larger than that of herring larvae, relative to their size (e.g., Wilson et al., 2018). The mackerel−herring larvae diet overlap observed in winter could be explained by phytoplankton consumption; however, herring larvae were mainly sampled nearshore in the Irish Sea, whereas mackerel were observed in Celtic Sea offshore waters. Therefore, this potential competition may not be such a concern.

In their life cycle, planktivorous SPF are consumers of organisms across the whole planktonic size spectra (e.g., phytoplankton, micro-, meso-, and macro- zooplankton), because with age and maturity, they can ingest prey of larger sizes (Bachiller et al., 2013). Often, when available, larger prey items are consumed, as they are more energetically valuable (Nikolioudakis et al., 2014). This study showed that larval species often consumed similar prey groups, such as copepod developmental stages in spring. Small copepods are particularly important to larval facultative filter-feeding species, such as sprat and herring, as low herring larval abundances have been associated with declines in copepods (Alvarez-Fernandez et al., 2015). The most critical phase of development for more specialist feeders such as herring are within the first few days, when they require sufficient suitable prey to successfully feed (Houde, 2008). Therefore, recruitment success can be impacted by suitable planktonic prey availability, which in turn is influenced by other factors such as environmental conditions. In fact, small copepods have experienced changes within the region and adjacent seas. In the Celtic Sea region, smaller copepods have seen a decline over the last few decades, showing a negative correlation with sea surface temperature (Bedford et al., 2020), whilst in the adjacent North Sea, a decline in recruitment of commercially important fish stocks was linked to a decline in small copepod abundance (since the 1990s) and to declining primary production (Capuzzo et al., 2022; Pitois & Fox, 2006).

3.4.3 Trophic levels

Although the prey composition changed throughout the year, there was no statistically significant difference in TL between seasons of the SPF. A possibility is that the major contributor in the prey composition (calanoid copepods) was relatively abundant in the diet throughout the year, whereas the low frequency prey groups changed between seasons. Horse mackerel for example did not change dominant prey groups, explaining the similar TLs calculated for the seasons sampled. The averaged TLs identified in this study for SPF species such as mackerel and anchovy were different from levels presented in FishBase (Froese & Pauly, 2009). This may be attributable to the different size ranges and life stage of the SPF species investigated. The data downloaded from FishBase was filtered for the region and to similar sizes; however, this was not always possible. For example, the relatively low TL calculated for mackerel, particularly in relation to those provided in FishBase (Froese & Pauly, 2009), is likely due to the size of mackerel investigated in the study; most of the mackerel stomachs considered were obtained from smaller fish, while the TL calculated in FishBase contains a mixture of juvenile and adults (Froese & Pauly, 2009). The waters southwest of the UK includes an important nursery area for mackerel, which may explain the prevalence of smaller mackerel found within this study. Fish are an important part of the diet of larger mackerel (Engelhard et al., 2013), and most of the larger mackerel tend to reside off the shelf area, outside the study area. The presence of phytoplankton in the stomachs of juvenile mackerel contributed to the reduction in this species' TL and is likely the result of available prey. In fact, mackerel could have consumed more phytoplankton in winter (52% of the diet) to meet their calorific requirements. Similarly, to mackerel, herring, horse mackerel, and sardine demonstrated lower TLs than in FishBase. In this study, sardine consumed phytoplankton, which was not present in the FishBase listed diet, and so explains the difference in TL. Horse mackerel in FishBase consumed finfish in the North Sea, which is a higher TL than the prey groups consumed by horse mackerel in this study. Interestingly, herring in FishBase demonstrated a higher TL than reported here; the consumption of bony fish (Ammodytidae) by herring reported in FishBase was the main difference between the TL calculations. Conversely, the reported TL in FishBase for anchovy was lower than in this study. This could be explained by the food items used for FishBase calculations containing more instances of phytoplankton, while the only instance of phytoplankton consumption in this study was 4% of diatoms in the autumn.

3.4.4 Potential impacts of environmental changes on SPF

SPF species pairings in this study does not always equate to competition, especially if there are enough food resources to achieve fish calorific intake and optimum fitness (Holt, 1987), and spatial segregation. In contrast, top-down control by these planktivorous species (consuming large vs. small copepods) and feeding strategy (generalist vs. specialist) can affect the zooplankton community.

Interactions may become apparent due to sea surface temperature changes in the Celtic Seas ecoregion, with a decadal mean of 0.66 ± 0.02°C (Lauria et al., 2012). This can change feeding conditions in the future and lead to shifting distribution scenarios (Pennino et al., 2020); in fact, European anchovy has increased its distribution in the study area (Beare et al., 2004), due to increased recruitment success of existing local northern stocks (Petitgas et al., 2012, Huret et al., 2020) and the ability of individuals to reach an overwintering size (Raab, 2013). After spawning in the southern North Sea, adult and juvenile anchovy overwinter in the relatively warmer waters of the western English Channel (Huret et al., 2020). This will have indirect as well as direct effects on SPF, possibly forcing changes in growth and survival of SPF species through prey availability and distribution variability (e.g., Corten, 2001; Cushing, 1990; Southward et al., 1995). It is difficult to predict how these potential changes in prey availability and distribution will affect SPF, due to their variable seasonal diet and the ability to switch from specialist to generalist diets (e.g., herring in this study switching from specialist in autumn and summer, to generalists in winter and spring). The importance of SPF is clear, as the abundance of the SPF can drive the abundance of demersal species in the region through a bentho-pelagic trophic link (Eme et al., 2022).

3.4.5 Considerations on the methods and recommendations

The methodology adopted to collect, collate, and analyse fish stomach contents data may present some limitations, which should be considered when interpreting the results. The main caveat of this study is the lack of concurrent planktonic community data; as such, the feeding strategies of the species studied cannot be ascertained, as consumption may reflect prey availability. The Costello diagram provides insight into the dominant prey group, or groups, from which we can begin to explore the possibilities of feeding strategies. We would recommend the collection of concurrent zooplankton community data to confirm these feeding strategies across seasons. A general overview of the seasonally available prey can be determined from several detailed studies in the region (Bedford et al., 2020; Capuzzo et al., 2022; Eloire et al., 2010; Pitois et al., 2021; Reygondeau et al., 2015; J. Scott et al., 2021; Widdicombe et al., 2010). The historical samples (adopted in this study) span a wide timeframe where changes in the planktonic community and composition may have occurred (e.g., see Bedford et al., 2020). However, we still find similar prey groups from the earliest decades to the latest (see the DAPSTOM database; Pinnegar 2014), supporting the relevance of our results and conclusions.

To analyse stomach contents, a visual inspection was used to identify prey organisms. This method is likely to underrepresent more easily digestible prey such as phytoplankton (Sikora et al., 1972), and gelatinous organisms. Molecular techniques can be used to identify these (e.g.,Bachiller et al., 2020; Lamb et al., 2019, references therein), but these methods return presence−absence of the prey type, rather than abundance and size. The use of abundance ratios in the diet can overemphasise the contribution of smaller prey groups in the stomach (Pinnegar, 2014; Van Der Lingen et al., 2006). To counteract this bias, the abundances can be converted to biomasses using existing length−weight relationships. As many of the prey groups were of low taxonomic resolution, there were large variations in prey sizes, and so the biomass estimates were judged to be uncertain. Pinnegar (2014) stated that the limitation of pooled data can underestimate prey numbers, but can also mask individual variation of feeding (e.g., individual variation observed in the Bay of Biscay; Bachiller & Irigoien, 2015). This variation could be due to gill raker size or feeding strategy by certain size fish species that can be even higher than differences in stomach contents of different species or different size ranges. The varying sample size may also have similar effects. Small sample sizes such as horse mackerel larvae in autumn and sardine in spring may overemphasise the importance of uncommon prey (Berg, 1979). An increase in sample number would reduce this bias and will also improve the capability of accounting for any variability found in fish feeding behaviour, and as such, would provide a more reliable representation of overall diet (Ferry & Cailliet, 1996; Winemiller, 1990).

3.4.6 Conclusions

This study provides novel insights into the diet composition of SPF across different seasons in the Celtic Seas ecoregion, showing that dietary overlap between SPF vary between seasons, with the highest overlaps occurring in autumn. Despite seasonal variability in prey consumption of the lower frequency prey groups, calanoid copepods represented a key component of diet in all seasons and the main contributor to the diet of the six SPF.

The results of this study may be generalised to other temperate locations with similar populations of SPF. In the North Sea, for example, 6 forage fish species co-occur and (partially) compete for the same planktonic food sources (Dickey-Collas et al., 2013; Raab, 2013). The results of this study may also provide important input to trophic models. These models often provide a platform to disentangle the complexities of food web functioning (trophic relationships), anthropogenic stressors, and the environment to predict how the ecosystem may respond to future scenarios (e.g., Boyd et al., 2020b). However, the accuracy of these models is dependent on ecosystem specific data (Essington, 2007; Han et al., 2020), including specific TL and diet matrices. Many existing Ecopath with Ecosim models (Christensen et al., 2014; Pauly et al., 2000) take into consideration only the annual consumption patterns rather than seasonal. Therefore, including a seasonally varying diet matrix, such as the one derived in this study, may improve such models, allowing them to be used to evaluate ecosystems effects of fishing, and to explore management policy options amongst many other ecological questions at a seasonal scale.

4

Assessment of standard Sentinel 3 - OLCI Chlorophyll-a in the waters southwest of the UK

Chapter 4 – Assessment of standard Sentinel 3 - OLCI Chlorophyll-a in the waters southwest of the UK

4.1 Introduction

Chapter 3 demonstrated the consumption of different phytoplankton types, (diatoms, dinoflagellates, and other phytoplanktonic types), in the diet of sardine, mackerel and larval sprat. Monitoring phytoplankton dynamics (i.e., temporal and spatial changes in abundance and composition), and size classes are key for understanding how energy is transferred through food webs (Werdell & Bailey, 2005). A proxy for phytoplankton biomass is phytoplankton chlorophyll, which can be derived from satellite remote sensing; a cost-effective monitoring tool (Wright & Jeffrey, 2006). Algorithms can be used to estimate phytoplankton size classes from these retrievals (e.g., Roy et al., 2013; Brewin et al., 2015), as the size structure is acknowledged as a critical component for controlling the ecological and biogeochemical functioning of pelagic ecosystems. The derived phytoplankton biomass and size classes (using satellite retrieved chlorophyll) can then be used as an input into food web models (e.g., Ecopath with Ecosim - Pauly et al., 2000) to evaluate energy transfer in ecosystems. However, before using satellite derived outputs it is imperative, they are validated against *in situ* measurements, to ensure they accurately represented, as will be explored in this Chapter.

Phytoplankton organisms contain three types of pigments (chlorophylls, carotenoids, and biliproteins), in their cells for harvesting light to fuel the photosynthetic process and for photoprotection (Wright & Jeffrey, 2006). Photosynthetic pigments absorb light from the orange-red and violet-blue wavelengths in the electromagnetic spectrum (Lodish et al., 2005). Photosynthetically available radiation (PAR) is the amount of light available for photosynthesis, which is in 400-700nm wavelength range. PAR can vary depending on latitude and season, with levels highest in summer at mid-day. While some pigments are limited to specific phytoplankton groups, chlorophylls and particularly Chlorophyll-a (Chl-a), are contained in all photosynthetic phytoplankton, as part of light-harvesting complexes in chloroplasts (Wright & Jeffrey, 2006). Therefore, Chl-a is considered a proxy (or index) of total phytoplankton biomass (excluding for prochlorophytes; Wright & Jeffrey, 2006). Environmental factors, such as irradiance, spectral composition of light, daylength, phytoplankton nutrient status and growth phase, affect the concentration of pigments present in the cell, although the type of pigments contained in the cell themselves do not change (Wright & Jeffrey, 2006). Consequently, it is important to consider spatial and temporal differences, such as region and season, as this may impact concentration of Chl-a. The above properties have led to using satellite derived Chl-a to map and quantify phytoplankton biomass and primary productivity at higher spatial and temporal resolutions.

Ocean colour (OC) sensors have provided a cost effective solution of investigating and resolving large scale spatial and temporal patterns in Chl-a, in offshore and coastal waters, supporting studies on biogeochemical cycles (e.g., Anugerahanti et al., 2018; Chang et al., 2015; Siegel et al., 2014) and single species individual based models (Atlantic Mackerel - Boyd et al., 2018, 2020). The 1978 satellite Coastal Zone Color Scanner Experiment (CZCS) was the first instrument devoted to the measurement of ocean colour (Chassot et al., 2011). Since 1997, there have been a succession of several operational satellites with sensors dedicated to ocean colour from various space agencies (Figure 4.1). These were mainly from the National Aeronautical Space Agency (NASA), and the European Space Agency (ESA). For example, NASA launched Moderate Resolution Imaging Spectroradiometer (MODIS), and Sea-Viewing Wide Field-of-View Sensor (SeaWiFS) and ESA launched MEdium Resolution Imaging Spectrometer (MERIS), and Sentinel 3 – Ocean Land Colour Imager (OLCI) (Figure 4.1). Over the years the sensors have changed through spectral and spatial resolution, revisit times, and also their lifespans (Table 4.1). Since SeaStar in 1997, there has been a succession of sensors and platforms providing a continuous data source of water properties. Consequently, researchers have been able to understand trends of Chl-a, with 20 years of continuous data. From this we understand the potential implications of factors such as climate change, with Chl-a increasing in some areas whilst decreasing in others (Behrenfeld et al., 2006; Dutkiewicz et al., 2019; Martinez et al., 2009; Wernand et al., 2013).

Ocean colour radiometry by satellite observations uses the detection of spectral variation of backscattered sunlight after hitting the water and its constituents from the ocean, this is known as reflectance or water-leaving radiance. Open ocean signals are primarily determined by phytoplankton, mainly Chl-a and other photosynthetic pigments and phytoplankton related detrital and coloured dissolved organic matter (CDOM), this is known as Case-1 waters. Coastal or Case-2 waters are more optically complex because of other re-suspended particles, terrestrial suspended particles or CDOM potentially from river run off separate of the phytoplankton assemblages and can be distinguished by the relationship with their Inherent Optical Properties, or IOPs (International Ocean-Colour Coordinating Group [IOCCG], 2000). Algorithms have been developed to estimate Chl-a or other optically active water constituents from ocean colour sensors depending on the characteristic of the water signal to the constituent of interest. This could be by empirical algorithms such as O'Reilly et al., (1998), semi-analytical approaches (e.g., Lee et al., 2002), or more recently neural networks (e.g., Brockmann et al., 2016). Empirical approaches such as O'Reilly et al., (1998), use a blue to green reflectance ratio, the use of reflectance band ratios is also known as a maximum band ratio. This is mainly because chlorophyll absorbs strongly in the blue spectral domain and weakly in the green. A key challenge to obtaining accurate measurements for all approaches is the correction of unwanted radiance contributions to the signal. The top of the atmosphere (TOA) signal that reach a sensor consists of atmospheric effects, water leaving radiance or reflectance, and water surface effects. The water leaving radiance contributes to around <10% of the TOA signal, with the remainder corrupted by atmospheric or surface effects (Wang et al., 2009). Highly accurate atmospheric correction processes take in all contributions to the signals in order to retrieve accurate apparent optical properties (AOPs) such as water- leaving radiance. Inaccuracies of AOPs can arise when the atmospheric correction is done incorrectly (IOCCG, 2010; Mobley, 1994; Wang, 2007). The estimates can then be used to derive water properties such as Chl-a (O'Reilly et al., 1998), total suspended matter (Miller & McKee, 2004; Son & Wang, 2012; M. Zhang et al., 2010) , CDOM, detritus as well as IOPs of the water e.g., absorption and scattering coefficients (Lee et al., 2002, Maritorena et al., 2002). Variations in absorption and backscattering co-efficient (IOPs) can affect the remote sensing reflectance and so the chlorophyll concentration (Hubert et al., 2010). Variations of algal size structure can also affect the phytoplankton absorption spectra and therefore the remote sensing of Chl-a.

Sentinel is one of the latest missions to deploy an OC satellite, which will provide another two decades of OC data. However, merging data from different sensors is not always straightforward, as factors such as resolution (spatial and spectral; Table 4.1) and water types (i.e., Case 1 and Case 2) are inconsistent and the level of confidence is different between the sensors and algorithms. As such, satellite derived Chl-a retrievals need to be validated against *in situ* measurements to ensure that they accurately represented and the accuracy and resolution of the variables from these satellite sensors are comparable (Lee & Carder, 2002; Young et al., 2011; Zieger et al., 2009).

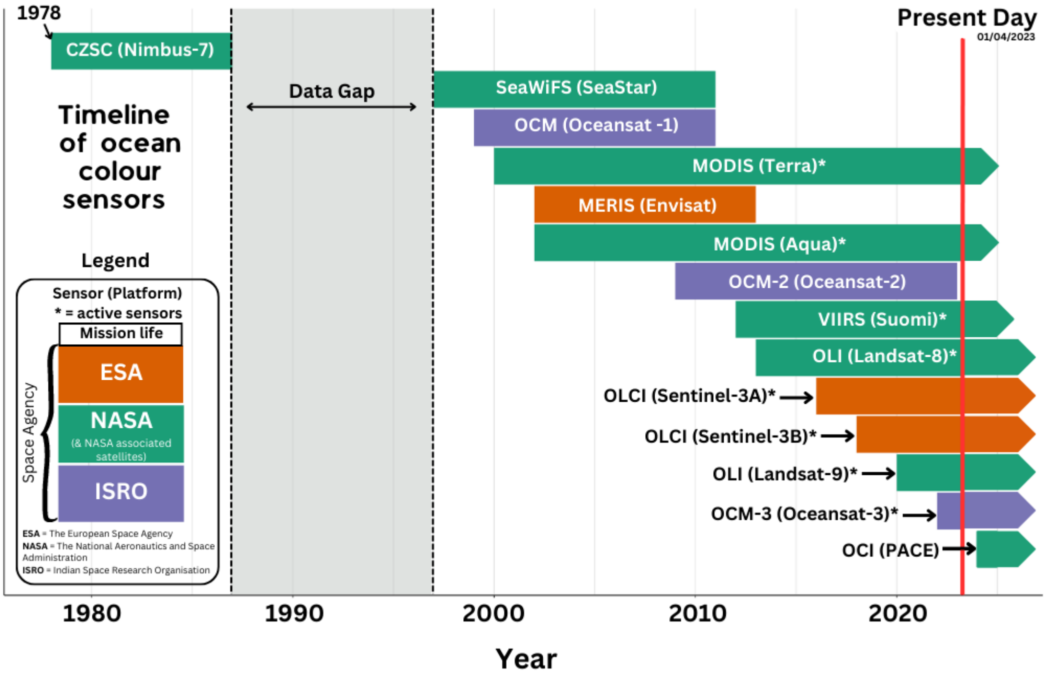


Figure 4.1 - Timeline of ocean colour sensors from 1978 to April 2023 for three space agency ocean colour satellite development. ESA – European Space Agency. NASA - National Aeronautics and Space Administration and their associated satellites. ISRO – Indian Space Research Organisation. Figure generated in R and Canva.

Table 4.1 - Previous, current, and future satellite sensors and platforms relevant to ocean colour. Adapted from Groom et al., (2019).

Status	Platform	Sensor	Spatial Resolution = Pixel Size	Spectral bands (400-1000nm)	Revisit frequency (at equator)	Launch (end)
Defunct	SeaStar	SeaWiFS	4 & 1 km	8	2 days	1997-(2010)
	Envisat	MERIS	1.2 & 0.3km	15	2 days	2002–(2012)
Current	Terra (T)/ Aqua (A)	MODIS	1km	9	Daily	1999/2000
	Oceansat-2	OCM-2	300m	8	2-3 days	2009
	Suomi	VIIRS	750m	7	Daily	2011
	Sentinel 3 A/B	OLCI	300m	21	Daily (with 2 satellites	2016/2018
	Oceansat-3	OCM-3	300m	13	2-3 days	2022
Future	PACE	OCI	1km	Hyperspectral; 5nm (340-890nm)	Daily	2024

High Performance Liquid Chromatography (HPLC) or spectrophotometric were the accepted measurement for *in situ* chlorophyll validation of the 1997 NASA launched SeaWIFS satellite (Mueller et al., 2003). Due to this, SeaWIFS bio-Optical Archive and Storage System (SeaBASS) and NASA's SeaWIFS bio-Optical Marine Algorithm Dataset were formed and are comprehensive databases of *in situ* Chl-a and other water constituents for satellite retrieval validation (Werdell & Bailey, 2005). These databases often contain many samples from coastal waters or where Chl-a is >0.1 mg m^{-3} (Brewin et al., 2016). In order to improve the number of match-up points, recent modifications were made to satellite validation process to measure Chl-a (see Neeley et al., 2018), which includes the use of ship-based flow-through systems such as FerryBox (Sørensen et al., 2007), measuring surface water properties at higher spatial and temporal resolution than discrete water sampling.

For newer satellites e.g. Sentinel 3, validation is currently ongoing, especially in complex waters (Case 2), where regional validation is required before they can be utilised (Toming et al., 2017). The Copernicus program launched Sentinel satellites to allow long-term monitoring of environmental parameters. OLCI was a continuation from MERIS (2002-2012), which launched on Sentinel 3A (S-

3A) in 2016 and 3B in 2017. OLCI has improved capabilities for Case 2 waters, more specifically a higher resolution of 300m (Donlon et al., 2012) compared to MODIS (1 km resolution) and spectral bands in the red and near-infrared (NIR). OLCI provides two Chl-a concentration algorithms as standard with their Level 2 products, ‘CHL OC4ME’ (Ocean Colour 4 MERIS), based off the algorithm used for MERIS and optimized for Case 1 waters (i.e., open oceans) and ‘CHL NN’ (Neural Net), a neural network generated for more optically complex waters, Case 2 waters (IMT, 2019). A few studies have aimed to regionally validate S-3A OLCI algorithms, such as Toming et al., (2017) in the Baltic, Moutzouris-Sidiris & Topouzelis (2021) in the Mediterranean, Cherif et al., (2021) in the Adriatic, and Harshada et al., (2021) in the east Arabian Sea. The Celtic Sea has been incorporated into wider area studies or for different satellites, for example Tilstone et al., (2017) validated OC4Me on the satellite MERIS in the northeast Atlantic, incorporating the Celtic Sea and English Channel. Whilst, Pahlevan et al., (2020) validated S-3A globally using coastal and inland waters and Tilstone et al., (2021) validated S-3A in comparison with MODIS-Aqua in the open ocean, oligotrophic waters of the Atlantic. However, as far as we are aware, there has yet to be a study focusing on standard Level 2 OLCI products in the Celtic Sea alone. Areas such as the Celtic Sea and Western English Channel can be considered optically complex (Darecki et al., 2003; Joint & Groom, 2000; McKee et al., 2007), and fall into two optical classes, Case 1 and Case 2.

The main purpose of this study was to evaluate the performance of two standard Level 2 Sentinel 3A - OLCI Chl-a calculating algorithms with FerryBox *in situ* data in the Celtic Sea, to estimate phytoplankton size classes to update the Celtic Sea Ecopath with Ecosim model (in Chapter 5). As far as we are aware this is the first time these algorithms will be validated for the Celtic Sea and will have great benefit to studies using satellite based Chl-a within the Celtic Sea. The first algorithm analysed for this study from S-3A, was Ocean Colour 4 for Meris (OC4Me), a 4th order polynomial equation and maximum band ratio. The second was the Neural Net (NN), designed for coastal waters or optically complex waters, that employs an Inverse Radiative Transfer Model (IMT, 2019) to calculate water quality parameters, e.g., Chl-a. The match ups were split by depth (<50m and >50m) and by mixed or stratified waters to understand whether the performance of the algorithm improves in coastal regions or in a particular water type. These algorithms were analysed with and without consideration of the standard error file associated with Chl-a retrievals, by removing values >30% error to understand the effectiveness of the algorithms in these two different scenarios. The two OLCI algorithms were also compared to MODIS-Aqua Chl-a algorithms, OCI+OC3, to advise on the best algorithm within the study area. An additional question, that arose through analyses in this study, was the effectiveness of the time window on the performance metrics and as such was investigated in this study.

4.2 Methodology

4.2.1 Study area

The study area is defined as the Celtic Sea and Western Approaches (Figure 1.1) located in the shelf-seas of the Northeast Atlantic to the Southwest of the United Kingdom. The two seasonal frontal systems as described in Section 3.2.1 result in gradients and patchiness of plankton distribution in this area, due to generating vertically mixed and stratified conditions of the water column (Johns, 2006). A spring and autumn (September-October) are the two main phytoplankton bloom events in the Celtic Sea (Pingree et al., 1976).

4.2.2 *In situ* measurements

The *in situ* chlorophyll data were collected on three multidisciplinary surveys in October 2016, 2017, and 2019 onboard the RV Cefas Endeavour, in the Celtic Sea and Western English Channel (Figure 4.2), as part of the annual autumn PELTIC survey. The surveys started in 2013 and focus on investigating the small pelagic fish community of the waters South-West of the UK and associated environmental conditions (Doray et al., 2021). Discrete water samples for analysis of phytoplankton pigments (including Chl-a) were collected from Niskin bottles on a rosette, at an approximate depth of 4 m. The samples were filtered through a 47mm Whatman GFF filter within one hour of collection and then wrapped in foil and stored in a -80 °C freezer on board. Pigment samples were then transferred to an accredited laboratory (DHI; Horsholm, Denmark) for quantification by High

Performance Liquid Chromatography (HPLC) using the method by van Heukelem, (2005), further details on the processing and analysis methods can be found in Capuzzo et al., (2022).

During the PELTIC surveys, in addition to collecting discrete water samples, a FerryBox system (4H-JENA©) recorded continuous subsurface (4 m depth) measurements of fluorescence (Seapoint Inc. USA), across the study area. These fluorescence measurements were converted to Chl-a (mg m^{-3}) by regressing the fluorescence measurements towards the discrete measurements of Chl-a collected from the same time and location from the HPLC analysis (Figure 4.3). Regressed fluorescence data was quality controlled and only those points that passed quality assurance (QA) and quality checks (QC) were used for validation. The QA checks are as follow QA1 = has had position and speed checks, flow rate checks, QA2 = QC per parameter including range and variance, checking instruments against each other, and QA3 = derived parameters or calibrated against bottle data.

Vertical profiles of temperature at sampling stations were recorded by using a SAIV CTD, to investigate the thermal stratification of the water column. In particular, thermal stratification was identified at a given location where the absolute temperature difference between surface and bottom temperatures was greater or equal to 0.5°C; otherwise, the water column was considered vertically mixed (Talling, 1971).

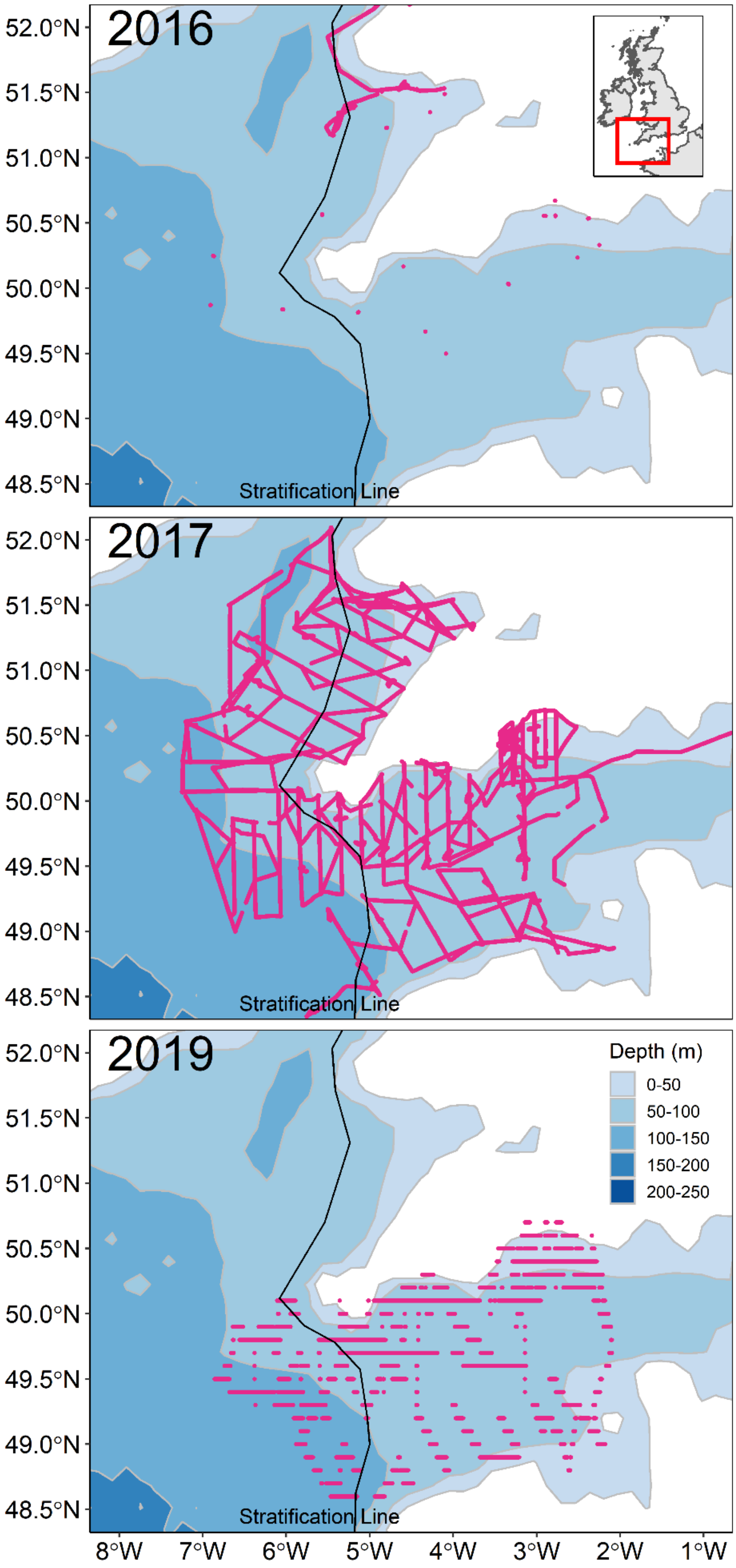


Figure 4.2 - FerryBox tracks from PELTIC Survey in the Celtic Sea and Western Approaches for 2016, 2017 & 2019 after QC checks. The stratification line provides an approximate separation between vertically mixed water column (on the right) and seasonally stratified waters (on the left) and was determined based on SAIV CTD temperature profiles.

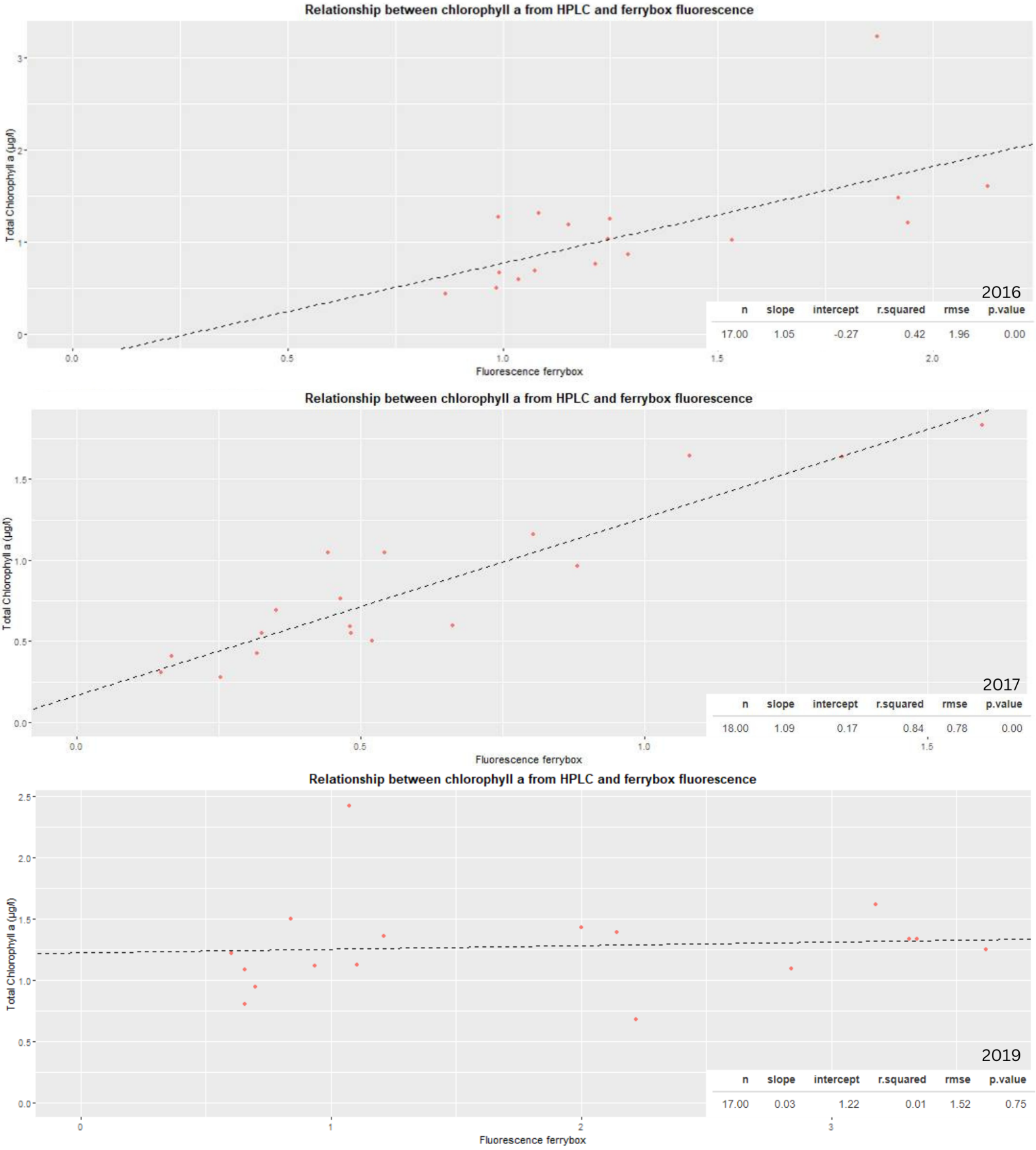


Figure 4.3- Relationship between discrete HPLC measurements (Total Chlorophyll) and FerryBox fluorescence for three Peltic Surveys, 2016, 2017, 2019 in the Celtic Sea. Figure generated by Kate Collingridge at Cefas.

4.2.3 Satellite Data Processing

Algorithms from ESA's Sentinel 3A – OLCI, OC4Me and NN, and from NASA's MODIS-Aqua, OCI+OC3 were examined for their efficiency of Chl-a estimation. The Sentinel 3A - OLCI retrievals were downloaded from EUMETSAT EO Portal (https://eoportal.eumetsat.int/) for October 2016, 2017, and 2019 and matched with *in situ* measurements spatially and temporally. Characteristics of the OLCI bands are presented in Table 4.2. All algorithms and their corresponding error files (if applicable) were processed in R Core Team (2021) using the 'raster' package (Hijmans et al., 2021). Each pixel with greater than 30% percentage error were removed to understand the effectiveness of the error file on Chl-a estimation. OC4Me is calculated using a Max Band Ratio (MBR). It uses a fourth order polynomial equation developed by Morel et al., (2007), as described in Equation 4.1 and the MBR (Equation 4.2) between the irradiance reflectance at wavelengths 443, 490, 510, and 555nm.

$$C = 10^{A_0 + A_1 \times R + A_2 \times R^2 + A_3 \times R^3 + A_4 \times R^4} \qquad (4.1)$$

where R = log_{10} (MBR) and coefficients A^0 = 0.450, A^1 = -3.259, A^2 = 3.522, A^4 = 0.949; C is the derived chlorophyll-a concentration in mg m^{-3}.

$$MBR = max((R_{443}, R_{490}, R_{510})/R_{555}) \qquad (4.2)$$

NN uses an Inverse Radiative Transfer Model and neural networks to estimate the water constituents (IMT, 2019). The initial development of this model was by Doerffer and Schiller (2007) for Case 2 waters and was later developed to become the Case-2 Regional Coast Colour (C2RCC).

The NN processor depends on a large database of simulated water leaving reflectance and related top of atmosphere radiances (Brockmann et al., 2016), inherent optical properties and the inversion of the spectrum for atmospheric correction train neural networks. Arithmetic conversion factors are used to convert IOPs into Chl-a.

NASA's MODIS-Aqua Level 2 images were downloaded at 1 km resolution from the NASA Ocean Colour Web portal (https://oceancolor.gsfc.nasa.gov). For MODIS-Aqua OC3 is utilised at Chl-a concentrations >0.2 mg m^{-3}. Like OC4Me, OC3 is a band ratio algorithm that uses one of two blue bands with blue-green $R_rs(\lambda)$, at 547 nm as the denominator (O'Reilly et al., 1998), as shown in Equation 4.3. MODIS-Aqua utilises the OCI (Ocean Colour Index) of Hu et al. (2012) at Chl-a concentrations <0.15 mg m^{-3}, based on the difference in R_rs between a green band and red and blue bands (Equation 4.4).

$$R = log_{10}\left\{max\left[\left(\frac{R_{rs}(443)}{R_{rs}(547)}\right), \left(\frac{R_{rs}(48)}{R_{rs}(547)}\right)\right]\right\} \tag{4.3}$$

where, OC3 coefficients are: a0 = 0.2424; b = 2.7423; c = 1.8017; d = 0.0015; e = 1.228.

$$CI = R_{rs}(\lambda_{green}) - [R_{rs}(\lambda_{blue}) + (\lambda_{green} - \lambda_{blue})/(\lambda_{red}) - \lambda_{blue}) * (R_{rs}(\lambda_{red}) - R_{rs}(\lambda_{blue}))] \tag{4.4}$$

Where *λ blue*, *λ green* and *λ red* are the instrument-specific wavelengths, these are 443, 547 and 667 nm, respectively. To remove erroneous satellite measurements, a set of quality flags (cloud and land cover) provided as standard with the measurements were applied as a mask to each pass. MODIS- Aqua is primarily optimised for Case 1 waters.

Table 4.2 - Characteristics of the bands of Sentinel 3-OLCI and their applications as defined in ESA (2021). Chl = Chlorophyll, abs = absolute, atmos. = atmospheric, corr. = correction.

OLCI Band	Band centre (nm)	Band Width (nm)	Application
Oa1	400	15	Aerosol correction, improved water constituent retrieval
Oa2	412.5	10	Yellow substance and detrital pigments (Turbidity).
Oa3	442.5	10	Chl absorption max biogeochemistry, vegetation
Oa4	442	10	High Chl, other pigments
Oa5	510	10	Chl, sediment, turbidity, red tide.
Oa6	560	10	Chlorophyll reference (Chl minimum)
Oa7	620	10	Sediment loading
Oa8	665	10	Chl (2nd Chl abs. max.), sediment, yellow substance/vegetation
Oa9	673.75	7.5	For improved fluorescence retrieval and to better account for smile together with the bands 665 and 680 nm
Oa10	681.25	7.5	Chl fluorescence peak, red edge

OLCI Band	Band centre (nm)	Band Width (nm)	Application
Oa11	708.75	10	Chl fluorescence baseline, red edge transition.
Oa12	753.75	7.5	O_2 absorption/cloud vegetation
Oa13	761.25	2.5	O_2 absorption band/aerosol corr.
Oa14	764.38	3.75	Atmospheric correction
Oa15	767.5	2.5	O_2A used for cloud top pressure, fluorescence over land.
Oa16	778.75	15	Atmos. corr./aerosol corr.
Oa17	865	20	Atmos. corr./aerosol corr., clouds, pixel coregistration.
Oa18	885	10	Water vapour absorption reference band. Vegetation monitoring.
Oa19	900	10	Water vapour absorption/vegetation monitoring (max. reflectance)
Oa20	940	20	Water vapour absorption, atmos./aerosol corr.
Oa21	1020	40	Atmos./aerosol corr.

4.2.4 Validation

Satellite retrievals were matched spatio-temporally with all available *in situ* FerryBox measurements using the nearest point match. From this initial match up four datasets were derived for validation metrics: 1) All points – the initial spatio-temporal matchup; 2) All points with error values removed – values > 30% error were removed from the initial match up. 3) Identical match up points – match ups where all three algorithms retrieved Chl-a values with exactly the same *in situ* measurements for ease of comparison of the algorithms; 4) Identical match up points with error values removed – as with previous but with values with >30% error removed.

Further to this the data of 1) and 2) was initially subset into Case 1 and 2 water using Matsushita et al., (2012), to evaluate the efficiency of the three algorithms for a particular water type. However, due to discrepancies in categorisation of the pixels this method was not used, and the dataset was split into stratified and mixed waters. Identification of mixed / stratified waters was based on analysis of temperature profiles from the SAIV CTD as described in Section 4.2.2. The data was also split by isobaths, <50m and >50m, used as a proxy for coastal and non-coastal waters again to understand the efficiency of the algorithms in different water types.

Alongside this there were varying time windows, where time window is the time between satellite overpass and *in situ* sample collection, as such, statistical metrics were calculated on each time window to understand the effect of the time window on the performance metrics. For example, the

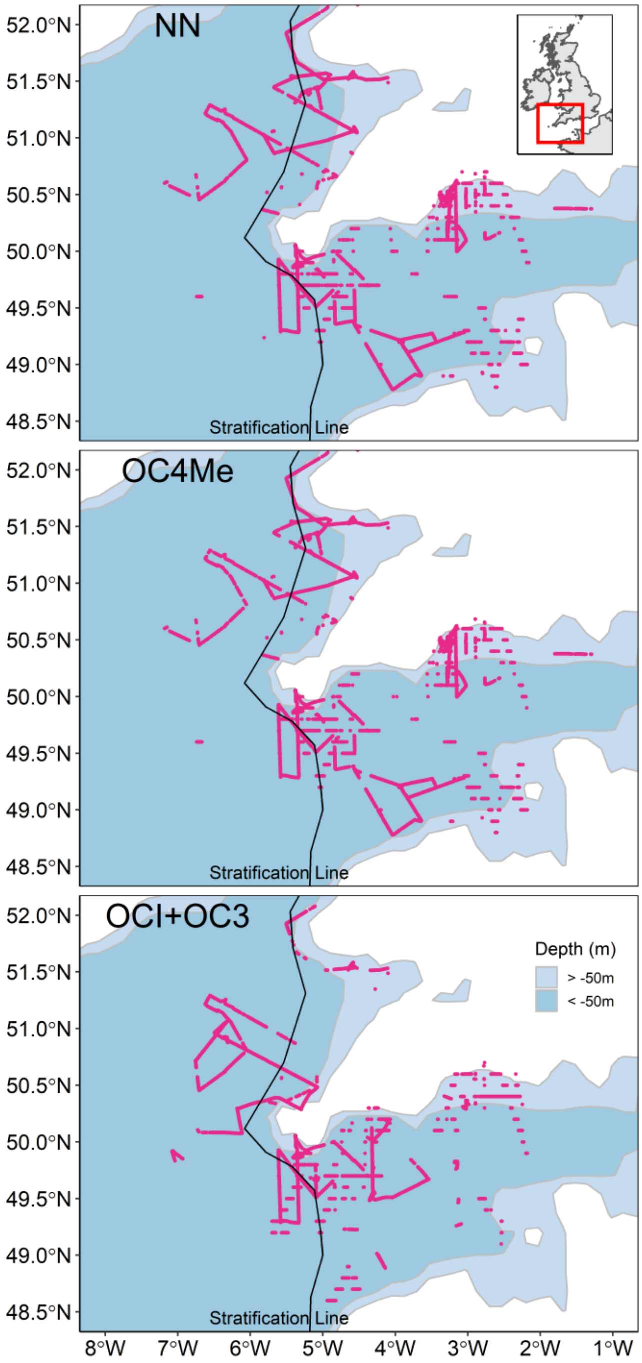


Figure 4.4 - All match up points of three algorithms, NN, OC4Me & OCI+OC3. Black line indicates stratification line. Depth is characterised by <50m and >50m isobaths. The stratification line provides an approximate separation between vertically mixed water column (on the right) and seasonally stratified waters (on the left) and was determined based on SAIV CTD temperature profiles.

in situ measurement was collected in the early hours of the morning or late at night and the satellite overpass between 8pm – 8am.

4.2.5 Statistical Metrics

The following statistical metrics were used to evaluated algorithm performance following Pahlevan et al., (2020): type-II regression slope (S), intercept (I), Pearson correlation coefficient (r), the bias (Equation 4.5), bias-corrected root-mean-square error (RMSE – Equation 4.6), and root-mean-square log error (RMSLE – Equation 4.7) which was computed with modulus, where estimated (E) Chl-a against that measured (M) *in situ*. The S, I, r, and RMSLE were computed in $\log_{10}$ space. To ease interpretation of these statistical metrics for satellite validation, the slope close to one and an intercept close to zero present a good fit between satellite and *in situ* data. Similarly, the higher the r/r^2 the better the linear consistency between the *in situ* and the satellite observations. The RMSE, RMSLE and bias provide information on the distribution of the data around the regression line and outliers, this information is not provided by slope, intercept, and correlation. RMSE and RMSLE is the bias corrected difference between satellite and in situ data and is sensitive to any outliers. The bias ($\log_{10}$) provides information on the under-estimate or over-estimate of the satellite data compared to the *in situ* data, with a value near zero indicating no systematic difference between the two data sets.

$$Bias = 10^{Z} \; where \; Z = \left[\sum_{i=1}^{n} \left(\log_{10}(E_i) - \log_{10}(M_i) \right) / n \right] \tag{4.5}$$

$$RMSE = \left[\frac{\sum_{i=1}^{N} (E_i - M_i)^2}{n} \right]^{1/2} \; \left(mg/m^3 \right) \tag{4.6}$$

$$RMSLE = \left[\frac{\sum_{i=1}^{N} \left(\log_{10}(E_i) - \log_{10}(M_i) \right)^2}{n} \right]^{1/2} \tag{4.7}$$

4.3 Results

4.3.1 Initial match up

There was a total of 124,628 FerryBox measurements collected throughout the Celtic Sea and Western English Channel, from which 41,914 were collected in 2017 and 51,528 in 2019. No points were removed through QC checks from either year. In 2016, 31,186 were collected and only 9,614 were taken further for analysis (Figure 4.2) due to samples not passing the QC checks. There was a maximum of 35 satellite images from Sentinel 3 (OLCI and NN) and 32 images from MODIS-AQUA (OCI+OC3) that contained match up points that were within 14 hours of *in situ* measurements (Table 4.3). From those satellite images a total of 12,202 for NN, 11,360 for OC4Me, and 11,543 for OCI+OC3 were extracted as match up points (Table 4.4; Figure 4.4). NN had over 40% of those samples removed as they contained a percentage error greater than 30% in comparison to OC4Me which had less than 1% of points removed. OC4Me produced less than 0.2% retrieval error (Table 4.4). Considering the data split based on the 50m isobath, for the areas <50m, there were 4115 satellite-*in situ* match ups for NN, 3917 for OC4Me, and 1632 for OCI+OC3. In comparison to >50 m where there were 8,087 match up for NN, 7,443 for OC4Me, and 9,911 for OCI+OC3. The data was also split by mixed or stratified conditions with the majority of match up points found within mixed waters, 10,387, 9,698, and 8,215 for NN, OC4Me, and OCI+OC3 respectively. Conversely, stratified waters where there were 1,815, 1,662, and 3,328 or NN, OC4Me, and OCI+OC3 respectively.

The *in situ* chlorophyll measurements from validated FerryBox fluorescence, had a range of 0.076 - 4.38 mg m^{-3} over the three years, (Figure 4.5) with the highest value in 2016. NN had a range of 0.01-16.3 mg m^{-3}; OC4Me had a smaller range of 0.022-11.8 mg m^{-3}, while OCI+OC3 had the largest range of 0.015-21 mg m^{-3} (Figure 4.5). A comparison of daily averaged FerryBox Chl-a overlaid on 8 day composite Sentinel 3A image demonstrates satellite derived Chl-a overestimates compared to FerryBox measurements (Figure 4.6; Figure 4.7; Figure 4.8.).

Table 4.3 - Number of satellite images used to generate match up points between in situ measurements and satellite retrieval algorithms. Points without errors have satellite retrieval values from the error files with >30% error removed. '>30% error points' in the table indicate the number of match up points that were removed.

Algorithm	**Time window (hours)**													
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**
NN														
Points without errors	12	18	21	22	26	28	28	28	29	29	29	30	32	32
>30% Error points	8	13	19	25	28	29	30	31	31	31	32	33	35	35
OC4Me														
Points without errors	12	18	22	25	28	29	29	29	29	30	31	32	35	35
>30% Error points	3	4	4	5	6	6	7	7	7	8	8	8	8	8
OCI+OC3														
All points	12	18	21	22	22	25	26	26	26	28	32	32	32	32

Table 4.4 - Number of match up points between in situ measurements and satellite retrieval algorithms. Points without errors have satellite retrieval values from the error files with >30% error removed. '>30% error points' in the table indicate the number of match up points that were removed. Identical match up points = all algorithms had the same equivalent *in situ* measurement.

Algorithm	**Time window (hours)**													
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**
NN														
All match up points														
Points without errors	409	871	1497	2023	2583	3167	3673	4332	5041	5680	6301	6654	6986	7014
>30% Error points	241	488	796	1220	1678	2200	2789	3277	3785	4212	4566	4911	5169	5188
% of points removed	37.08	35.91	34.71	37.62	39.38	40.99	43.16	43.07	42.88	42.58	42.02	42.46	42.53	42.52
Identical match up points														
Points without errors	92	189	375	562	698	850	1000	1173	1331	1532	1740	1835	1963	1981
>30% Error points	124	246	321	441	526	655	803	925	1032	1172	1348	1515	1660	1668
% of points removed	57.41	56.55	46.12	43.97	42.97	43.52	44.54	44.09	43.67	43.34	43.65	45.22	45.82	45.71
OC4Me														
All match up points														
Points without errors	603	1179	2010	2915	3883	4937	5909	6997	8155	9130	10029	10692	11246	11292
>30% Error points	10	16	18	19	20	27	30	30	31	40	50	58	68	68
% of points removed	1.63	1.34	0.89	0.65	0.51	0.54	0.51	0.43	0.38	0.44	0.5	0.54	0.6	0.6
Identical match up points														
Points without errors	210	428	689	996	1217	1498	1796	2091	2356	2697	3081	3343	3616	3642
>30% Error points	6	7	7	7	7	7	7	7	7	7	7	7	7	7
% of points removed	2.78	1.61	1.01	0.7	0.57	0.47	0.39	0.33	0.3	0.26	0.23	0.21	0.19	0.19
OCI+OC3														
All match up points														
All points	667	1309	2317	3268	4110	5175	6208	7286	8460	9513	10280	10865	11375	11537
Identical match up points														
All points	171	389	690	1014	1320	1690	2039	2423	2774	3178	3356	3398	3613	3649

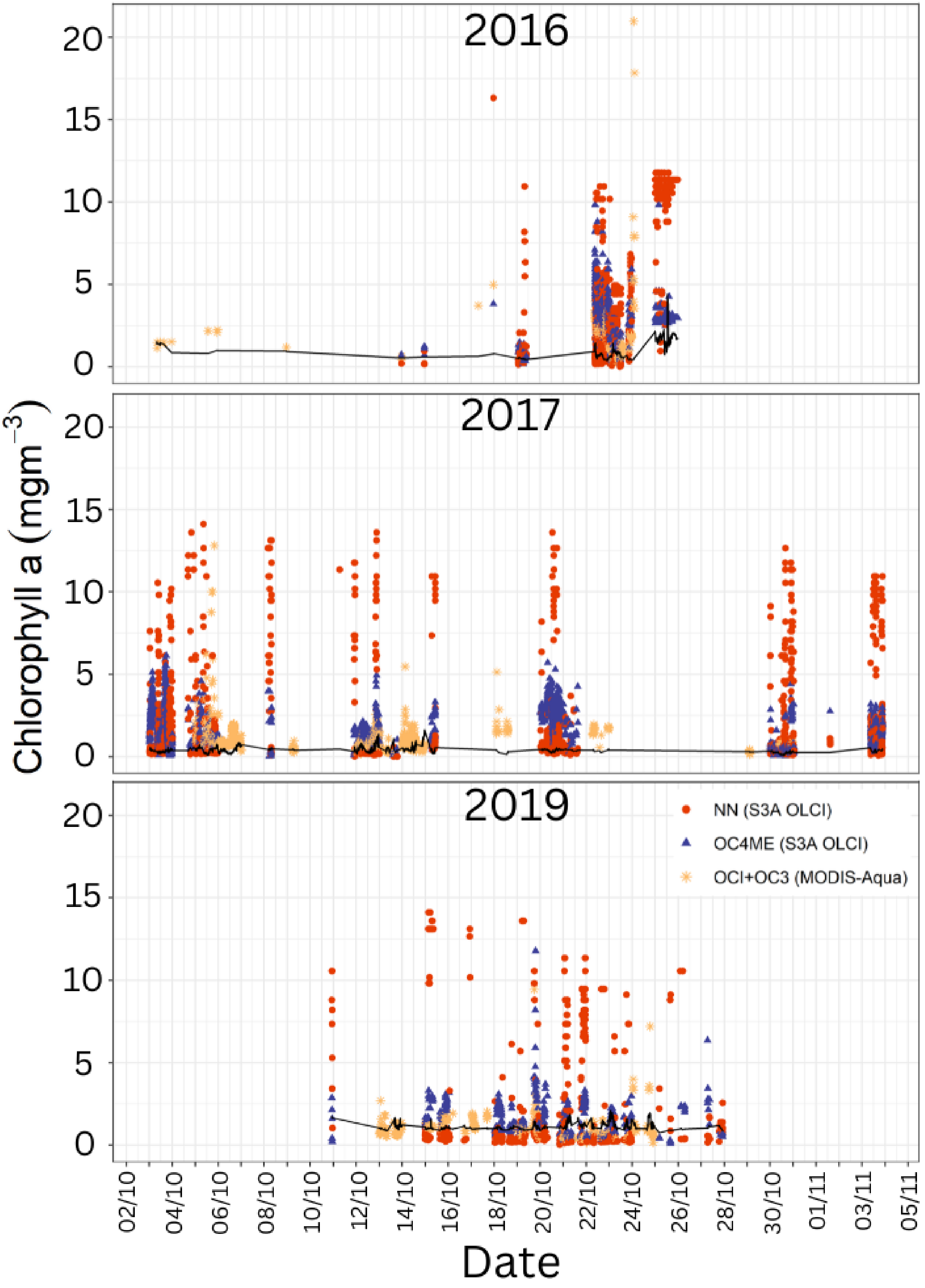


Figure 4.5 - Range of satellite retrievals on each sampling date of all possible match up points. Black line indicates *in situ* measurement points on dates by minute sampled.

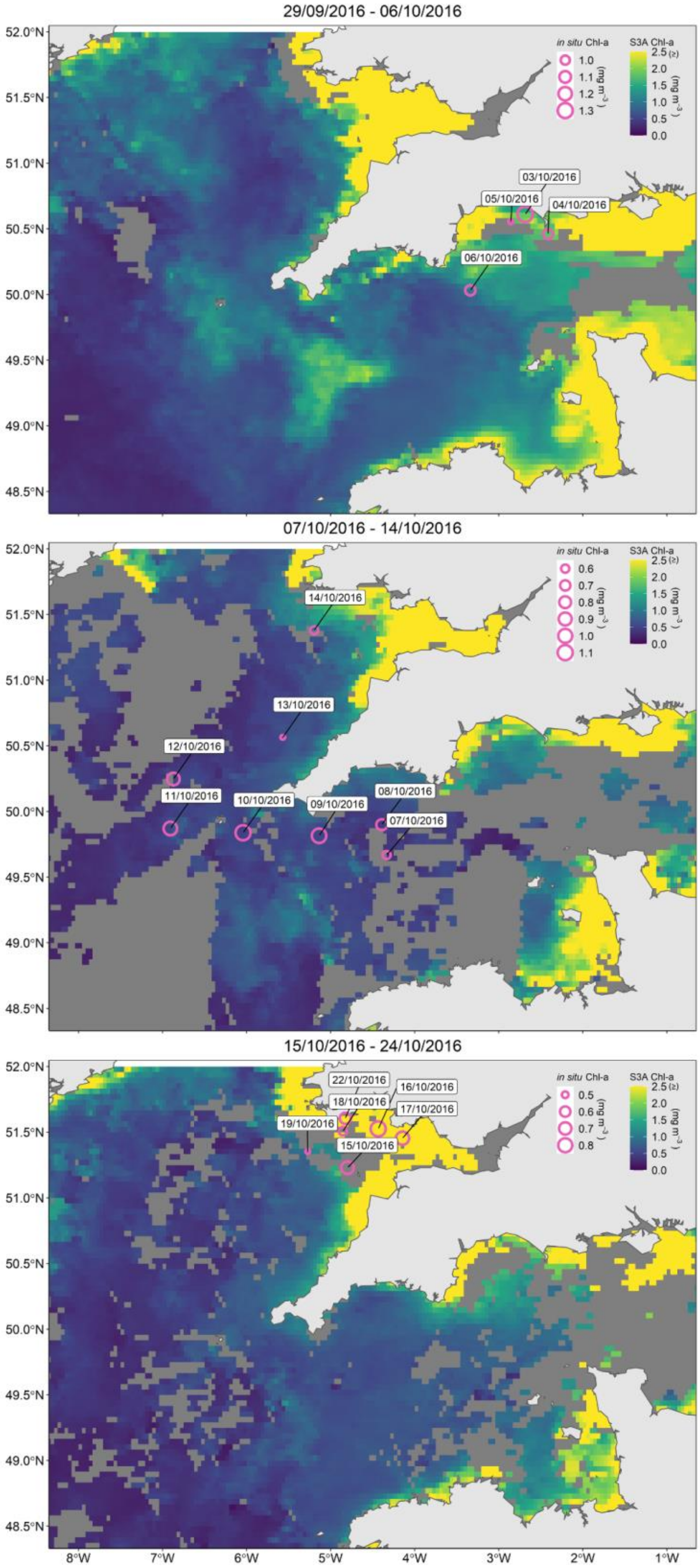


Figure 4.6 - Eight-day composite Sentinel 3A Chl-a (Chlorophyll -a) at 4km resolution in 2016 of the Celtic Sea, with points of daily average calibrated FerryBox from the PELTIC survey. Size of point indicates daily averaged Chl-a concentration and spatially. Dark grey values indicate no data available, light grey represents land. Satellite images downloaded from https://oceancolor.gsfc.nasa.gov/.

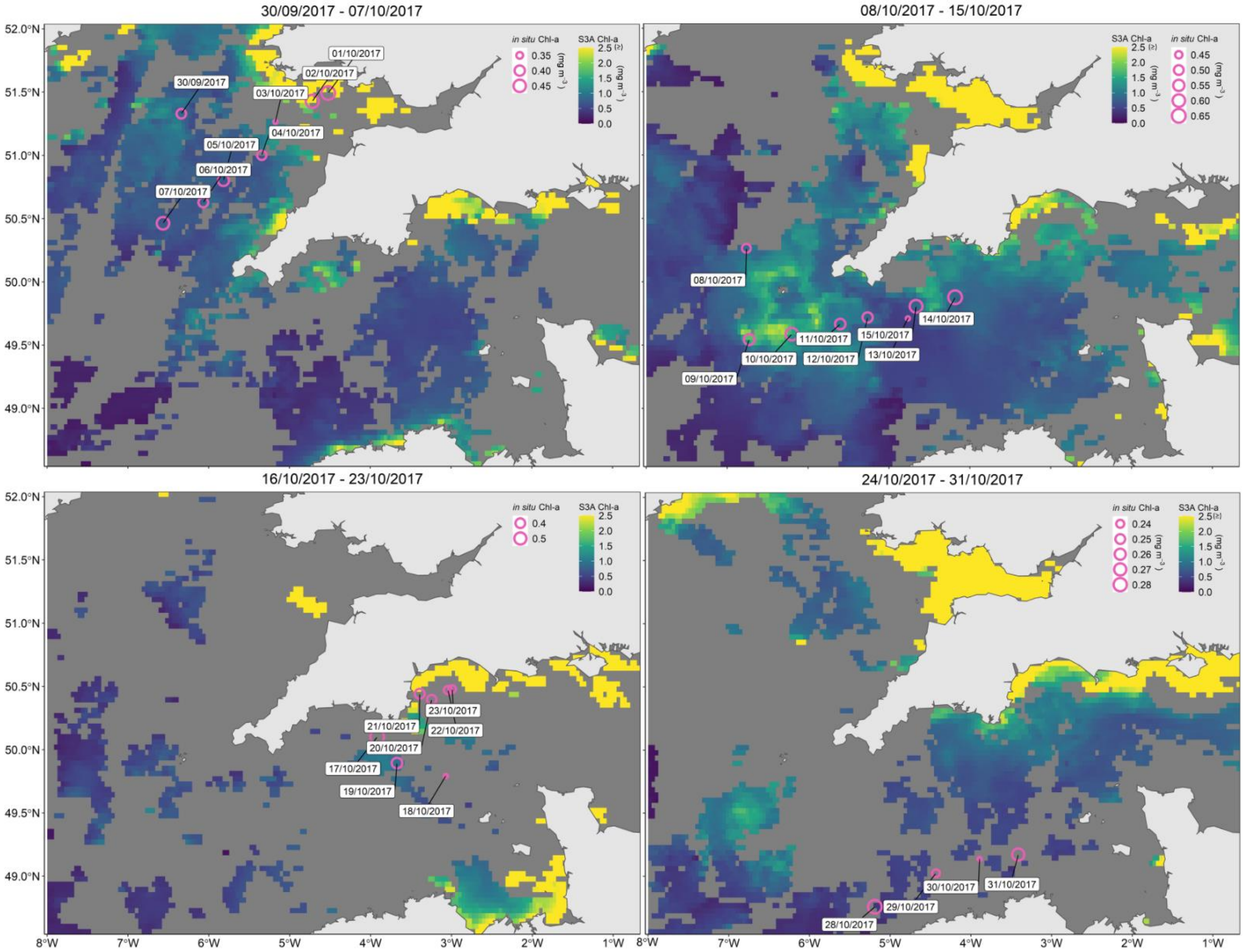


Figure 4.7 - Eight-day composite Sentinel 3A Chl-a (Chlorophyll -a) at 4km resolution in 2017 of the Celtic Sea, with points of daily average calibrated FerryBox from the PELTIC survey. Size of point indicates daily averaged Chl-a concentration and spatially. Dark grey values indicate no data available, light grey represents land. Satellite images downloaded from https://oceancolor.gsfc.nasa.gov/.

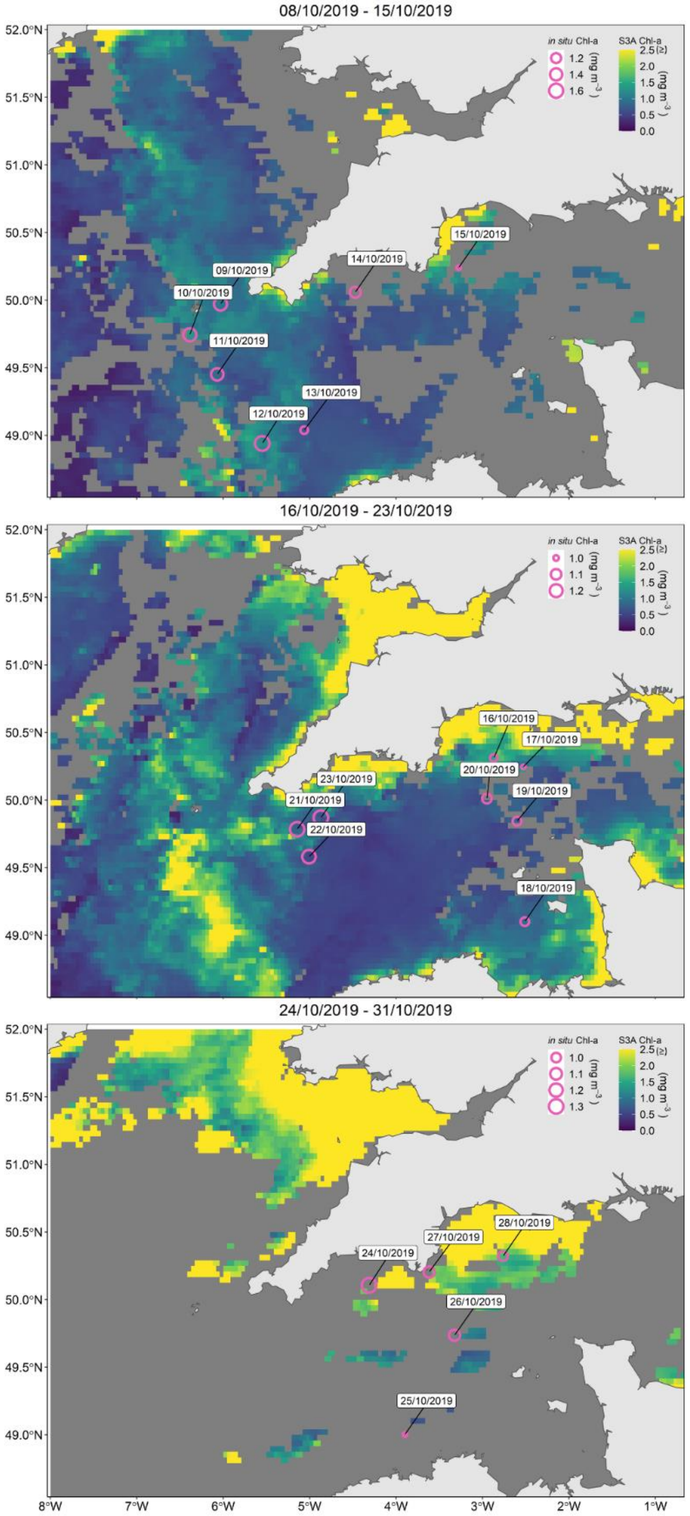


Figure 4.8 - Eight-day composite Sentinel 3A Chl-a (Chlorophyll -a) at 4km resolution in 2017 of the Celtic Sea, with points of daily average calibrated FerryBox from the PELTIC survey. Size of point indicates daily averaged Chl-a concentration and spatially. Dark grey values indicate no data available, light grey represents land. Satellite images downloaded from https://oceancolor.gsfc.nasa.gov/.

4.3.2 Validation and metrics

4.3.2.1 Accuracy assessment of ocean-colour algorithms in the Celtic Sea

The NN algorithm had a slope greater than 0.5, an intercept close to zero, a low bias, low RMSLE and a high RMSE when error points were not removed (Table 4.5; Figure 4.9) . There was an improvement in slope when the values with > 30% error were removed to 0.827, the intercept was higher at 0.313 and many of the underestimated points were classed as high error. The RMSE and RMSLE were also higher than with error values. The identical match up points with error values, generated closer values to when there all points were considered. The slope remained similar, 0.545, the intercept was negative -0.13, there was a lower RMSE and lower RMSLE, and low adjusted r^2 (Figure 4.9A; Table 4.5). Identical match ups with error removal, resulted in a higher slope, an intercept of 0.198, higher adjusted r^2, a higher bias, RMSE and RMSLE compared to identical match up points with errors. Overall, the removal of error values improved the performance metrics of NN (Table 4.5; Figure 4.9).

The OC4Me algorithm had a slope of 0.234, an intercept of 0.177, a low adjusted r^2 and high RMSE and RMSLE values (Table 4.5; Figure 4.9A) . These results are very similar to (Table 4.5; Figure 4.9C), as only 7 values were removed due to high error values. Just as before, when the identical match up points had errors removed the values did not change, due to a very small percentage of points removed.

For MODIS there were only two sets of performance metrics, without errors and with the points with identical match up points to the other two algorithms. The identical match up points did not improve the slope values, there was slight decrease in intercept, the adjusted r^2, bias, RMSE and RMSLE were lower (Table 4.5; Figure 4.9).

All three algorithms performed better in mixed rather than stratified waters (Table 4.7; Figure 4.10). NN had a lower bias, RMSE and RMSLE and higher slope and adjusted r^2 when the errors were not removed (Figure 4.10). Similarly, to mixed waters, in stratified waters the bias, RMSE, RMSLE was higher when the errors were removed. However, in this case, the slope, was also slightly higher. Removing the errors improved the intercept (Table 4.7; Figure 4.10). OC4Me metrics did not change much when the errors were removed for both mixed and stratified waters. There was a slight improvement in the slope from a negative value (-0.186) to almost 0 (-0.058) for OC4Me. OCI+OC3 performed better mixed waters than stratified waters (Table 4.7; Figure 4.10).

Table 4.5 - Performance metrics of three chlorophyll-a retrieval algorithms in the Celtic Sea and Western approaches. * and bold = best metric for data processing category.

Algorithm	All	Error values removed	Identical match up points	Error values removed + identical match up points
NN				
n	12202	7014	3649	1981
Slope	**0.578***	**0.827***	**0.545***	**0.838***
Intercept	**-0.001 ***	0.313	-0.13	0.198
Adj. r2	**0.089***	**0.208***	**0.06***	**0.133***
Bias	**0.089***	0.348	**-0.063 ***	0.221
RMSE	152.817	213.872	71.098	110.161
RMSLE	**9.779***	29.182	**3.794***	**9.841***
OC4Me				
n	11360	11292	3649	3642
Slope	0.234	**0.22***	0.205	0.183
Intercept	0.177	0.179	0.12	0.118
Adj. r2	0.045	0.042	0.029	0.023
Bias	0.341	0.345	0.237	0.238
RMSE	102.439	102.838	45.783	45.83
RMSLE	36.31	36.632	14.31	14.339
OC3+OCI				
n	11543	11543	3649	3649
Slope	0.072	0.072	**0.017***	**0.017***
Intercept	-0.023	**-0.023 ***	**-0.028 ***	**-0.028 ***
Adj. r2	0.006	0.006	0	0
Bias	0.174	**0.174***	0.117	**0.117***
RMSE	**39.83***	**39.83***	**15.761***	**15.761***
RMSLE	18.717	**18.717***	7.083	**7.083**

Table 4.6 - Performance metrics of three chlorophyll-a retrieval algorithms in the Celtic Sea and Western approaches when split by mixed and stratified waters. * and bold = best metric for data processing category.

Algorithm	**Mixed**		**Stratified**	
	All	**Error values removed**	**All**	**Error values removed**
NN				
n	10387	6098	1815	916
Slope	**0.649***	**0.939***	**0.095***	**0.007***
Intercept	**0.037***	0.36	-0.269	**-0.058 ***
Adj. r2	**0.107***	**0.264***	**0.003**	-0.001
Bias	**0.108***	0.373	**-0.023 ***	**0.187***
RMSE	155.824	215.329	23.46	36.237
RMSLE	**11.006***	29.1	**0.975***	**5.669***
OC4Me				
n	9698	9680	1662	1612
Slope	0.298	0.289	-0.186	-0.22
Intercept	0.217	0.217	**-0.087 ***	-0.075
Adj. r2	0.074	0.07	**0.04***	**0.076***
Bias	0.362	0.363	0.218	0.238
RMSE	104.446	104.524	**15.519***	16.044*
RMSLE	35.627	35.67	8.868	9.544
OC3+OCI				
n	8215	8215	3328	3328
Slope	0.079	0.079	-0.017	-0.017
Intercept	-0.007	**-0.007 ***	**-0.087 ***	-0.087
Adj. r2	0.006	0.006	0	0
Bias	0.146	**0.146***	0.243	0.243
RMSE	**33.413***	**33.413***	21.683	21.683
RMSLE	13.254	**13.254***	14.036	14.036

Table 4.7 - Performance metrics of depth category, <50m and >50m for three algorithm, OC4Me, NN and OCI+OC3 in for different processing methods. * = best metric for the processing category.

	<50m		>50m	
Algorithm	**All**	**Error values removed**	**All**	**Error values removed**
NN				
n	4115	2341	8087	4673
Slope	**0.939***	**1.145***	**0.334***	**0.529***
Intercept	**0.185***	0.532	-0.137	**0.138***
Adj. r2	**0.169***	**0.389***	**0.036***	**0.094***
Bias	**0.192***	0.519	**0.036***	0.263
RMSE	138.001	193.608	89.271	124.99
RMSLE	**12.321***	25.116	**3.223***	**17.975**
OC4Me				
n	3917	3917	7443	7375
Slope	0.043	0.043	0.135	0.119
Intercept	0.382	0.382	**0.031***	0.033
Adj. r2	0.003	0.003	0.019	0.016
Bias	0.503	0.503	0.255	0.261
RMSE	110.037	110.037	46.73	47.057
RMSLE	31.483	31.483	22.019	22.384
OC3+OCI				
n	1632	1632	9911	9911
Slope	0.298	0.298	0.023	0.023
Intercept	0.28	**0.28***	-0.077	-0.077
Adj. r2	0.072	0.072	0.001	0.001
Bias	0.398	**0.398***	0.137	**0.137***
RMSE	**49.478***	**49.478**	**22.907***	**22.907***
RMSLE	16.09	**16.09***	13.67	**13.67***

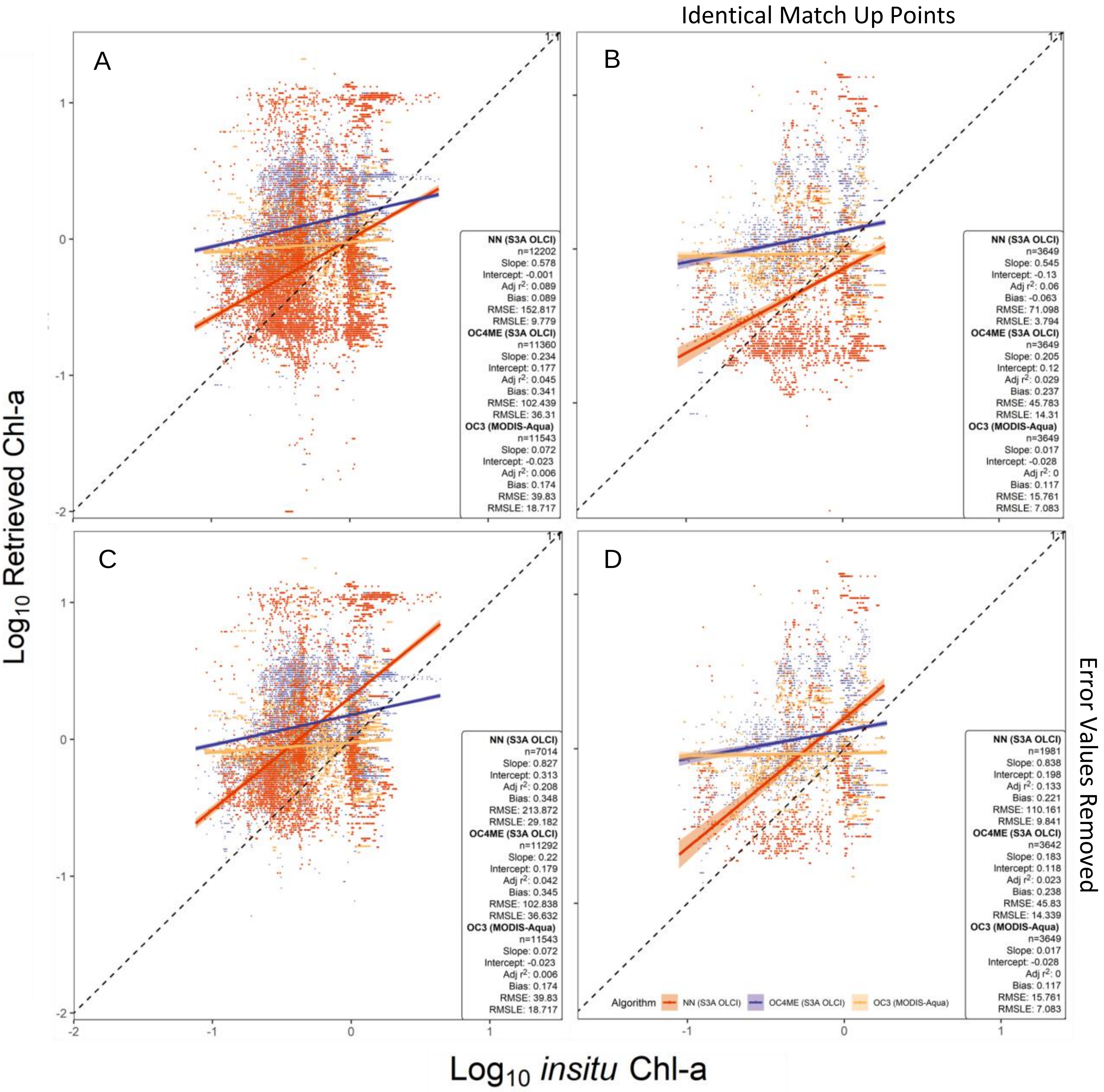


Figure 4.9 - Log$_{10}$ *in situ* and modelled chlorphyll-a (Chl-a) performance metrics of OC4ME and NN algorithms and OC3 =OCI+OC3 Modis Aqua (1:1 line [dotted line]). A) All match up points; B) Identical match up points between the three algorithms; C) All match up points with errors removed; D) Identical match up points with error values removed. Adjusted r^2 (log$_{10}$); Bias (log$_{10}$); Root Mean Square Error (RMSE [mg m^{-3}]); Root Mean Square Log Error (RMSLE [log$_{10}$]).

The algorithms performed poorly in both depth categories. The only metric that improved when errors were removed in <50m depth category for NN was the adjusted r^2 (Figure 4.11; Table 4.7). When compared with the >50m depth category, NN had a higher slope, intercept, and adjusted r^2, the bias, RMSE, and RMSLE were lower. As with the <50m depth category, when the errors are removed for >50m category, the bias, RMSE, and RMSLE are higher, the slope, intercept and adjusted r^2 are higher (Figure 4.11; Table 4.7). In <50m for OC4Me, there were no match up points removed due to satellite retrieval errors, as such the metrics were the same. The scatter plot demonstrated that the algorithm (OC4Me) was overestimating estimates of chlorophyll-a, as the majority of the points are found above the 1:1 line (Figure 4.11). Only few error points were removed from >50m, therefore the metrics are very similar (Table 4.7). For OCI+OC3, performed better in >50m depth category (Table 4.7), most satellite retrieval points overestimated predicted values of chlorophyll-a (Figure 4.11; Table 4.7).

4.3.2.2 Comparison of algorithms

When satellite retrievals were not removed and there was a varying number of match ups, the results were 'weak' in terms of slope and r^2. NN performed better than OC4Me and OCI+OC3 with a low RMSLE (9.779), intercept of almost 0, the highest r^2 out of the three with 0.089, and highest slope of 0.578, in terms of performance metrics (Table 4.5). However, NN had the largest range of chlorophyll-a values (Figure 4.5) compared to the other algorithms. The intercept was also closest to 0 (Figure 4.9a) indicating a better fit. After removing the errors, NN had almost 50% reduction in match up points (Table 4.4), but slope and adjusted r^2 improved, with all higher values in all other metrics. Values of intercept, bias, RMSE and RMSLE for OC4Me were all lower in comparison to NN. OCI+OC3 and NN outperformed OC4Me when there were identical match ups and when the error was removed from identical match ups (Table 4.5) in all metrics other than slope and adjusted r^2, where NN performed better. Overall, between all three algorithms, OCI+OC3 and NN performed marginally better.

All three algorithms performed better in mixed rather than stratified waters (Table 4.6; Figure 4.10). NN had a higher slope, the highest adjusted r^2, lowest bias, and RMSLE for mixed waters when errors were included. When the errors were removed, many of the underestimated values were removed (Figure 4.10). NN had a larger range of Chl-a retrieval values in comparison to OC4Me and OCI+OC3 and OC4Me had the smallest range of Chl-a retrieval values (Figure 4.5). No algorithm performed better in stratified with and without errors removed, NN and OCI+OC3 performed better than OC4Me in mixed waters. NN had better metrics in <50m depth category when error values were not removed, with the lowest RMSLE, lowest bias, highest slope (Figure 4.11; Table 4.7). However, NN has the largest deviation from the 1:1 line in comparison to the other algorithms (Figure 4.11). For the >50m depth category, the slope was closer to one for NN, but less than 0.2 for OCI+OC3. When the high errors were removed, OCI+OC3 had the lowest RMSE, RMSLE, bias and an intercept close to 0. However, the slope was also close to 0 (Table 4.7).

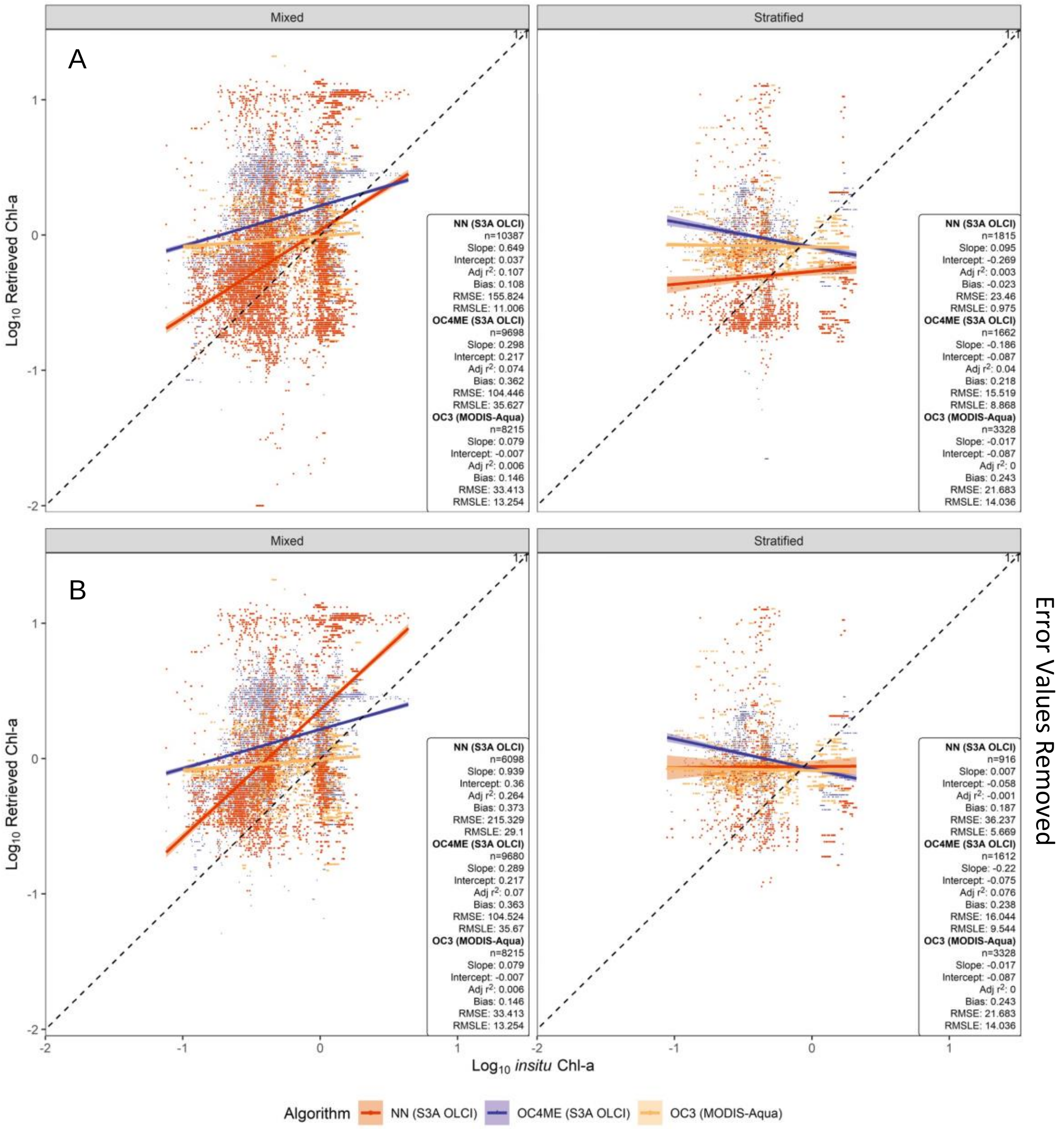


Figure 4.10 - Log$_{10}$ in situ and modelled chlorophyll-a performance metrics for mixed and stratified waters for OC4ME and NN algorithms and OC3 = OCI+OC3 (1:1 line [dotted line]). A) Where all match ups are considered, B) Where, error values were removed. Adjusted r^2 (log$_{10}$); Bias (log$_{10}$); Root Mean Square Error (RMSE [mg m^{-3}]); Root Mean Square Log Error (RMSLE).

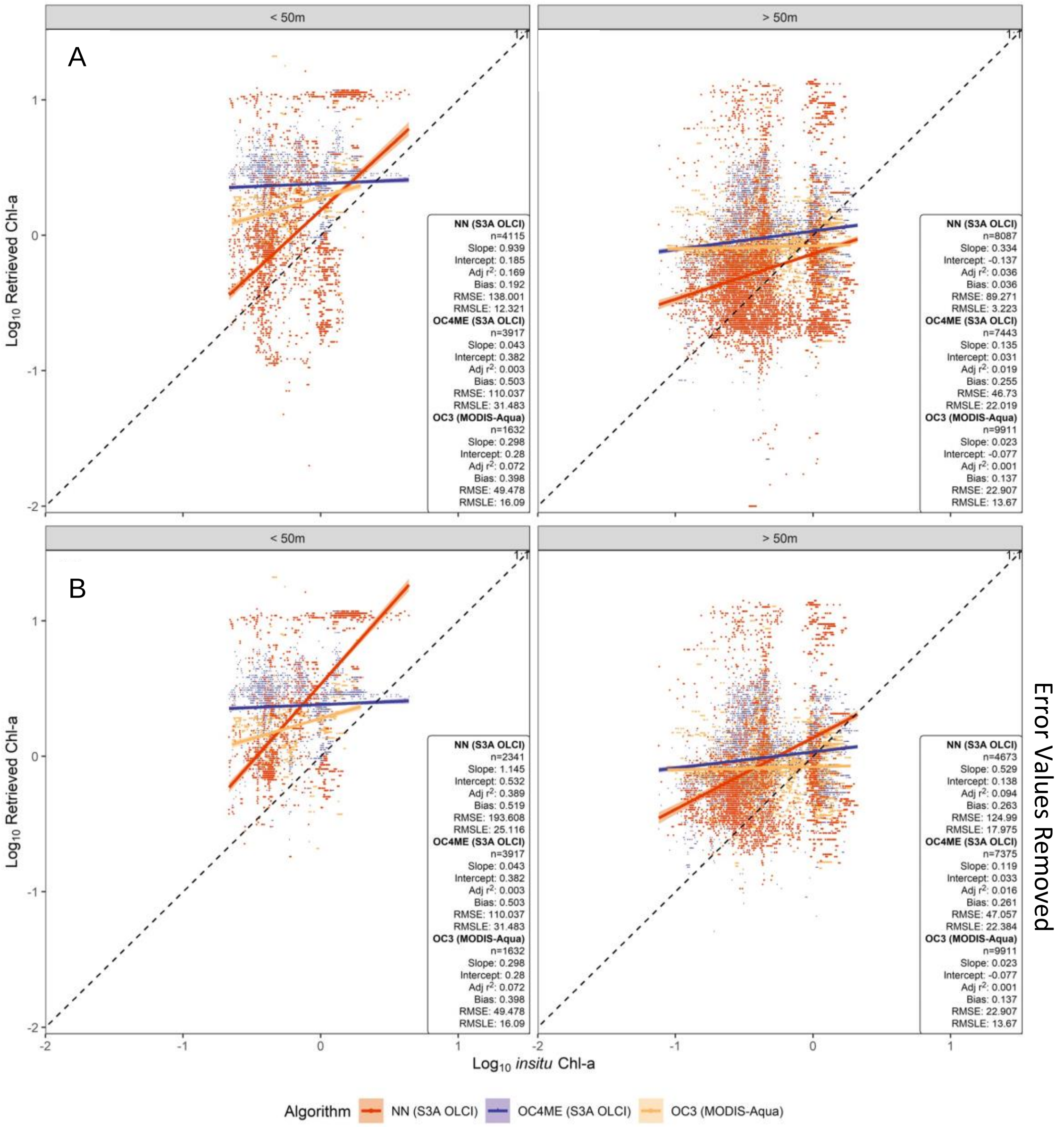


Figure 4.11 - Log$_{10}$ *in situ* and modelled chlorophyll-a (Chl-a) for <50m and >50m depth categories for OC4ME, NN and OC3 = OCI+OC3 (1:1 line [dotted line]). Adjusted r^2 (log$_{10}$); Bias (log$_{10}$); Root Mean Square Error (RMSE [mg m^{-3}]); Root Mean Square Log Error (RMSLE). A) Where all match ups are considered; B) Where, error values were removed.

4.3.3 Time window

Generally, all algorithms followed the same pattern across the time window (Figure 4.12). The first-time window (0-1 hour) resulted in the highest slope, bias and r^2, with the lowest RMSLE (Figure 4.12). As time between satellite overpass and *in situ* measurements increased, the slope, bias and adjusted r^2 decreased and the RMSLE increased. The metrics for the Sentinel 3 algorithms indicate that the OC4Me algorithm shows very little difference when the 30% error is removed, compared to

NN where there is a larger difference in values (Figure 4.12). OC3+OCI combination performed poorly in comparison to NN and OC4Me for the slope and adjusted r^2 in all time windows.

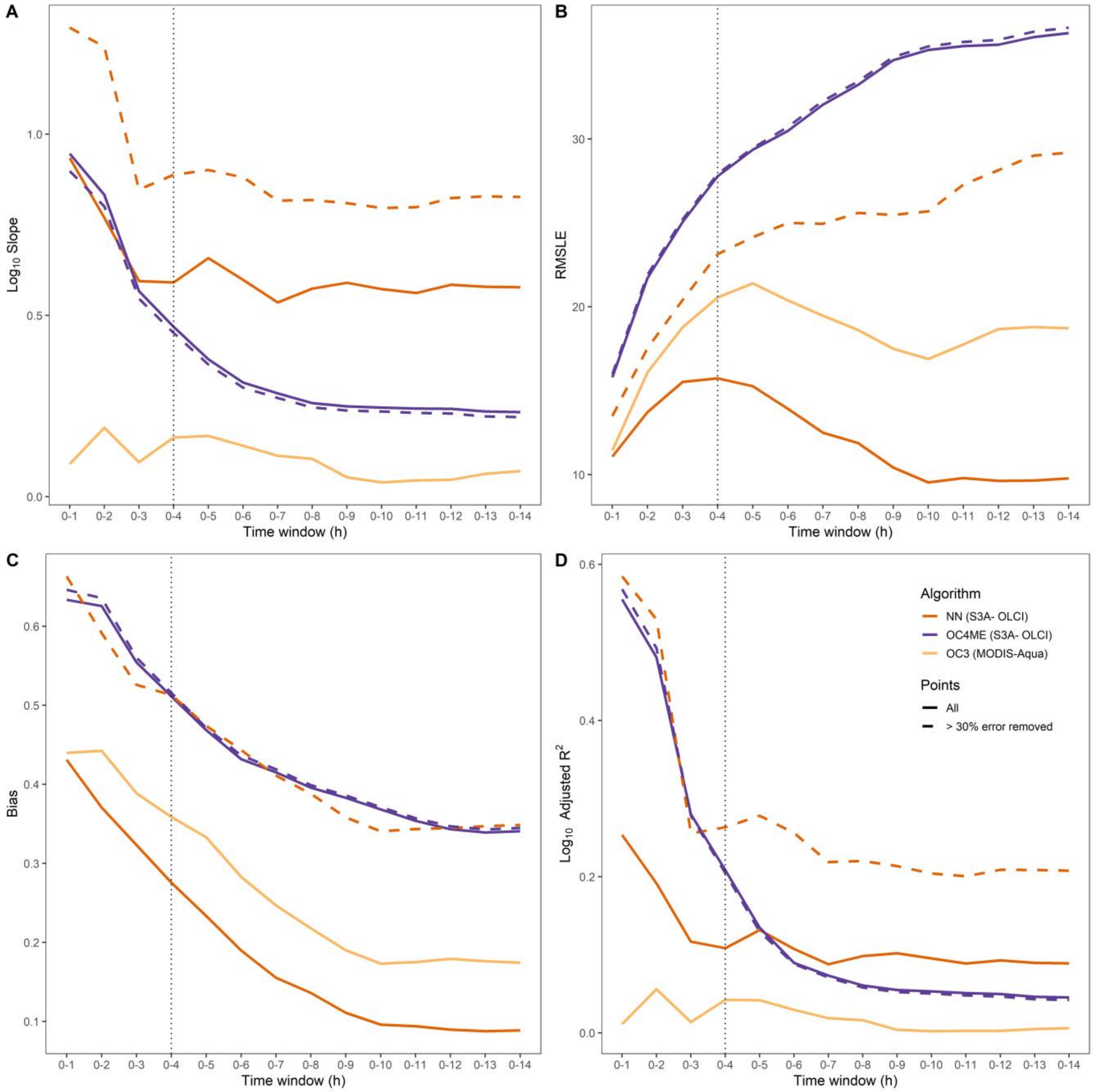


Figure 4.12 – Performance metrics of Log_{10} modelled chlorophyll-a match ups to *in situ* measurements (FerryBox), in Autumn 2016, 2017, 2019 in the Celtic Sea and Western Approached for three algorithms, OC4ME, NN, and OC3 = OCI+OC3 with errors (dashed line) and without errors removed (solid line) across different time windows. A) Log_{10} Slope; B) Root Mean Square Log Error (RMSLE); C) Bias ($\log_{10}$); D) Adjusted r^2 ($\log_{10}$); Bias ($\log_{10}$).

Table 4.8 - Comparison of OLCI performance metrics in different study areas. Dashed line represents no information available. * = This study.

Study Location	Sensor	Algorithm	Intercept	Slope	r^2	r	bias	RMSE mg m^{-3}	RMSLE	units	Reference	Considerations
Adriatic - Slovenia	OLCI	NN	-	-	0.1	0.31	-	-	0.43	log	Cherif et al. 2021	-
Adriatic - Slovenia	OLCI	NN	-	-	0.01	0.11	-	1.41	-	mg m^{-3}	Cherif et al. 2021	-
Adriatic - Slovenia	OLCI	OC4Me	-	-	0.33	0.58	-	0.46	-	log	Cherif et al. 2021	-
Adriatic - Slovenia	OLCI	OC4Me	-	-	0.27	0.52	-	1.12	-	mg m^{-3}	Cherif et al. 2021	-
Atlantic Ocean	OLCI	OC4Me	0.604	1.881	0.76	0.875	0.205	-	-	log$_{10}$ unless specified	Tilstone et al. 2021	-
Baltic Sea	OLCI	C2RCC	-1.61	2.56	0.56	-	-	-	-	mg m^{-3}	Toming et al. 2017	-
Baltic Sea	OLCI	C2RCC	-0.49	0.75	0.43	-	-	-	-	mg m^{-3}	Toming et al. 2017	-
Mediterranean Sea	OLCI	NN	-	-	0.16	0.4	0.19	-	-	mg m^{-3}	Moutzouris-Sidris & Topouzelis 2021	Case 2 (0-2 hour windows)
Mediterranean Sea	OLCI	OC4Me	-	-	0.55	0.74	0.19	-	-	mg m^{-3}	Moutzouris-Sidris & Topouzelis, 2021	Case 2 (0-2 hour windows)
Northwest European waters	MERIS	OC4Me	0.46	0.76	0.67	0.68	-	2.04	0.32	mg m^{-3}except RMSLE	Tilstone et al., 2017	Coastcolour AC processor
Northwest European waters	MERIS	OC4Me	0.63	0.83	0.55	0.62	-	2.14	0.43	mg m^{-3}except RMSLE	Tilstone et al., 2017	MEGS 8.0 AC Processor
South-eastern Arabian Sea	OLCI	C2RCC	0.0198	1.14	0.75	-	0.075	0.567	0.148	log unless stated otherwise	Harshada et al. 2021	-
World - inland and coastal waters	OLCI	OC4	-	0.581	-	-	1.645	3364.6	1.309	log10	Pahlevan et al. 2020	Same metrics as this study
Celtic Sea*	OLCI	NN	0.198	0.838	0.133	0.36	0.221	110.161	9.841	log$_{10}$ unless specified	This study	Error + identical match ups (0-14 hour time window)
Celtic Sea*	OLCI	OC4Me	0.118	0.183	0.023	0.15	0.238	45.83	14.339	log$_{10}$ unless specified	This study	Error + identical match ups (0-14 hour time window)

4.4 Discussion

The results indicate that none of the satellite retrieval algorithms for the Celtic Sea tested in this study (NN, OC4Me, OC3 MODIS-Aqua) reproduced chlorophyll-a with high accuracy, and all the algorithms generally overestimated chlorophyll-a concentrations compared to the *in situ* measurements. Out of the three algorithms, NN produced the best performance metrics, but due to the large range of values deviating from ground truthing data (i.e., high RMSE/RMSLE values), it also produced many errors. Through the different processing stages over half of the NN points were removed due to high error values. The values removed were often underestimated values of chlorophyll, therefore resulting in an overestimation of the remaining chlorophyll values.

NN performed better than the other algorithms for mixed and <50m waters; this was expected, as it was designed to estimate Chl-a in coastal waters (ESA, 2019). Overall, OC4Me did not have many high error values, and the range of values were smaller compared to NN and OCI+OC3, but performed poorly overall, in terms of the metrics. The observed overestimations by NN and OC4Me, have been documented in the product notice from ESA (ESA, 2019).

In mesotrophic and oligotrophic waters, the Chl-a retrievals from OC4Me are within a 30% uncertainty, compared to *in situ* data. There have been no reliable comparisons for *in situ* measurements and OC4Me in eutrophic waters. The product notice states that NN product validation is preliminary. It should take into consideration water types and is recommended for use in mesotrophic and eutrophic waters that exceed Chl-a concentrations of 0.1 mg m^{-3} (ESA, 2019). *In situ* Chl-a values were often below 1 mg m^{-3} and varied within a small range (0.076 - 4.38 mg m^{-3}). These low values, as stated in ESA (2019), may be a reason for poor validation results by NN.

NN retrieved chlorophyll requires the determination of multiple coefficients (training). A training data set for the region may improve Chl-a calculations (IMT, 2019; Ioannou et al., 2013), as such lack of regional data could explain algorithm performance as seen in this study. The standard error files have not yet been validated, (ESA, 2019), and the results from this study indicate that it is important to take into consideration the error file when working with NN.

4.4.1 Comparison with other regional studies

When compared with other studies validating Sentinel 3 – OLCI products, the results are quite varied (Table 4.8). Pahlevan et al., (2020) was only one study that produced higher RMSE values, than those found within this study. Similar results were demonstrated in the Mediterranean Sea (Moutzouris-Sidiris & Topouzelis, 2021), with poor performance of NN within coastal waters. Moutzouris-Sidiris & Topouzelis (2021) split the data into hourly time windows and found the optimum range to be 0-2 hours. These results are comparable to the 0–2 hour window found within this study for OC4Me (0.76 in this study when high errors were removed). However, NN had a stronger r^2 value in this study (0.36) than in Moutzouris-Sidiris & Topouzelis' study. This difference could be due to the number of match up points. For the 0-2 window, we used 191 match up points for NN, when high errors were removed, compared to 67 and 89 for Case 1 & 2 waters respectively used by Moutzouris-Sidiris & Topouzelis (2021). To directly compare these results with Moutzouris-Sidiris & Topouzelis (2021), the same relationship for classifying waters in terms of Case 1 and Case 2 was applied, where Case 1 waters were defined as absorption coefficient of 412nm divided by absorption coefficient of 443 nm is equal or less than 1.2. However, when this was implemented for this study, there were areas that were considered Case 1 waters (from *in situ* measurements) but resulted in Case 2 from the relationship defined above or vice versa. Therefore, depth (<50m and >50m) and mixed and stratified waters were used as a proxy to Case 1 and 2 waters.

The study by Moutzouris-Sidiris & Topouzelis (2021) also found an underestimation of Chl-a estimates by NN and overestimation by OC4Me in Case 2 waters, differing from this study, which found NN to overestimate results independently of water type. A possible reason is that not all *in situ* samples were collected using the same method in the Mediterranean Sea. The study by Toming et al., (2017) in the Baltic Sea calculated similar r^2 values to those in the Mediterranean Sea and this study, reporting 0.56 in coastal waters and 0.43 in open waters for NN. All three studies (this one included) used standard products released by ESA. As such, the atmospheric correction (AC) processors were the same.

Tilstone et al., (2017) took into consideration the effect of atmospheric correction processors on the performance of OC4Me, from the satellite MERIS in the Northeast Atlantic (including the Celtic Sea). The coefficients of determination (r^2) for two AC processors, COASTCOLOUR and MEGS8.0, were comparable to the value of 0.76 for adjusted r^2 for the 0-2 hour window using OC4Me in this study. Therefore, the atmospheric processor may play a key role in the outcome in the accuracy of the modelled Chl-a values. More recently, S-3A algorithms were analysed for performance with *in situ* data collected from the Atlantic Meridional Transect (AMT), in the Atlantic oligotrophic waters (Tilstone et al., 2021). Tilstone et al., (2021) calculated performance metrics for OC4Me, for samples within a 0-1 hour time window, with different AC processors, reiterating the importance of AC processors on the outcome of modelled Chl-a estimates. The POLYMER model through an iterative optimisation scheme, separates radiometric contribution of water from contributions from the atmosphere and surface through a spectral matching algorithm, which uses the full spectra available. This AC model was found to have great promise in providing more accurate estimations (0.01 – 1 mg m^{-3}), especially in regions where partial cloud cover and sun glint can affect the retrieval, such as the Celtic Sea (Tilstone et al., 2021). Analysing the effect of the AC processors on the accuracy of Chl-a estimations were outside the scope of this study, as the aim was to test the effectiveness of standard products that users may implement into research.

Pahlevan et al. (2020) undertook a global study using coastal and inland data of Chl-a and found that a Mixture Density Model (MDN) outperforms many of the current existing algorithms (e.g., OC4) by improving bias (logarithmic) by 40-60% and the RMSLE improved two to three times over.

4.4.2 Differences between OLCI algorithms and MODIS

The performance of MODIS differed from that of OLCI (Table 4.5). Generally, OCI+OC3 algorithm has poor performance within the region compared to OLCI algorithms. One key difference between MODIS and OLCI is the spatial resolution, one MODIS pixel is equivalent to 3 x 3 OLCI pixels, resulting in a smaller number of match-up points compared to OLCI, which can capture the smaller-scale variability on a pixel basis. MODIS was launched in 2002 and was designed to be operational for ~6 years. Given it has been operational for 20 years, MODIS-Aqua becomes the longest running ocean colour sensor. Due to its longevity, there have been multiple papers that demonstrate the degradation in MODIS-Aqua R_rs (Meister et al., 2011; Meister & Franz, 2014), which has been compensated for in R2018 reprocessing. Very few studies have compared MODIS with OLCI products (e.g., Li et al., 2019; Tilstone et al., 2021), with the latter reporting MODIS-Aqua was more accurate than OLCI OC4Me standard product (pb 2), as is the case of this study. A major difference is that Tilstone et al., (2021) investigated algorithm efficiency in the open ocean along the AMT, compared to the complex waters of the Celtic Sea considered within this study. Li et al., (2019) found that MODIS-Aqua and OLCI overestimated in the R_rs spectra in the open ocean of the China Sea. Atmospheric artefacts such as glint and other water constituents can affect the R_rs spectral shape, and it is the spectral shape that determines the accuracy of the ocean colour Chl-a algorithms. This was investigated by Tilstone et al., (2021) on OC4Me by collecting in situ R_rs to estimate Chl-a; they found ~25% underestimate in Chl-a, due to an overestimate in the maximum band ratio. It was concluded that there was a significant bias of OC4Me in the Atlantic Ocean. This contradicts the findings presented here, which demonstrates an overestimate of Chl-a from all algorithms in the region.

4.4.3 Limitations

Within the study there are number of limitations in the satellite Chl-a and also the *in situ* measurements. For example, the *in situ* measurements only spanned one month across the year, therefore it does not accurately reflect the annual range of chlorophyll within the Celtic Sea. Even though the autumn bloom on occurrences has been bigger than the spring bloom (Smyth et al., 2010), the range of values used to validate the algorithms in the region was not large enough to cover all phytoplankton conditions. The blooms were also temporally and spatially limited, and so the number of corresponding *in situ* measurements were small. There were many values below 1 mg m^{-3}, which may have increased uncertainties and errors in algorithms performance. The *in situ* measurements were continuous, therefore many observations were captured within a pixel. As such, the *in situ* data points should be averaged over one pixel to ensure that each matchup uses an independent satellite pixel. However, in 2019 FerryBox outputs had coarser spatial resolution (i.e., to 1 or 2 significant figures), which caused FerryBox measurements at a given latitude and longitude to collect data at different times of the day (i.e., 1am and 6pm on 15th October 2019 - See Appendix B [Table B 1]). This can be corrected for by using a smaller time window e.g., ± 1 hour time window of overpass, such as that performed by Tilstone et al., (2021). Considering an aim of this Chapter was to investigate the effect of the time window on the performance metrics of the algorithms, *in situ* measurements were not averaged.

There are also limitations in the accuracy of FerryBox derived Chl-a from the regression with HPLC. Even though the use of FerryBox to validate satellite observations has been in a number of validation studies (Toming et al., 2017), the regression and conversion is calculated individually for each year therefore it is not the same year in year out, as seen in Figure 4.3, and the difference could be up to a factor of 2 (Kratzer et al., 2022). Fluorometric measurements are also known to be influenced by other pigments (Gibbs, 1979; Welschmeyer, 1994). As there was such a poor match between HPLC and FerryBox, especially 2019, the satellite retrievals may be performing better than that reported in this study.

The satellite-based estimations of Chl-a are also susceptible to inaccuracies due to dissolved organic and suspended material at, or close to, the sea surface, such as coloured dissolved organic matter and total suspended matter. There are many riverine inputs into the Celtic Sea and Western approaches, such as the River Severn into the Bristol Channel, with the greatest influx of freshwater (and nutrients - Ruiz-Castillo et al., 2019) in Winter (Uncles, 2010). However, these were not taken into consideration, which could explain poor algorithm performance, particularly within the Bristol Channel (potentially classified as Case 2 coastal waters; ESA, 2019).

4.4.4 Recommendations & Conclusion

This is the first local scale study to investigate the efficiency of OLCI satellite retrieval algorithms in the Celtic Sea. We found NN to perform better than other algorithms in <50m and mixed waters. OC4Me did not perform as expected and did not perform better in >50m and stratified waters compared to the algorithms. However, there is still large uncertainty in the best performing satellite retrieval algorithm as demonstrated here for the Celtic Sea. Even though, NN and OCI+OC3 performed better than OC4Me, the algorithms were still error prone. The standard error files included are key if using the NN algorithm as it removes many underestimated outliers, this does, however, then cause an overestimate in the derived Chl-a. Clear reservations also lie within the accuracy of the *in situ* FerryBox measurements, and further investigation is required into especially understanding the poor regression shown in 2019.

Further investigation is also required to understand the causes of the uncertainties satellite retrievals, by taking a wide range of *in situ* measurements throughout the year, including in bloom and non-bloom seasons and also using just discrete HPLC samples. Comparing *in situ* R_rs spectra, with satellite derived spectra, and subsequently deriving Chl-a for OC4Me, as reported in Tilstone et al., (2017) would provide a better understanding of how the algorithm performs in the area. This will also provide understanding of the effect of the AC processor within the region. In terms of NN, providing the collected *in situ* observations into the training dataset may improve the quality of performance of the algorithm. Taking into consideration the other water quality parameters (such as coloured dissolved organic matter) will provide an overall picture of the complexity of the waters, and whether the presence of a particular parameter is causing the overestimates in the region.

It has been demonstrated that there is promise for the improvement of these algorithms in the wider Celtic Sea region. Our results currently show a ’weak’ correlation between *in situ* measurements and satellite retrievals. As such, further investigation into the causes of the uncertainties is required. Due to these uncertainties, the use of satellite retrieved Chl-a to calculate phytoplankton size classes (e.g., Roy et al., 2013; Brewin et al., 2015), in this study area, cannot be recommended at this stage.

It was beyond the scope of this study to further investigate improving the satellite algorithms or FerryBox regression, to generate more accurate chlorophyll estimates for use in an SPF model. Therefore, Chapter 5 will not include phytoplankton size classes generated from these algorithms as input into Ecopath with Ecosim. Instead, outputs from the state-of-the-art UK Earth System Model (CMIP6), were considered for use.

5

Understanding the role of small pelagic fish in the Celtic Sea using an ecosystem model

Chapter 5 –Understanding the role of small pelagic fish in the Celtic Sea using an ecosystem model

5.1 Introduction

Over the past few decades, human activities such as overfishing, climate change, and pollution have affected marine ecosystems dynamics (Ottersen et al., 2004; Pauly et al., 1998; Votier et al., 2004), biodiversity and trophic interactions (Stokstad, 2006). Therefore, understanding the functioning of marine ecosystems is key for conservation and sustainable management practices. Food webs govern the structure and functioning of marine ecosystems (Libralato et al., 2014), and are often modelled using trophodynamic models as explained in Section 2.2. Changes to a component of the food web (e.g., predator or prey) can have potential consequences on another component via trophic linkages. Studies have shown that human activities such as fishing (a potential stressor) as a top-down control can generate trophic cascades (Österblom et al., 2007), and reduce the mean trophic level (Pinnegar et al., 2002). Climate change, on the other hand, can change basal productivity by influencing the distribution and composition of planktonic communities, and thereby the bottom-up control of the system (Beaugrand, 2005; Conversi et al., 2010). These changes may in turn affect the mid-trophic species, e.g., small pelagic fish, a key link to apex predators (Mavor et al., 2005).

An ecosystem-based approach is recognised as an important management tool (Craig & Link, 2023), as it provides an opportunity to recreate complex trophodynamics (Fulton, 2010). It can further focus on specific species interactions, e.g., predator prey interactions, and explore the effects of fishing and climatic changes (Fulton & Smith, 2004). Ecopath with Ecosim (EwE) is a modelling software used to understand trophodynamics of ecosystems through a multi species approach and has been applied to address ecological and policy questions (Christensen & Walters, 2004).

The Celtic Sea ecosystem has seen changes in the past decades, which are mostly attributed to fishing of demersal species (Hernvann & Gascuel, 2020). Fishing in the Celtic Sea is mostly driven by commercial or industrial fleets (Hernvann & Gascuel, 2020). Although fishing has previously been considered a major driver in the Celtic Sea it is thought that there might be a shift from fishing induced changes of the past to environmental changes as a result of climate change (Hernvann et al., 2020). For example, there has been a change to the SPF community composition: with an increase of warm water species like European anchovy (*Engraulis encrasicolus*) to the region since the late 1990s (ICES, 2016), and recent decline in cold-water herring leading to a reduction in fishing effort (ICES, 2021). Changes to other SPF within the Celtic Sea have also been recorded. SPF are important to the region as they can control the system through bottom-up and top-down control. Therefore, it is important to understand the role these species play within the ecosystem, especially due potential environmental and anthropogenic changes that may occur within the Celtic Sea.

Pre-existing EwE models of the Celtic Sea have mainly focused on assessed stocks (e.g., cod and anglerfish) within the region (Moullec et al., 2017; Hernvann et al., 2020), with biomasses of SPF taken from demersal surveys. The diet matrix of the SPF for these models have used stomach content analyses from neighbouring seas or from FishBase (Froese & Pauly, 2009; Moullec et al., 2017). Stomach content analyses are a key input into ecosystem models, such as EwE, as they provide information on predator-prey and trophic interactions. Therefore, it is ideal to use data only from the region of interest if available. Hernvann et al., (2022) developed an R package ‘EcoDiet’ (Théro et al., 2020), to improve the diet composition input for ecosystem models by using a Bayesian hierarchical model, to combine multiple data types, stable isotopes, stomach content analyses, and literature knowledge. However, input data on SPF both in terms of diet as well as biomass, were relatively limited. Therefore, updating the diet matrix of Hernvann et al., (2020), using EcoDiet, with data provided from Chapter 3, and biomasses from pelagic surveys, could improve the understanding of trophic interactions of SPF in the Celtic Sea.

The primary objective of this study is to update the pre-existing EwE models for the Celtic Sea (Hernvann et al., 2020; Moullec et al., 2017), focusing on small pelagic fish, mackerel, sardine, anchovy, herring, horse mackerel, and sprat, using data from 2013 - 2021. To update the model, diet data for SPF from Chapter 3 and updated biomass data from Cefas' PELTIC survey were used, as well as ensuring all SPF were a single species functional group. Small scale mono specific fishing fleets for SPF were included, due to social importance of these fisheries to the region. Guidelines outlined by Heymans et al., (2016), pre-balance diagnostics, 'PRE-BAL' (Link, 2010), and stepwise fitting from Scott et al., (2016) were conducted to evaluate the initial static energy budget and the model fitting from 2013 - 2021. Ecosystem network analysis indicators were used to assess the role of SPF in the system, more specifically how an increase of biomass of functional groups (FG) impacts SPF. Annual niche overlap (modified Pianka Index) was calculated to compare with results of Chapter 3. Understanding the role of SPF in the Celtic Sea ecosystem, especially regarding an increase to anchovy in the region, can inform us of potential structural and functional changes of the Celtic Sea ecosystem.

5.2 Methods

5.2.1 Study Area

The study area as previously described, is the Celtic Sea (Figure 1.1; Figure 5.1), delineated by the 200m depth contour of the Northwest European continental shelf. There are two seasonal fronts systems that develop during spring: the Celtic Sea front (separating the Celtic Sea from the Irish Sea) and the Ushant Front, which develops from the coast of Brittany and extends to the western English Channel (OSPAR, 2000), it is in these areas where there are the greatest gradients and patchiness of plankton distribution in this area (Johns, 2006). There are two main phytoplankton bloom events, a spring bloom (e.g., March), and an autumnal bloom, September-October, (Pingree et al., 1976). The sea area is also characterized by both warmer water and colder water systems and both Lusitanian and Boreal fish species are found in the area (Dinter et al., 2001).

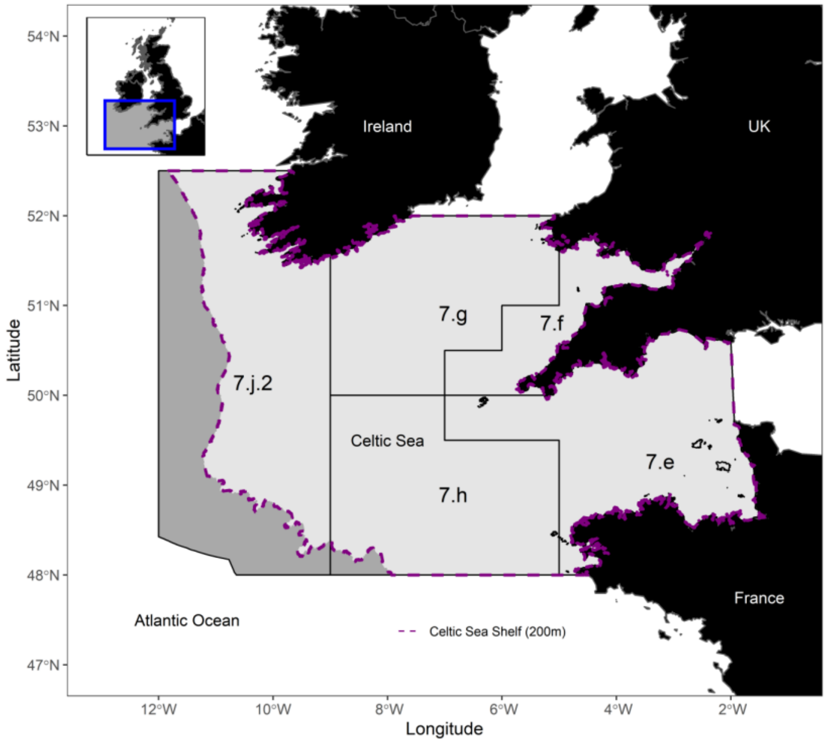


Figure 5.1 - General location of the Celtic Sea (top left corner) and delimitation of the study area regarding physical and management boundaries. The Celtic Sea EwE model (purple dashed contour) is updated for the shelf area shallower than 200 m depth matching ICES divisions (polygons) 7.e (Western English Channel), 7.f (Bristol Channel), 7.g (Celtic Sea North), 7.h (Celtic South) and 7.j.2 (Southwest of Ireland- East belonging to the NE Atlantic Fisheries Commission regulatory area)

5.2.2 Ecopath

To understand the trophic relationships of the Celtic Sea food web particularly for pelagic fish, Ecopath with Ecosim, a steady state simulation program, was used. The software is used to analyse ecosystem dynamics through the creation of model food webs (Pauly et al., 2000). The initial concept was developed by Polovina, (1984) and was combined with network analysis and system maturity indices of Ulanovicz & Puccia, (1990) and Odum, (1969).

The model is structured by species that can be aggregated by their ecology (e.g., life history, diet composition, habitat), these are represented as functional groups (FGs) and connected through predator/prey interactions based on diet composition. These FGs can consist of one species or life history traits (i.e., juvenile vs adults), or multiple species. For some FGs, species were grouped according to taxonomic similarities (e.g., lobsters), whilst others are aggregated by trophic guilds (e.g., small benthivorous fish) or similar feeding strategy (e.g., seabird offshore divers).

Ecopath requires input for each functional group *i*, this is in terms of biomass (B t km^{-2} y^{-1}), production/biomass (P/B y^{-1}), which in most conditions relates to the total mortality rate or instantaneous mortality (Z = fishing mortality + natural mortality), consumption/biomass (Q/B y^{-1}) and ecotrophic efficiency (EE), which the proportion of the net annual production consumed by higher trophic levels (Christensen and Walters, 2004). Ideally, EE is estimated from the software, and B, P/B, and Q/B are entered for all groups. These values are often taken from literature, stock assessments, and ecological studies.

In addition to the parameters stated, the model also requires information on diet composition and fisheries landings and discards. In the Ecopath model an equilibrium condition is assumed, where inputs and outputs are equivalent. A biomass budget equation is used to establish the equilibrium and is determined for each functional group (*i*), considered as Equation 5.1.

$$Production\ (i) - predation\ (i) - non\ predation\ losses\ (i) - export\ (i) = 0 \qquad (5.1)$$

Ecopath mass-balance over a given time period relies on two master equations, with the first describing the production of FG, *i* (Equation 5.2).

$$B_i \times \left(\frac{P}{B}\right)_i = \sum_{j=1}^{N} B_j \times \left(\frac{Q}{B}\right)_j \times DC_{ji} + \left(\frac{P}{B}\right)_i \times B_i \times (1 - EE_i) + Y_i + E_i + BA_i \qquad (5.2)$$

where B_i is the biomass of the FG; $(P/B)_i$ is the production rate (assumed to be the total mortality, Z), EE_i is the ecotrophic efficiency (proportion of the production used in the system), Y_i is the fisheries yield, E_i is the net emigration rate, and BA_i is the biomass accumulation. B_j is the biomass of one of the N predators of functional group *i,* which eats functional group *i* in DC_{ji} proportion, whose consumption rate is $(Q/B)_j$. For each FG, i, Y_i and DC_{ji} are input parameters, and three out of the following four parameters B_i, $(P/B)_i$, $(Q/B)_i$ and EE_i, are to be specified. The unspecified fourth parameter is estimated by Ecopath. Ideally, EE should be the parameter estimated by Ecopath (Heymans et al., 2016).

The second master equation of Ecopath defines an FG's productivity in terms of its consumption and maintenance needs (Equation 5.3).

$$Q_i = P_i + R_i + UA_i \tag{5.3}$$

where Q_i is the consumption of functional group *i*, P_i its production, defined in Equation 5.2 as $B_i \times \left(\frac{P}{B}\right)_i$, R_i its respiration, and UA_i the unassimilated food. Therefore, Equation 5.3 expresses that consumption is the sum of growth (somatic and gonadal combined), metabolic costs and waste products (Winberg, 1956).

5.2.3 Ecosim

Ecosim represents temporal changes of biomass in an ecosystem in response to changes in trophic interactions, fishing, environmental changes (Christensen et al., 2008; Christensen & Walters, 2004). It relies on a set of differential equations, to express changes in biomass of each FG *i,* over a given time period d_t (Equation 5.4).

$$\frac{dB_i}{dt} = g_i \times \sum_{j=1}^{N} Q_{ji} - \sum_{j=1}^{N} Q_{ij} + I_i - (M0_i + F_i + e_i + i_i) \times B_i \tag{5.4}$$

The growth rate of a FG *i* over time interval d_t, is given by the difference in matter produced by FG *i,* through migrations (immigration i_i and emigration e_i), losses in FG_i, through fishing (fishing mortality rate F_i), natural mortality due to predation (sum of Q_{ij} by functional group *i*'s predator) or other causes (mortality rate $M0_i$). The matter produced by FG *i,* is expressed by the consumption of all FG *i*'s prey (product of food consumed), and the growth net efficiency through the ratio of two parameters *(Q/B)_i* and *(P/B)_i*. These consumptions are based off the 'foraging' arena theory, by dividing prey biomasses into vulnerable and invulnerable compartments (either accessible or inaccessible to predators, respectively) (Ahrens et al. 2012). For a predator-prey pair (*i,j*), the consumption of *i* by *j*, is estimated by Equation 5.5.

$$Q_{i,j} = \frac{a\prime_{i,j} * v_{i,j} * B_i * P_j * T_i * T_j * \frac{M_{i,j}}{D_j}}{v_{i,j} + v_{i,j} * T_i * M_{i,j} + a\prime_{i,j} * M_{i,j} * B_j * \frac{T_j}{D_j}} * S_{t,j,}(e_e, t) \tag{5.5}$$

where B_j is the biomass of the predator *j*; $a'_{i,j}$ is the rate of effective search of predator *j* for prey *i*; T_i and T_j correspond to the prey and predator relative feeding time, respectively; $M_{i,j}$ is the mediation effect that a third organism can impose on the (*i,j*) trophic relationship; and D_j is the handling time of the predator *j* for its prey. The vulnerability coefficient $v_{i,j}$ controls the transfer rate of the prey between the vulnerable and invulnerable compartments and it can range from 1 to infinity. For values of $v_{i,j}$ greater than 2, a large increase in B_j results in a large increase in $Q_{i,j}$. Therefore, values of $v_{i,j}$ greater than 2, the quantity of prey *i,* consumed by predator *j* is mainly influenced by predator *j* abundance, which is a top-down control. A bottom-up control is when $v_{i,j}$ is close to 1, a large increase in B_j has a lower impact on $Q_{i,j}$; Initially the vulnerability co-efficient is set to 2, as a trade-off between the bottom-up and top-down control, this can be estimated through Ecosim model fitting to time-series. They are estimated to minimise the weighted sum of square deviations. The number of vulnerability coefficients that can be estimated are limited to the number of time-series, which is either chosen by the modeller or through the stepwise fitting procedure (Scott et al., 2016), this determines the vulnerability coefficients based on best fit to time series data based on Akaike Information Criterion (Akaike, 1974).

The Ecosim model can also be forced by using environmental or fishing time-series. Forcing time-series of fishing mortality can be applied to FG's that the fisheries target, this simulates the temporal impact of fishing. It is directly applied through Equation 5.4. There are two ways that Ecosim can model environmental change. The first uses an observed time-series of primary production (PP). The production of primary producer (phytoplankton groups) PP_i is determined from its biomass as shown in Equation 5.6.

$$PP_i = \frac{r_i.B_i}{1+B_i.h_i} * pp_{i,t}^{rel} \tag{5.6}$$

where r is the largest possible production/biomass ratio, r_i/h_i is the maximum net primary production when the biomass is not limiting production. $pp_{i,t}^{rel}$ is a time-series of primary production used to simulate the impact of observed changes in the production of lower trophic levels. For example, from the Chl-a from satellite remote sensing, such as that assessed in Chapter 4.

The second way is through FG_i, to model mean species consumption or mortality on specific environmental drivers. This can be done using one or several functional responses f_e related to environmental variables e_e to express a temporal forcing of the trophic group consumption. The functional response f_e, could represent a preference function to water temperature (Bentley et al., 2017; Corrales et al., 2017; Serpetti et al., 2017) or oxygen concentration (de Mutsert et al., 2016). It would provide a multiplier of the consumption that vary according to the conditions in the ecosystem.

5.2.4 Updates to the Celtic Sea EwE

5.2.4.1 Model Structure

The Ecopath model in this thesis was based on data from 2013, updating Moullec et al., (2017) and Hernvann et al., (2020) for small pelagic fish in the Celtic Sea. The FGs of the Celtic Sea Ecopath model were extracted from Hernvann et al., (2020) with one exception. Anchovy (*Engraulis encrasicolus*) was previously incorporated into group ‘Pelagic fish – Medium’, this group was repurposed to solely represent anchovy (see Appendix - [Table C 1]). Hernvann et al., (2020) stated that the main contributor of the group was anchovy. The other species in the group present a much smaller contribution within the Celtic Sea ecosystem; therefore, it was decided for ease of interpretation to remove these species and repurpose the FG for anchovy alone (see Appendix C – [Table C 1] for full list of functional groups).

Fishing fleets in the model remained the same as Hernvann et al., (2020), specifically targeting one functional group (mono-specific) but with the addition small scale mono-specific fleets with data from Sea Around Us (SAU - Pauly et al., 2020) and Fisheries Dependent Information (FDI - STECF, 2020) for small pelagic fish.

5.2.4.2 Inputs to Ecopath

Biomass data for small pelagic fish, notably anchovy, sprat, and sardine became available from 2013, from the PELTIC survey. The PELTIC survey is a pelagic survey that investigates phytoplankton to small pelagic fish and top predators within the Celtic Sea area in autumn. As such the biomasses of SPF stated above for 2013 were updated, as previously the only biomasses were taken from demersal surveys that are not designed for SPF and are likely to have underestimated the values. Biomass for phytoplankton and zooplankton groups were taken from the UK Earth System Model, UKESM1-0-LL historical data, as part of Coupled Model Intercomparison Project (CMIP6; Eyring et al., 2016), downloaded from https://esgf-index1.ceda.ac.uk/search/cmip6-ceda/ and extracted through Python (v3.8 – van Rossum & Drake, 2009) package ‘nctoolkit’ (v0.8.6) on the Reading Academic Computing Cluster (Linux).

P/B and Q/B were taken from Moullec et al., (2017) if available or calculated using empirical model of Pauly, (1980) for P/B (annual production rate) and empirical models of Pauly et al., (1990) and Christensen & Pauly, (1992) for Q/B ratios with inputs to the models taken from FishBase (Froese & Pauly, 2009).

5.2.4.3 Diet Matrix

The diet matrix from Hernvann et al., (2020) was updated based on results from Chapter 3/Patel et al., 2023. The outputs from Patel et al., (2023) were computed annually and localised to the Celtic Sea only for SPF. The new diet data for SPF was combined with Celtic

Sea biotracer, and literature data from Hernvann et al., (2020; 2022) in a Bayesian hierarchical model, through ‘EcoDiet’ R Package (Hernvann et al., 2022; Théro et al., 2020) in R (v4.1.2 – R Core Team, 2021). The outputs for anchovy, sardine, herring, mackerel, sprat, and horse mackerel were updated from the 1985 diet matrix (Table 5.1; see Appendix C – [Table C 2] for full diet matrix input).

Table 5.1 - Diet matrix update from 1985 Ecopath model to this study (2013) for small pelagic fish in the Celtic Sea Ecopath model using the Bayesian hierarchical model from Hernvann et al. (2022).

Prey \ predator	1985	2013	1985	2013	1985	2013	1985	2013	1985	2013	1985	2013
	Mackerel		Horse mackerel		Sprat		Sardine		Herring		Pelagic fish - Medium	Anchovy
Seabirds - Divers												
Seabirds - Surface feeders												
Baleen whales												
Toothed cetaceans / Seals												
Pelagic sharks												
Carnivorous demer. elasmobranchs												
Benthivorous demer. elasmobranchs		0.029										
Sea bass												
Anglerfish large												
Anglerfish small												
Hake large												
Hake small			0.001									
Cod large												
Cod small			0.001									
Whiting			0.006									
Haddock										0.020		
Pouts		0.031		0.044						0.021		
Megrim												
Sole												
Plaice												
Piscivorous demer. fish												
Epibenthivorous demer. fish			0.002	0.046								
Endobenthivorous demer. fish												
Suprabenthivorous demer. fish		0.029	0.044	0.044						0.027		
Small benthivorous demer. fish			0.001	0.045						0.020		
Mackerel		0.030										
Horse mackerel		0.033										
Boarfish												
Sprat		0.038	0.001	0.046						0.041		

Blue whiting	0.052	0.033	0.019	0.004								
Pilchard												
Herring			0.008							0.071		
Pelagic fish - Large												
Pelagic fish - Medium	0.004		0.006						0.002			
Squids	0.001	0.034	0.006	0.045								
Benthic cephalopods		0.035		0.040						0.021		0.048
Commercial crustaceans												
Nephrops												
Commercial bivalves												
Shrimps	0.015	0.026	0.058	0.046	0.083	0.028			0.013	0.016		0.060
Carnivorous/Necrophagous benth. inv.		0.040	0.008	0.046	0.051	0.043		0.061	0.004	0.021	0.021	0.063
Suspension/Surface detritus feeder benth. inv.		0.042	0.001	0.046	0.113	0.076	0.093	0.168	0.021	0.036	0.077	0.074
Subsurface deposit feeder benth. inv.											0.014	0.041
Suprabenthos	0.010	0.036	0.004	0.046							0.095	0.059
Benthic meiofauna								0.071				0.086
Macrozooplankton	0.523	0.090	0.341	0.047	0.014	0.014	0.107	0.103	0.236	0.240	0.023	0.023
Mesozooplankton - Large	0.271	0.059	0.370	0.211	0.177	0.177	0.350	0.102	0.509	0.185	0.253	0.193
Mesozooplankton - Small	0.123	0.412	0.124	0.234	0.562	0.660	0.447	0.447	0.214	0.280	0.516	0.350
Microzooplankton												
Bacteria												
Phytoplankton - Large		0.002	0.000	0.009		0.003	0.003	0.003				0.003
Phytoplankton - Small												
Discards												
Detritus								0.047				
Import												
Sum	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
(1 - Sum)	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

5.2.4.4 Model Balancing

When the Ecopath model input parameters were updated for 2013, the model was parameterised, and the missing parameters estimated by Ecopath to achieve mass balance. Model balancing was performed using a pre-balance diagnostic (PREBAL; Link, 2010) through a set of guidelines as a form of a checklist. As the model was balanced previously through Hernvann et al., (2020) and Moullec et al., (2017) the PREBAL diagnostic did not differ from the pre-existing models (see Appendix -Table C 4;Figure C 1).

A functional group is imbalanced when the EE > 1, where the fishing or predation of a particular group exceeds the production or mortality of that particular FG. The initial Ecopath parameterisation produced estimated SPF EE >1. The diet matrix was scrutinised for the predator of these species, and through the use of DAPSTOM (Pinnegar, 2014), minor changes were made to the diet matrix to reduce predation on SPF.

5.2.4.5 Ecosim parameterisation

The Ecosim model was initially fitted through observed biomass time series (2013-2021) from ICES stock assessments, abundance indices from surveys (EVHOE - Duhamel et al., 2018; PELTIC - Doray et al., 2021), phytoplankton and zooplankton biomass from CMIP6 (https://esgf-index1.ceda.ac.uk/search/cmip6-ceda), and catch time-series from ICES, FDI (STEFC, 2020) and Sea Around Us (Palomares et al., 2018; Pauly et al., 2020). For assessed stock, fishing mortality was used as forcing function; and for non-assessed stocks, catch time series were used as in Hernvann et al., (2020). Before calibration, model stability was tested over a 100-year period (Figure C 2). The calibration of the Ecosim model was done through the stepwise fitting procedure outline in Scott et al., (2016) and the protocol from (Bentley et al., 2019), for determination of the predator-prey dynamics (vulnerabilities) for estimation. The forcing was carried out similar to Hernvann et al., (2020), with fishing only first, then by environmental and fishing dynamics, initially separately then combined. For environmental forcing, primary production (PP) monthly time series were taken from the Vertically Generalised Production Model (VGPM; Behrenfeld & Falkowski, 1997) for 2013-2021. The VGPM model uses satellite retrieved Chl-a from SeaWIFS and MODIS-Aqua to compute PP over the water column (Morel & Berthon, 1989). This time series was used to force phytoplankton groups. Sea Surface Temperature (SST) was taken from MODIS-Aqua Level 3 outputs and averaged over the Celtic Sea area as an environmental forcing time series. Sea Surface Salinity (SSS) was also used as an environmental forcing variable downloaded from Copernicus Marine Services (marine.copernicus.eu). Environmental preferences for the FGs were generated from Aquamaps (Kaschner et al., 2019) using R package 'aquamapsdata'

(Kaschner et al., 2019) and imported into EwE though the import tool. SST was applied to functional groups with an environmental preference of SST i.e., pelagic groups rather than demersal groups that are more likely to be affected by Sea Bottom Temperature (SBT).

To quantify the relative contribution of each driver, model fitting iterations were compared through sum of squares between observed and predicted time-series and bias corrected Akaike Information Criterion of the model (Akaike, 1974). A no hake and cod fishing scenario were implemented to understand the effect of SPF predators and commercially assessed species, on the biomass of SPF.

5.2.5 Mixed trophic Impact

Mixed trophic Impact (MTI) is a routine within the EwE software (Ulanowicz & Puccia, 1990). It is based on the Ecopath steady state model and can be used to better describe trophic relationships within the ecosystem. It shows direct and indirect influences (including competition) of variations in biomass of an FG on other FGs, thus can provide insight to how short-term variations in the food web can affect the whole ecosystem. However, it is important to consider that the MTI routine is not a function to predict future changes on trophic interactions, these are addressed in the dynamic model Ecosim, described in Section 5.2.4.5. MTI was applied to the balance Ecopath model of the Celtic Sea, as described in Section 5.2.4.4, to assess the impacts of increased biomass (10%) of a particular FG on the biomass of others in the ecosystem.

MTI is calculated by generating an $n\ x\ n$ matrix, where the i, jth terms represent the interaction between the impacting group i and impacted group j (Equation 5.7).

$$MTI_{i,j} = DC_{i,j} - FC_{j,i} \tag{5.7}$$

Where $DC_{i,j}$ is the diet composition of how much j contributes to the diet of i; $FC_{j,i}$ is the host composition term giving the proportion of the predation of j that is due to i as the predator. Fishing fleets are considered as ‘predators’. Direct and indirect increase of the impacted group j are calculated through the multiplication of the matrix. Direct impacts describe the effect of the increase of the impacting group has on the biomass of the impacted group. Whereas indirect effects can be associated with trophic cascades and inter-FG competition (e.g., density dependent effects).

5.2.6 Niche Overlap

The niche overlap routine (in terms of prey) in Ecopath uses a modified Pianka index by (Christensen et al., 2005). The main difference from Pianka index described in Section 3.2.5 is instead of using the geometric mean implied in the denominator of Equation 3.2, an arithmetic mean is used (Equation 5.8). If one of the groups (j) only overlaps with one other group (k) then p_{ij} will be zero for all values of i but $i = k$, where it will reach a value of 1. In such a case, the denominator of Equation 3.2 in Section 3.2.5 will always be 1, and the overlap index will equal p_{ik}, whereas a value between p_{ik} and p_{ij} would be more reasonable.

$$O_{jk} = \frac{\sum_i^n p_{ij} p_{ik}}{\sum_i^n ({p_{ij}}^2 + {p_{ik}}^2/2)} \tag{5.8}$$

As with Pianka Index explained in Section 3.2.5, the index assumes values from 0 to 1, where 0 = no overlap and 1 = complete overlap, all intermediary values show a partial overlap in resource utilization.

5.3 Results

5.3.1 Ecopath parameterisation

The results of parameterisation of the balanced Ecopath model are shown in Table 5.2, and the biomass contributions presented in Figure 5.2Figure 5.2 - Voronoi treemap of biomass (t km-2 yr-1) model output. Groups from Table 5.2 has been amalgamated for ease of interpretation. The trophic level of each FG is calculated through the diet composition (Table

5.1). Mackerel, herring, horse mackerel had a higher trophic level than the reported in Chapter 3, due to non-phytoplankton consumption.

The total fisheries catch amounted to 1.009 t km^2 yr^{-1} with a mean trophic level of 3.628. The highest catches were from hake and commercial bivalves, and the highest discards were large anglerfish.

Table 5.2 - Ecopath model outputs, B = Biomass; P/B = Production/Biomass; Q/B = Consumption/Biomass; EE = Ecotrophic Efficiency for all functional groups in the Celtic Sea Ecopath model. Bold values indicate values estimated by Ecopath.

Group no.	Group name	Trophic level	B ($t\ km^{-2}\ yr^{-1}$)	P/B (/year)	Q/B (/year)	EE
1	Seabirds - Divers	**4.50**	0.00	0.15	135.26	**0.00**
2	Seabirds - Surface feeders	**3.93**	0.00	0.25	114.47	**0.00**
3	Baleen whales	**3.60**	0.07	0.04	4.77	**0.00**
4	Toothed cetaceans / Seals	**4.85**	0.03	0.14	12.00	**0.00**
5	Pelagic sharks	**4.74**	**0.10**	**0.20**	**1.96**	0.60
6	Carnivorous demer. elasmobranchs	**4.44**	**0.01**	**0.47**	**3.13**	0.65
7	Benthivorous demer. elasmobranchs	**3.95**	**0.23**	**0.52**	**3.48**	0.65
8	Sea bass	**4.20**	0.03	0.28	1.52	**0.87**
	Anglerfish					
9	Anglerfish large	**4.68**	0.29		2.38	**0.65**
10	Anglerfish small	**4.49**	0.05		6.97	**0.05**
	Hake					
11	Hake large	**4.53**	0.31		2.52	**0.42**
12	Hake small	**4.05**	0.17		5.56	**0.15**
	Cod					
13	Cod large	**4.17**	0.08		4.61	**0.93**
14	Cod small	**3.95**	0.02		9.14	**0.70**
15	Whiting	**4.22**	0.29	1.12	3.70	**0.28**

16	Haddock	**3.43**	0.40	0.91	3.33	**0.47**
17	Pouts	**3.61**	**1.55**	**1.35**	5.40	0.95
18	Megrim	**4.17**	0.30	0.45	**2.24**	**0.33**
19	Sole	**3.31**	0.04	0.47	**2.58**	**0.55**
20	Plaice	**3.31**	0.06	0.81	**4.50**	**0.25**
21	Piscivorous demer. fish	**4.43**	**0.18**	**0.64**	3.21	0.85
22	Epibenthivorous demer. fish	**3.67**	**0.93**	**0.86**	4.30	0.95
23	Endobenthivorous demer. fish	**3.30**	**0.14**	**1.09**	5.45	0.95
24	Suprabenthivorous demer. fish	**3.42**	**0.89**	**1.88**	7.52	0.95
25	Small benthivorous demer. fish	**3.45**	**0.98**	**1.84**	7.34	0.95
26	Mackerel	**3.67**	0.70	0.56	**2.24**	**0.63**
27	Horse mackerel	**3.71**	1.49	0.85	**3.40**	**0.99**
28	Boarfish	**3.29**	2.14	**1.20**	4.80	**0.00**
29	Sprat	**3.17**	1.93	0.85	7.00	**0.42**
30	Blue whiting	**3.72**	0.60	**1.48**	5.90	**0.75**
31	Pilchard	**3.14**	1.21	0.84	6.80	**0.16**
32	Herring	**3.61**	0.84	0.78	4.59	**0.99**
33	Pelagic fish - Large	**4.32**	**0.09**	**0.42**	2.80	0.90
34	Anchovy	**3.35**	0.04	1.18	9.27	**0.99**
35	Squids	**4.10**	**0.20**	**3.90**	13.00	0.90
36	Benthic cephalopods	**3.91**	**0.18**	**3.90**	13.00	0.90
37	Commercial crustaceans	**3.60**	**0.88**	0.55	**3.67**	0.80
38	Nephrops	**3.31**	0.25	0.60	**4.00**	**0.91**
39	Commercial bivalves	**2.00**	0.30	3.50	**17.50**	**0.72**
40	Shrimps	**3.09**	**1.59**	3.00	**20.00**	0.95
41	Carnivorous/Necrophagous benth. inv.	**2.75**	**13.80**	1.89	**12.57**	0.95
42	Suspension/Surface detritus feeder benth. inv.	**2.05**	**27.72**	2.80	**14.00**	0.95

43	Subsurface deposit feeder benth. inv.	**2.48**	**27.07**	1.60	**8.00**	0.90
44	Suprabenthos	**2.36**	**4.88**	2.80	**14.00**	0.95
45	Benthic meiofauna	**2.09**	**7.72**	10.00	**50.00**	0.95
46	Macrozooplankton	**2.69**	2.25	**7.50**	25.00	**0.89**
47	Mesozooplankton - Large	**2.31**	3.84	**8.01**	26.69	**0.66**
48	Mesozooplankton - Small	**2.06**	6.34	**25.35**	84.50	**0.31**
49	Microzooplankton	**2.15**	5.29	**33.70**	112.32	**0.51**
50	Bacteria	**2.00**	**4.26**	54.48	**136.20**	0.65
51	Phytoplankton - Large	**1.00**	7.00	76.45		**0.96**
52	Phytoplankton - Small	**1.00**	10.10	76.45		**0.85**
53	Discards	**1.00**	0.25			**0.49**
54	Detritus	**1.00**	325.70			**0.92**

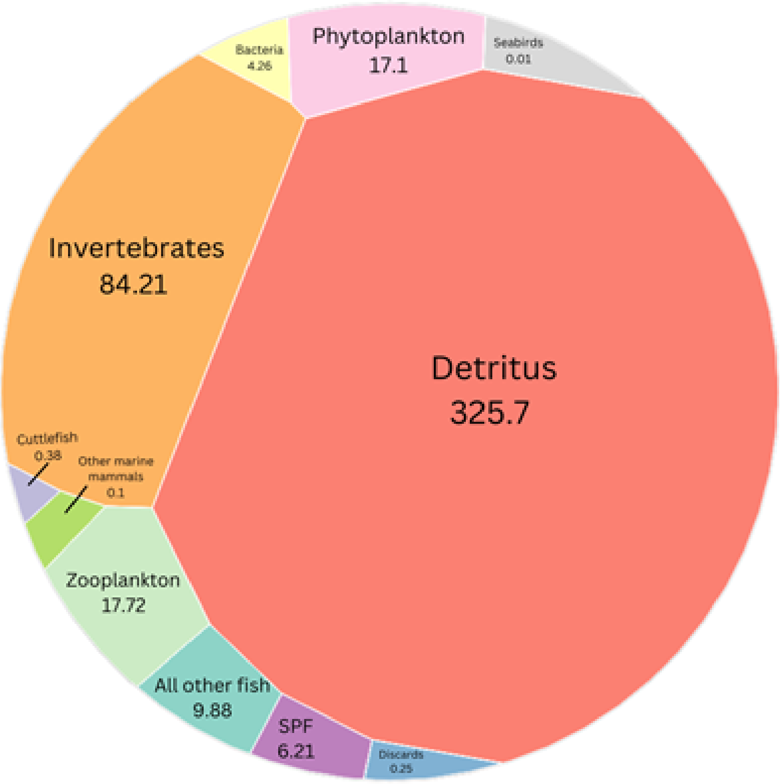


Figure 5.2 - Voronoi treemap of biomass (t km^{-2} yr^{-1}) model output. Groups from Table 5.2 has been amalgamated for ease of interpretation.

5.3.2 Mixed Trophic Impact

The MTI routine on the balanced Ecopath model for six pelagic functional groups, anchovy, herring, mackerel, horse mackerel, sardine, and sprat, and the functional groups affecting the SPF are shown in Figure 5.3. SPF are positively impacted by planktonic groups, mesozooplankton – large (Figure 5.3). Sardine, anchovy, horse mackerel, mackerel, and herring were negatively impacted by an increase in seabird biomass, particularly, surface feeders (-0.133; -0.057; -0.046; -0.14; -0.013 respectively), compared to sprat which had a small positive effect (-0.022). Fleets of cod, whiting, and hake had the same positive effect on anchovy (0.011; 0.0935; 0.054 respectively). Macrozooplankton negatively affected anchovy (-0.104), while mesozooplankton of both size classes had a positive effect (mesozooplankton small = 0.163; mesozooplankton large = 0.071). Herring had the largest negative impact by an increase in its own biomass (-0.321), which was the same for sardine (-0.229), mackerel (-0.283), and sprat (-0.089). Sprat and sardine had the largest positive impact from an increase in mesozooplankton – small (0.350; 0.201 respectively). Sprat had the largest negative impact, -0.249, from horse mackerel increase and other small pelagic species (Figure 5.3). From the small-scale fishing fleets, herring (-0.016) and sardine (-0.011) were two species negatively impacted by an increase in fishing effort (Figure 5.3).

5.3.3 Niche Overlap

The six pelagic species had at least four of the six SPF as their highest Pianka indices (Figure 5.4), only the highest six groups in terms of Pianka index are represented. Mackerel, sardine, herring, and sprat all had high overlaps with suprabenthivorous demersal fish. This indicates that there is overlap in prey items between SPF and suprabenthivorous demersal fish. Sprat, anchovy, horse mackerel had high overlaps with baleen whales. Five of the six SPF had their highest overlap with another SPF, the exception being herring that had the highest overlap with suprabenthivorous demersal fish (Figure 5.4). Mackerel and sardine had the highest overlaps with each other (0.92; Table 5.3). For mackerel, the next highest groups were anchovy (0.88), sprat (0.86), herring (0.82), suprabenthivorous demersal fish (0.80), and horse mackerel (0.79). Sardine had the same groups as mackerel for high overlaps; sprat (0.90), anchovy (0.90), herring (0.80), suprabenthivorous demersal fish (0.79), and horse mackerel (0.74). Sardine was also the highest overlap for sprat (0.90) and had the overall lowest overlap (0.68), with herring, the same value as horse mackerel and boarfish. Only horse mackerel had boarfish as a top six Pianka index.

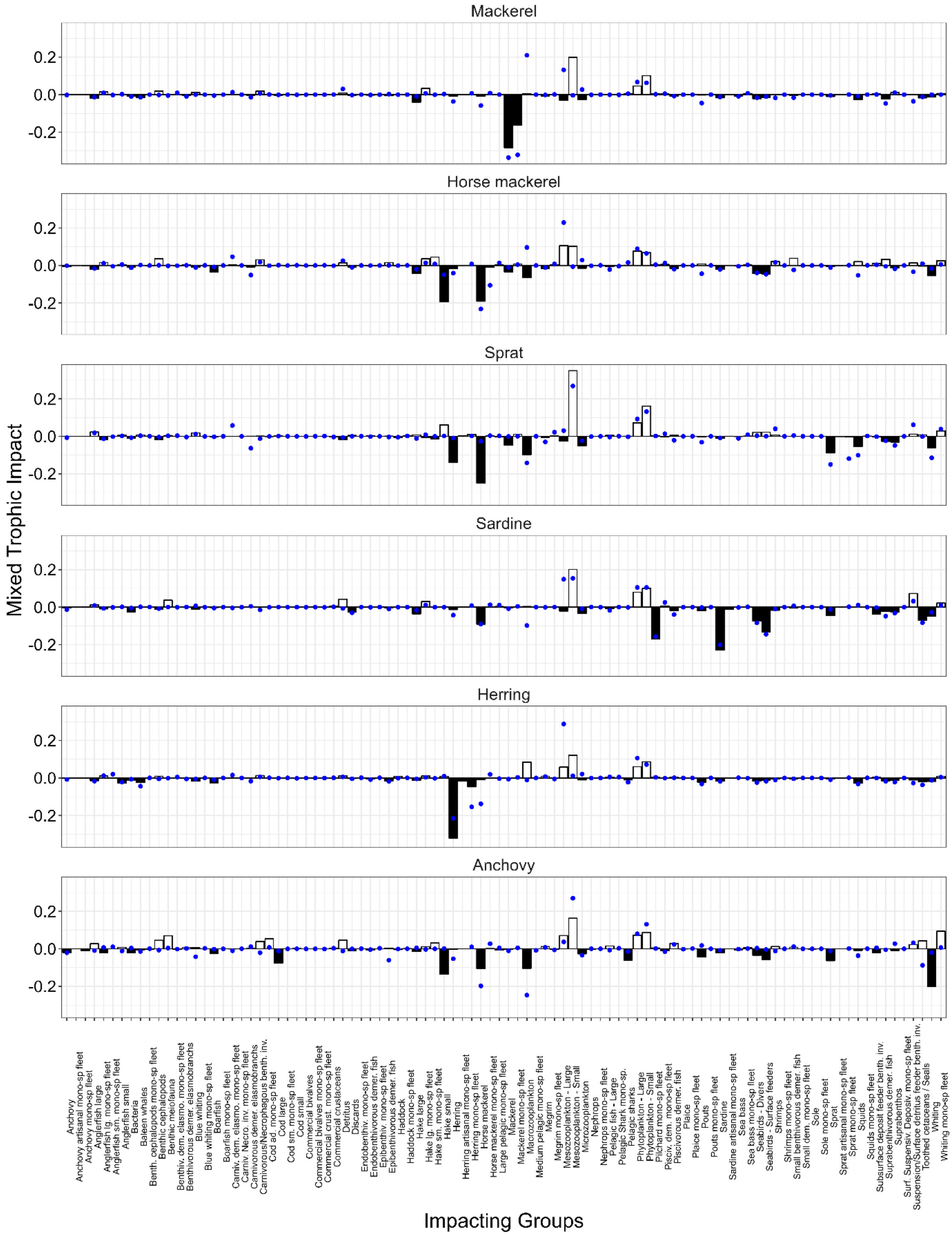


Figure 5.3 – Comparison of Mixed Trophic Impact analysis between Hernvann et al. (2020) and this this study. Shown here in the Celtic Sea ecosystem of 6 pelagic species (impacted groups) response to increase of other functional groups biomass (impacting groups) in the Ecopath balanced model. Positive impacts are shown above the black line above 0 (white bars) and negative impact below the black line (black bars). Blue dots represent values from 1985 model re-run following Hernvann et al. (2020).

Table 5.3 - Pianka index of six pelagic species from the balanced Celtic Sea Ecopath model for 2013.

	Mackerel	Horse mackerel	Sprat	Sardine	Herring
Horse mackerel	0.79				
Sprat	0.86	0.66			
Sardine	0.92	0.74	0.90		
Herring	0.82	0.82	0.68	0.80	
Anchovy	0.88	0.88	0.83	0.90	0.79

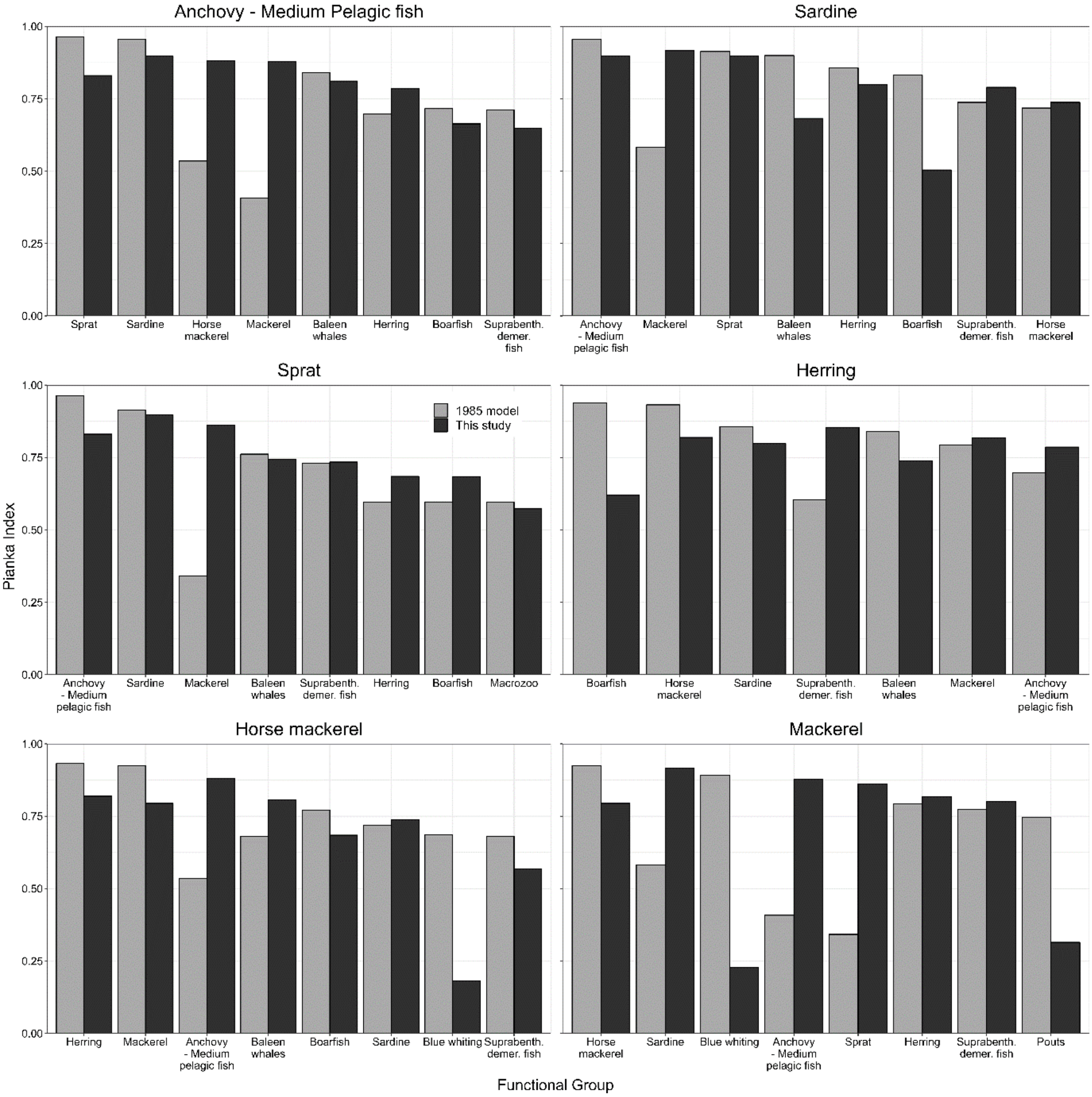


Figure 5.4 - Niche overlap (modified Pianka index) of six pelagic species and the six largest overlap from the balanced Ecopath model of the Celtic Sea in 2013 (dark grey) and 1985 model re-run of Hernvann et al. (2020). Suprabenth. demer. fish = suprabenthivorous demersal fish.

5.3.4 Ecosim fitting

Statistically the best model fit was the baseline and trophic interactions when there was environmental forcing (sea surface temperature), however fishing did not improve the model fitting (Table 5.4). The limited change in sum of squares (SS) suggests that fishing was not the main driver during the eight-year model period. Environmental forcing improved the model with those species with thermal preferences outside or towards the limit of Celtic Sea's temperature range. For example, herring fit slightly improved with the forcing of SST. Fishing did not improve the time series fitting for the six pelagic species (Figure 5.5), the difference between the best baseline and fit and fishing fit was minimal (Figure 5.5). The time series fitting for the other SPF was not correctly captured by Ecosim, especially in mackerel and anchovy (Figure 5.5; Figure 5.6). Anchovy time series presented an increase in biomass over the eight-year period, however, anchovy in Ecosim decreased. For mackerel, with only four observations, the predicted values demonstrate a decrease, whilst the observations had a slight increase in biomass. When there was a cessation of cod and hake fishing, therefore more cod in the system, sardine, horse mackerel, sprat, anchovy, mackerel all decreased (Figure 5.5). Only herring had a slower decline than the baseline (Figure 5.5).

Table 5.4 - Stepwise fitting scenarios, with and without environmental forcing (sea surface temperature). Vs = Number of vulnerability parameters estimated. NSpline = primary production anomaly points. SS = minimum sum of squares. AICc = Akaike Information Criteria. PP = Primary production. Bold = best setup fitting. Pre-existing model best fit taken from Hernvann et al. (2020).

Scenario		Vs	NSpline	SS	AICc
No environmental forcing	Baseline	0	0	2241	577
	Trophic Interactions	**2**	**0**	**2136**	**566**
	Fishing	0	0	2781	636
	Fishing + trophic interactions	3	0	2628	627
Environmental forcing	Baseline	0	0	2186	570
	Trophic Interactions	**2**	**0**	**2044**	**556**
	Trophic Interactions + PP anomaly	2	2	2044	560
	Fishing	0	0	2718	630
	Fishing + trophic interactions	3	0	2562	620
	Fishing + trophic interactions + PP anomaly	3	2	2562	624
Pre-existing model outputs best fit	Fishing + Trophic interactions + Temperature + Plankton	46	0	340	-3365

RMSE (Root Mean Squared Error) and bias over the 8-year duration were lower for mackerel and horse mackerel and highest for sprat (Table 5.5). When calculated over a four year period (2013-2016), the overall values were much higher, with the lowest values for herring and the highest values for sprat (Table 5.5).

Table 5.5 - Root Mean Squared Error (RMSE) and Bias of six pelagic fish species outputs of best fit Baseline and trophic interactions (Table 4.4) and best fit for the pre-existing model (Hernvann et al., 2020) from the full duration of the model and comparison of the overlapping years from both models. Model outputs from Hernvann et al. (2020) were taken using plotdigitzer. Bold values indicated the best fit for the pelagic species. '–' indicates no data available for comparison.

Species	**This study (2013-2021)**		**Hernvann et al. (2020) (1985 - 2016)**		**This study (2013-2016)**		**Hernvann et al. (2020) (2013-2016)**	
	RMSE	**Bias**	**RMSE**	**Bias**	**RMSE**	**Bias**	**RMSE**	**Bias**
Herring	0.088	-0.031	**0.081**	**0.014**	**0.148**	**-0.085**	0.188	0.094
Sprat	0.883	-0.334	**0.039**	**0.007**	1.390	-0.802	**0.787**	**0.393**
Sardine	0.408	-0.144	**0.092**	**-0.016**	0.269	0.155	**0.086**	**0.043**
Horse Mackerel	**0.016**	**0.006**	3.379	0.597	0.123	0.071	**0.052**	**0.026**
Anchovy	0.040	-0.014	-	-	-	-	-	-
Mackerel	0.008	-0.004	-	-	-	-	-	-

The basal productivity of the Celtic Sea ecosystem also had no clear trend for the period 2013-2021 and remained constant. The planktonic groups demonstrated a constant trend, with phytoplankton – small groups producing the highest biomass around 10 t km^{-2}, followed by mesozooplankton – small near 6.5 t km^{-2}. Both, phytoplankton – large and microzooplankton remained constant around 6 t km^{-2}, with mesozooplankton – large near 4 t km^{-2} and macrozooplankton, 2.5 t km^{-2}. The higher trophic levels, that have stock assessments, were captured better by Ecosim.

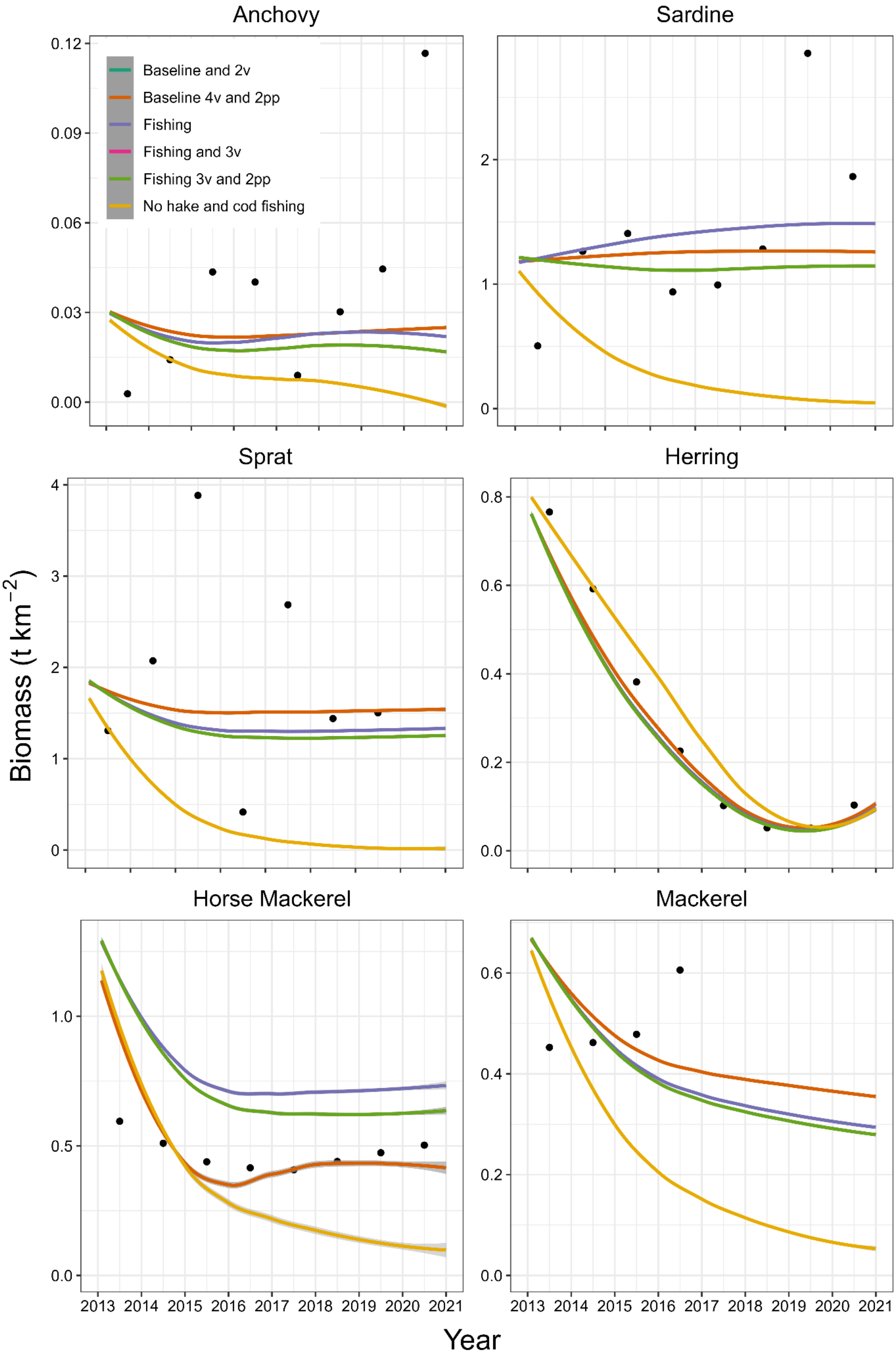


Figure 5.5 - Model predictions (lines) vs time series points for updated Ecopath with Ecosim model from 2013 – 2021 for six pelagic species in the Celtic Sea. Solid lines = different scenarios. Black dots = observations.

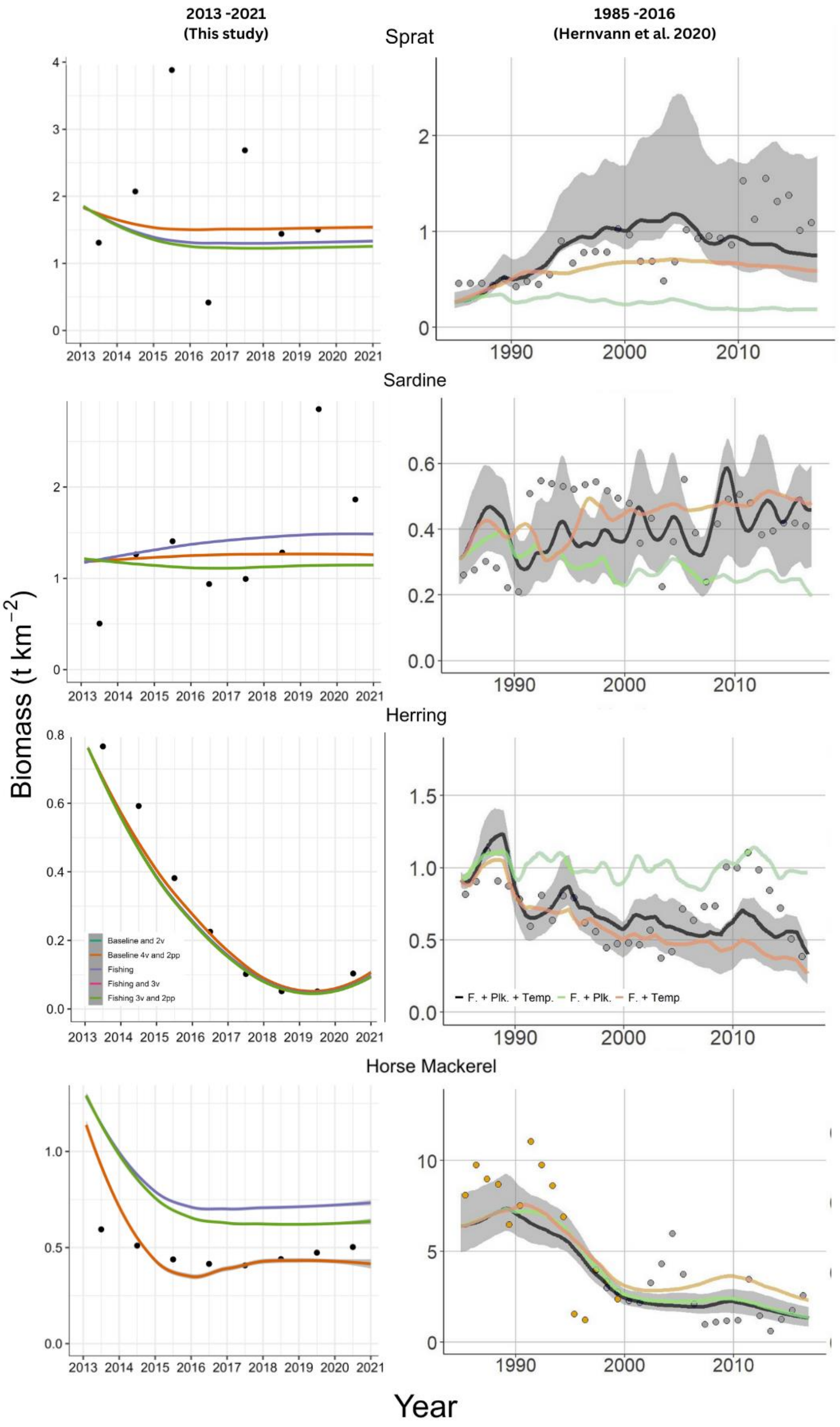


Figure 5.6 - Comparison of best fit of relative biomass of four pelagic species, sprat, sardine, herring and horse mackerel from this study (left hand panels) and pre-existing model (right hand panels; taken from Hernvann et al. 2020). Points represent observations and lines represent model outputs.

5.4 Discussion

In this chapter, an updated Ecopath model for Celtic Sea has been presented. This model was built on a combination of Hernvann et al., (2020) and Moullec et al., (2017), and was updated using improved diet and biomass inputs for Small Pelagic Fish (SPF) presented in Chapter 3. The present study has demonstrated that the six SPFs selected for the Celtic Sea ecosystem, are facilitators of energy transfer from lower trophic to higher trophic levels and their biomasses are influenced by environmental conditions and fishing mortality of higher trophic levels. The changes in their biomass can influence, in particular, the commercially assessed species hake and cod, and seabirds (MTI results).

5.4.1 Trophic dynamics in the Celtic Sea

This model identified that commercial demersal species such as cod and hake have a negative effect on the SPF, and as expected the commercial fisheries of cod and hake therefore have a positive effect, particularly for horse mackerel (Mahe et al., 2007). As horse mackerel is a dominant prey group for hake (>23cm; Mahe et al., 2007), if more hake is taken out of the system by fishing, there could be an increase in their prey. The negative impact on herring by herring could be due to the cannibalistic nature of herring. Cannibalism on larvae has been reported for herring and is not uncommon for other clupeoids (Valdes et al., 1987), and so possibly the negative effect of sardine on sardine. Both, herring, and sardine were negatively impacted by small scale fisheries. These species have been key part of the Cornish fishing community since at least the 16th century and play an important role socially and economically within the region (Southward et al., 1988). In recent years there has been a reduction in fishing effort of the Celtic Sea herring (ICES, 2021), due to a decline in stock. However, the drivers that caused the decline are poorly understood. Considering the stock is yet to recover, despite negligible quota, indicates there might be an environmental driver involved. Historic evidence demonstrates that herring and sardine show opposite trends, linked to warmer periods (Southward et al., 1988), with sardine currently increasing, indicating that warmer temperatures in the Celtic Sea may be a contributing factor for herring.

Our model reveals an increase of zooplanktonic groups has a positive impact on SPF, due to copepods being a main prey group for these species (Chapter 3/Patel et al., 2023). These zooplanktonic groups play a major role in ecosystem functioning and structure, as they are impacted by environmental changes. Studies have shown that SPF are impacted by changes in zooplanktonic composition, their prey (e.g., Coll et al., 2008; Heneghan et al., 2023). Zooplanktonic groups within the model are currently of low taxonomic resolution. Thus, increasing their resolution could improve understanding how their biomass fluctuations can impact functional groups within the ecosystem. Especially, as there have been changes to zooplanktonic community composition attributed to environmental change (e.g., SST – Bedford et al. 2020).

The trophic levels (TLs) for all SPF presented in this study are higher than the estimated average in Chapter 3. Anchovy in spring was the only species that reported a higher trophic than the annual EwE estimate (3.51 in Chapter 3; 3.35 in this Chapter). The results from Chapter 3, only consists of stomach content analyses, which only represents a snapshot of time. As the diet matrix was generated through EcoDiet (Hernvann et al., 2022), it contains stable isotope analyses that provide longer timeframe than stomach content analyses. Therefore, the functional group may have consumed prey of a higher TL than found in stomach content analyses and could explain the higher TLs generated by Ecopath.

5.4.2 Niche overlap of SPF in the Celtic Sea

Overall, the niche overlap results from this modelling study are in agreement with those obtained from stomach samples presented in Chapter 3 (Patel et al., 2023). The top six overlaps of each SPF species within Celtic Sea were mostly ‘in competition’ with another SPF. Thus, comparable to other regions (e.g., by Bachiller & Irigoien, 2015 - Bay of Biscay; Raab et al., 2012 - North Sea). As the diet matrix used stomach sample data from Chapter 3/Patel et al., (2023) as an input to EcoDiet, it was expected that results would be similar. However, as the diet data was calculated annually and to a lower taxonomic resolution for Ecopath input, there are greater number of high overlaps between the SPF, rather than a mixture of overlap categories when calculated seasonally and at higher resolution (Patel et al., 2023).

Baleen whales, suprabenthivorous demersal fish, and boarfish were the non-SPF groups with highest overlaps. Baleen whales (fin, minke, and humpback), are regularly observed in the Celtic Sea, and have been linked to high density herring and sprat areas (Volkenandt et al., 2016). Isotopic mixing models have confirmed that fin and humpback whales are both planktivorous and piscivorous in the Celtic Sea. Both species consume krill, which represents around half of the diet of fin whales and lower proportions in humpback whales (Ryan et al., 2014). Humpback whales select a more piscivorous diet than fin whales, preferring age 0 sprat and herring (Ryan et al., 2014). The high diet overlap calculated between SPF and baleen whales, is due to the consumption on mesozooplanktonic groups (krill) (Patel et al., 2023). However, as the isotopic mixing model is not an exhaustive representation of baleen whale diet, they may feed on other SPF, such as sardine and anchovy, and other zooplanktonic groups, such as calanoid copepods (Ryan et al., 2014). The overlap in niche between baleen whales and SPF will vary dependent on prey availability as fin and humpback whales are generalist feeders switching between zooplankton and fish (Friedlaender et al., 2019) and SPF identified as predominantly generalist in Chapter 3/Patel et al., 2023. However, baleen whales are obligate batch feeders, requiring prey fields of suitable size and magnitude (Goldbogen et al., 2011; Piatt et al., 1989; Piatt & Methven, 1992). If baleen whales are consuming both SPF and SPF prey (krill and calanoid copepods), this might have consequences on SPF populations through direct consumption and indirectly through food competition.

Suprabenthivorous demersal fish, such as sandeels, gobies and pouts are important facilitators of organic matter from the pelagic to demersal compartment. Within this functional group, sandeels are considered small pelagic fish (family Ammodytidae). The lesser sandeel (*Ammodytes marinus*), small sandeel (*A. tobianus*), smooth sandeel (*Gymnammodytes semisquamatus*), greater sandeel (*Hyperoplus lanceolatus*), and Corbin’s sandeel (*H. immaculatus*) are the five sandeel species thought to be present within the Celtic Sea. The functional group considers four out of five of these sandeels, with the lesser sandeel not found within the functional group (Hernvann et al., 2020 suppl. Material). However, recent eDNA sampling has suggested that the lesser sandeel is the dominant species in the study area (Ratcliffe et al., 2021). Lesser sandeels consume a similar diet to the SPF in this study, preferring large copepods e.g., *Calanus*, with greater sandeels mainly feeding on fish (Macer, 1966). Sandeels spend most of their life within the seabed, emerging during the day in spring and summer to feed on zooplankton, and return at night to the seabed (Campanella & van der Kooij, 2021). From autumn, they remain buried in the seabed until spring, only to emerging to spawn. As such, the niche overlap between sandeels and SPF would be seasonal, rather than annual as calculated through Ecopath. This overlap may become important with environmental changes, as sandeel larvae records have demonstrated a decrease within the Celtic Sea, but an increase in the Irish Sea (Lynam et al., 2013). A possibility for the decrease in the Celtic Sea could be the decline of *Calanus finmarchius*, within the region (Johns, 2006), an important prey item for sandeels (Campanella & van der Kooij, 2021). The lesser sandeel itself contributes to the diet of many predators, both demersal (when emerging from the seabed floor) and pelagic when in mid water. Breeding seabirds such as terns (Stienen, 2006), auks (Wanless et al., 2005), and kittiwakes (Frederiksen et al., 2004) rely on their high calorific content. Studies have indicated that food conditions play an important role in driving observed variation in sandeel size (Olin et al., 2022). This implies that climate driven changes in sandeel prey (zooplankton) may impact sandeel growth rates and affect the structure of the local kittiwake populations. Therefore, it is important to consider the addition of lesser sandeel into Celtic Sea EwE model and the model would benefit from being run seasonally to account for winter hibernation.

Boarfish (*Capros aper*) were the other functional group (outside of the six SPF focused on in this study), that had high overlaps with horse mackerel. Boarfish are also considered small pelagic fish and have a strong calanoid copepod-based diet (Pinnegar et al., 2014), similar to horse mackerel (Patel et al., 2023), explaining the high overlap with horse mackerel.

5.4.3 The Celtic Sea between 2013-2021 and beyond

The updating of the 2013 Ecopath model from a combination of Hernvann et al., (2020) and Moullec et al., (2017) has demonstrated the importance of SPF in the Celtic Sea ecosystem in particularly for the commercially assessed species hake and cod, and also seabirds (MTI results). Although, the model built in this study, did not significantly improve the existing model by Hernvann et al., (2020), we did not expect significant changes in RMSE and bias values. We have added more locally informed diet data, more accurate biomass for SPF, and a specific anchovy functional group to apply the model in the future for exploring the growing presence of anchovies, given the changes in the ecosystem.

Piscivorous fish, such as cod and hake, key predators for SPF have shown to impact each species of SPF differently. Generally, it is commonly understood that harvesting of SPF may indirectly affect piscivorous fish that consume them (Engelhard et al., 2013; Pikitch et al., 2014). The cessation of fishing of hake and cod decreased the biomass of sprat, sardine, anchovy, horse mackerel and mackerel, due to more cod and hake in the system to consume them. In contrast, fishing of hake and cod increased the biomass of horse mackerel and sardine in particular, as there are less cod and hake in the system to predate on SPF. Intricacies between these two trophic levels have been documented in the Baltic Sea, where fishing for SPF (herring and sprat) may prevent a fishing-induced collapse of the cod (Soudijn et al., 2021). SPF stocks tend to fluctuate widely in biomass, and quite often recover easily (Hutchings, 2000), and collapses often attributed to primary productivity or fishing (Essington et al., 2015; Siple et al., 2019). Due to changes within the SPF community (i.e., herring decline and anchovy increase) of the Celtic Sea, fishing effort on predators and SPF must be managed carefully. Declines in SPF in the Celtic Sea can also impact Balearic shearwaters and bluefin tuna, which have recently increased within the region (Darlaston & Wynn, 2012; Horton et al., 2021; Jones et al., 2014; Wynn & Yésou, 2007). Balearic Shearwater increase could be a consequence of increasing SST and changes in prey (SPF) distributions, for example the increase of anchovy. Re-iterating the importance of managing SPF communities, possibly through fishing effort to ensure sufficient energy transfer to higher trophic levels.

5.4.4 Limitations and recommendations

Overall, the update of the Celtic Sea Ecopath model shows promise. Our model only ran for eight years (2013-2021) compared to 1985-2016 in Hernvann et al., (2020), therefore the SS or AICc obtained for these two models in response to inclusion of time series fishing and environmental variables, are not directly comparable. The Hernvann et al., model (Hernvann et al., 2020) included relatively high fishing mortality for assessed stocks up until 2000, at which point the fishing mortality declined considerably (Hernvann & Gascuel, 2020). Therefore, it is expected that the ecosystem modelled here for more recent times (i.e., after 2000) might be less controlled by fishing than what was found in the earlier model (Hernvann et al., 2020). Further addition of Sea Bottom Temperature (SBT) for the demersal functional groups, which was not done in this work, and may change or improve the model predictions. SBT was used in the previous model for forcing for functional groups identified by Generalised Additive Models (GAM) as an important variable. This was not included in this study, as we initially tested the environmental preferences of functional groups using Aquamaps (Kaschner et al., 2019), which does not include SBT only SST. Aquamaps uses a standardised trapezoidal shape for environmental preferences, which may cause sudden changes within the biomass predictions by Ecosim. Other species distribution models or envelope models generate curves as such may improve the model predictions e.g., GAMs (Grüss et al., 2018, 2020). The methodology employed by Grüss et al., (2018, 2020), and implemented in the pre-existing model, is a more flexible approach that allows that can incorporate as many variables as desired. Another potential limitation of the model in this study is the planktonic time series, taken from CMIP6 (UK Earth System Model) outputs. Studies have shown that even though the UK earth system model outputs (CMIP6) are state of the art, they do not model the planktonic groups accurately, and are better at representing global planktonic dynamics rather than regional (Petrik et al., 2022). The improvement of the planktonic groups in the current model may improve the overall fitting.

The model presented in this chapter could begin to address management questions specifically, around SPF (e.g., anchovy fishing), and the potential consequences for higher trophic levels. Optimising this model for the lower trophic levels will provide further clarification on the potential changes within the Celtic Sea ecosystem because of environmental and anthropogenic drivers and help provide an ecosystem-based management approach.

6

Discussion and Conclusion

Chapter 6 – Discussion and Conclusion

In this thesis the role of lower trophic levels, in particular of Small Pelagic Fish (SPF), in the Celtic Sea has been evaluated. The aim of this research was to evaluate the role of SPF and to develop an ecosystem (food web) model to understand the temporal dynamics of SPFs in the Celtic Sea. This section will discuss the main findings across all chapters whilst drawing on published research for comparison.

6.1 Importance of regional stomach content analyses of SPF

Environmental and anthropogenic drivers have altered marine ecosystem structure and functioning across the globe, potentially resulting in long term threats to biodiversity (Guldberg & Bruno, 2010; Pauly et al., 2005; Planque et al., 2010). For example, the North Sea ecosystem has been strongly impacted by climate change, altering ecosystem structure (Aebischer et al., 1990; Beaugrand, 2004; Frederiksen et al., 2004, 2006). Not all marine ecosystems are equally sensitive to change and can respond differently to perturbations within the system according to their own history and resilience (Beaugrand et al., 2008). The Celtic Sea, the region of study in question, is an important ecosystem, in terms of biodiversity as it sustains both Lusitanian and Boreal species (Dinter et al., 2001). However, it is understudied compared to the North Sea, with little currently known about SPF in the region. For this reason, this thesis focused on understanding lower trophic pelagic energy transfer by investigating the role of a key functional groups, small pelagic fish, on the functioning of the Celtic Sea ecosystem. The pelagic pathway is key for the transfer of energy from primary production to zooplankton to higher trophic levels including to commercially important species such as cod and hake. This energy transfer differs from ecosystem to ecosystem. Therefore, it is important to understand these pathways through trophic interactions (e.g., predator – prey dynamics) within an ecosystem. Diet studies such as stomach content analyses provide a way to do this. As small pelagic fish can control marine ecosystems, through top-down and bottom-up controls, stomach contents analyses of these species are of particular importance. Many diet studies of SPF have been conducted in seas neighbouring the Celtic Sea (e.g., Bay of Biscay – Bachiller and Irigoien, 2015 and the North Sea – Raab et al., 2012), but there have only been a limited number within the Celtic Sea region itself (see Section 2.4). Chapter 3 aimed to use multispecies approach to investigate feeding strategies (i.e., generalist vs specialist) and potential interspecific competition. This chapter has added to the knowledge base through the collection of new stomach content data for small pelagic fish, especially for underrepresented species in the region e.g., anchovy. Since the 1990s there has been an increase in Anchovy within the region, making it an important species to consider (ICES, 2016). Anchovy consumed planktonic groups, in line with planktonic seasonal changes. Therefore, the diet of these species may change between seasons. Consequently Chapter 3 investigated this seasonality, using a combination of newly collected data and historical data, of SPF diet in the Celtic Sea and utilising an overlap index to begin to understand the potential competition between SPF. Overall, Chapter 3 demonstrated that calanoid copepods were consistently consumed regardless of seasons.

Lauria (2012) separated zooplanktonic functional group in the EwE model, to have copepods separately. Separating calanoid copepods into a standalone functional group may provide a more realistic pathway to understand how lower trophic levels function within the Celtic Sea ecosystem. Calanoid copepods are not only an important food source for SPF but also for specialist demersal fish larvae such as hake and cod (Morote et al., 2010; Rowlands et al., 2008), although SPF were not found to have a high diet overlap with either in Chapter 5. Instead, the main prey for hake-small were macrozooplankton, with only a small consumption of mesozooplanktonic groups. Morote et al., (2011) on the other hand, identified that larvae hake are specialist feeders, consuming mainly adult calanoid copepods. Relative abundance of whiting, hake and plaice as inferred by catch per unit effort (CPUE) increased when *C. finmarchicus* were abundant in the plankton community (Kempf et al., 2022), indicating the importance of the separation of calanoid copepods from the mesozooplankton functional group within the EwE model. One of the main prey groups for hake-adult are horse mackerel, as such an increase in hake fishing has a positive effect on horse mackerel biomass (MTI results).

The SPF in this study region is changing. Mackerel and sardine populations growing, anchovy expanding their range, and declines in herring, and sprat. Understanding how the changes of SPF may impact predators such as bluefin tuna, hake and seabirds is complex, and tools such as EwE provide an opportunity to disentangle the complexities of the Celtic Sea and predict potential biodiversity changes. Therefore, it is vital that new diet studies continue, to inform changes in trophic interactions at a regional scale.

An important outcome of this study is that the data from Chapter 3 has been added to DAPSTOM allowing it to be used in other studies. The PELTIC survey stomach sampling campaign in 2019 has been incorporated into DAPSTOM, allowing it to be used and is now a main contributor to stomach samples in the Celtic Sea. This contribution has increased anchovy stomach samples by 200%, sprat by 138%, sardine by 95%, and horse mackerel by 16%. DAPSTOM is a widely used data source and has been incorporated into models such as Irish Groundfish EwE model (Bentley et al., 2019), Atlantis, and for food web indicators in environmental change assessments (Thompson et al. 2020), which have been used to support management decisions.

6.2 Using satellite retrieved phytoplankton estimates

Over the last two decades the use of satellite remote data has been increasingly utilised in marine ecology (Anugerahanti et al., 2018; Boyd et al., 2018; Boyd et al., 2020; Chassot et al., 2011; Garrido et al., 2008; Siegel et al., 2014). Satellite derived PP estimates have the potential to become routine in many marine ecosystem models, and currently are commonly implemented (Abdou et al., 2016; Christensen et al., 2009; Grüss et al., 2016; Hernvann et al., 2020). Phytoplankton Colour Index (PCI), from the Continuous Plankton Recorder (CPR) survey has been used as a proxy for standing biomass of phytoplankton and has shown measurable changes in the Celtic Sea (Lauria, 2012; Hernvann et al., 2020). Chapter 3 has demonstrated that sardine, mackerel, and larval sprat also consume phytoplankton of various sizes. The pre-existing EwE model has used CPR PCI as time series data; however, satellite remote sensing can provide direct observations at a higher spatial and temporal resolution and employ phytoplankton size class algorithms such as Roy et al., (2013). In combination with CPR PCI data, and other available *in situ* survey data, this may provide a more accurate representation of the phytoplankton community within the Celtic Sea. Chapter 4 demonstrated a need for further validation of satellite outputs before these can widely be used, especially for newer sensors such as OLCI and the subsequent algorithms OC4Me and NN and also the use of FerryBox data in validation. Implementation of the phytoplankton size structure algorithms can be an invaluable input into models such as Ecopath with Ecosim (Chapter 5). The Ecopath model in Chapter 5 was built in 2013, however from the three algorithms (OC4Me - OLCI; NN - OLCI; OC3+OCI - MODIS-Aqua) analysed in Chapter 3, only MODIS-Aqua data was available, as Sentinel 3-OLCI was launched in 2016. OCI+OC3 performed better than OC4Me, however this due to be decommissioned, in favour of sensors such as OLCI. Even though the outputs of Chapter 4 showed limited agreement with *in situ* data, there is promise for OLCI neural network, as it begins to be optimised for complex waters (Case 2) such as coastal regions of the Celtic Sea. Chl-a retrievals from satellite remote sensing is widely used and are key contributors to many models (Anugerahanti et al., 2018; Boyd et al., 2018; Boyd et al., 2020; Chassot et al., 2011). Therefore, expanding the *in situ* Chl-a measurements for validation with satellite retrievals at different times of year (i.e., different bloom conditions) and with HPLC samples alone, could provide a greater understanding of the efficiency of the algorithm in the Celtic Sea.

6.3 Celtic Sea ecosystem model

Increasingly, ecosystem models are being used for decision making, to meet a growing need to predict future scenarios. Currently, there is limited use of these models for fisheries and ecosystem management, however Ecopath with Ecosim is the most widely used approach. EwE can be used to evaluate bottom-up, top-down and middle-out processes on ecosystems, and as such can quantify potential trade-offs that have arisen by natural or anthropogenic perturbations of management scenarios (Craig & Link, 2023). These models can help disentangle indirect and direct effects placed on the ecosystem through trophic interactions (Christensen and Pauly, 2004). To understand how these models have been used in resource management throughout the world Craig & Link, (2023) analysed 10 case studies of many hundreds of EwE models. Irish Sea Groundfish Fishery (Bentley et al., 2020, 2021), is an example where advice was facilitated by a specific question related to management decisions, i.e., fishing mortality rates for assessed single stock species. With further development, by use of inclusion of stakeholder workshops, the Celtic Sea ecosystem model built in Chapter 5 can begin to address management specific questions such as those in the Irish Sea (Bentley et al., 2020, 2021). The development of multiple models in the Celtic Sea (e.g., Lauria et al., 2016; Hernvann et al., 2020; this study), can help understand area model uncertainty within the region (Craig & Link, 2023). Demersal fisheries in the Celtic Sea are considered a mixed fishery, i.e., many demersal fish are caught together, therefore exploitation patterns of one stock may influence another (Kempf et al., 2022; Moore et al., 2019), indicating the importance of carefully considering the treatment of fleets within EwE models for demersal fisheries. Changes to larger pelagic fish in the Celtic Sea have also been observed, with an increase of bluefin tuna, *Thunnus thynnus* (Horton et al., 2021), and Balearic Shearwater (Phillips et al., 2021), predators of mackerel, sardine, sprat, herring, and European anchovy (Olafsdottir et al., 2016; Pleizier et al., 2012), with a potential negative impact. The Ecosim model developed in this study shows promise for addressing management of specific questions targeted towards role of SPF in the ecosystem especially associated with climate change, fishing, and spatial management (marine protected areas and renewable energy infrastructure).

6.4 Conclusions and future work

The research reported in this thesis represents new insight in the understudied Celtic Sea ecosystem and provides greater understanding of changes in the lower trophic pelagic pathway within this ecosystem. Through the collection of new regional diet studies, and the local biomass data of SPF, research findings have clearly highlighted the importance of data types used to develop ecosystem-based modelling approaches, such as EwE. Additionally, it has demonstrated how its application can offer opportunities to further disentangle key components of the pelagic system. Further development of the EwE model will no doubt increase our understanding of anthropogenic impacts upon the Celtic Sea ecosystem. This coupled with development into the lower trophic levels, through the use of remote sensing techniques, can provide a source for decision making in future management and conservation policy of the region.

Further studies are recommended in regard to Chapter 3 to understand how the SPF consumption reflects prey availability. Combining data from the Plankton Imager (to provide an overview of prey availability) collected alongside the PELTIC stomach sampling in 2019, would improve such knowledge, although this would be limited to autumn only.

Chapter 4 validation would require data for other the seasons, not just autumn, especially during the spring bloom, and of varying chlorophyll levels to understand how the Sentinel 3 algorithms perform within the region under different conditions alongside comparison with HPLC samples. To improve the model further and to gain a greater understanding of the pelagic pathway in the Celtic Sea, we recommend the following adjustments are made to the model presented in Chapter 5 within future studies:

- Bluefin tuna (*Thunnus thynnus)* as a separate functional group. This species has increased in the region recently and is a main predator of SPF, particularly anchovy. The use of tagging studies could be useful in estimating abundances in the region.
- Sandeels as a separate functional group. Sandeels are also an important facilitator of energy and are a link between the pelagic and demersal pathways. With EVHOE (Duhamel et al.2018) surveys undertaken during Quarter 4 when lesser sandeels (considered the most abundant in the Celtic Sea area through eDNA analyses –

Ratcliffe et al. 2021) are hibernating. Inclusion of other survey data if available could fill in potential data gaps.

- Addition of eDNA, SIA, SCA methods to further update the trophic interactions for diet matrix input to the EwE model, as part of the next phase of development of EcoDiet (Hernvann et al. 2022).
- Develop seasonal models of the Celtic Sea ecosystem, as Chapter 3 has demonstrated the importance of seasonal changes on the lower trophic levels.
- Improve the input zooplankton data within the EwE model through use of combined data sources for zooplankton biomass such as CPR and zooplankton suitability habitats (as used in Hernvann et al. 2020) and data obtained from the Plankton Imager.
- Update Chapter 5 model to be temporally and spatially explicit using Ecospace.

References

Abdou, K., Halouani, G., Hattab, T., Romdhane, M. S., Lasram, F. B. R., & Le Loc’h, F. (2016). Exploring the potential effects of marine protected areas on the ecosystem structure of the Gulf of Gabes using the Ecospace model. *Aquatic Living Resources*, *29*(2), 202.

Adebola, T., & Mutsert, K. (2019). Spatial simulation of redistribution of fishing effort in Nigerian coastal waters using Ecospace. *Ecosphere*, *10*(3), 02623.

Aebischer, N. J., Coulson, J. C., & Colebrook, J. M. (1990). Parallel long-term trends across four marine trophic levels and weather. *Nature*, *347*, 753–755.

Agawin, N. S. R., Duarte, C. M., & Agustí, S. (2000). Nutrient and temperature control of the contribution of picoplankton to phytoplankton biomass and production. *Limnology and Oceanography*, *45*(3), 591–600. https://doi.org/10.4319/lo.2000.45.3.0591

Ainsworth, C. H., Samhouri, J. F., Busch, D. S., Cheung, W. W., Dunne, J., & Okey, T. A. (2011). Potential impacts of climate change on Northeast Pacific marine foodwebs and fisheries. *ICES Journal of Marine Science*, *68*(6), 1217–1229.

Akaike, H. (1974). A new look at the statistical model identification. *IEEE Transactions on Automatic Control*, *19*, 716–723. https://doi.org/10.1109/TAC.1974.1100705.

Alder, J., Campbell, B., Karpouzi, V., Kaschner, K., & Pauly, D. (2008). Forage Fish: From Ecosystems to Markets. *Annual Review of Environment and Resources*, *33*(1), 153–166. https://doi.org/10.1146/annurev.environ.33.020807.143204

Alheit, J., & Hagen, E. (1997). Long-term climate forcing of European herring and sardine populations. *Fisheries Oceanography*, *6*(2), 130–139. https://doi.org/10.1046/j.1365-2419.1997.00035.x

Alheit, J., Roy, C., & Kifani, S. (2009). Decadal-scale variability in populations. In *Climate Change and Small Pelagic Fish* (pp. 64–87). Cambridge University Press. https://doi.org/10.1017/CBO9780511596681.007

Almende, B. V., Benoit, T., & Titouan, R. (2019). https://CRAN.R-project.org/package=visNetwork

Alvarez-Fernandez, S., Licandro, P., van Damme, C. J. G., & Hufnagl, M. (2015). Effect of zooplankton on fish larval abundance and distribution: A long-term study on North Sea herring (Clupea harengus). *ICES Journal of Marine Science*, *72*(9), 2569–2577. https://doi.org/10.1093/icesjms/fsv140

Amundsen, P., Gabler, H. M., & Staldvik, F. J. (1996). A new approach to graphical analysis of feeding strategy from stomach contents data—Modification of the Costello (1990) method. *J Fish Biol*, *48*(607).

Amundsen, P., & Sánchez-Hernández, J. (2019). Feeding studies take guts—Critical review and recommendations of methods for stomach contents analysis in fish. *J Fish Biol*, *95*(1364).

Anugerahanti, P., Roy, S., & Haines, K. (2018). A perturbed biogeochemistry model ensemble evaluated against in situ and satellite observations. *Biogeosciences*, *15*(21), 6685–6711.

Arim, M., Bozinovic, F., & Marquet, P. A. (2007). On the relationship between trophic position, body mass and temperature: Reformulating the energy limitation hypothesis. *Oikos*, *116*(9), 1524–1530. https://doi.org/10.1111/j.0030-1299.2007.15768.x

Audzijonyte, A., Pethybridge, H., Porobic, J., Gorton, R., Kaplan, I., & Fulton, E. A. (2019). Atlantis: A spatially explicit end-to-end marine ecosystem model with dynamically integrated physics, ecology and socio-economic modules. *Methods in Ecology and Evolution*, *10*(10), 1814–1819. https://doi.org/10.1111/2041-210X.13272

Bacha, M., & Amara, R. (2009). Spatial, temporal and ontogenetic variation in diet of anchovy (Engraulis encrasicolus) on the Algerian coast (SW Mediterranean. *Estuar Coast Shelf Sci*, *85*(257).

Bachiller, E., Albo-Puigserver, M., Giménez, J., & MG, P. (2020). A trophic latitudinal gradient revealed in anchovy and sardine from the Western Mediterranean Sea using a multi-proxy approach. *Sci Rep*, *10*(17598).

Bachiller, E., Cotano, U., Boyra, G., & Irigoien, X. (2013). Spatial distribution of the stomach weights of juvenile anchovy (*Engraulis encrasicolus* L.) in the Bay of Biscay. *ICES Journal of Marine Science*, *70*(2), 362–378. https://doi.org/10.1093/icesjms/fss176

Bachiller, E., Giménez, J., Albo-Puigserver, M., & MG, P. (2021). Trophic niche overlap between round sardinella (Sardinella aurita) and sympatric pelagic fish species in the Western Mediterranean. *Ecol Evol*, *11*, 16126 16142.

Bachiller, E., & Irigoien, X. (2015). Trophodynamics and diet overlap of small pelagic fish species in the Bay of Biscay. *Marine Ecology Progress Series*, *534*, 179–198. https://doi.org/10.3354/meps11375

Bachiller, E., Skaret, G., Nøttestad, L., & Slotte, A. (2016). Feeding Ecology of Northeast Atlantic Mackerel, Norwegian Spring-Spawning Herring and Blue Whiting in the Norwegian Sea. *PLOS ONE*, *11*(2), e0149238. https://doi.org/10.1371/journal.pone.0149238

Bakun, A. (2006). Wasp-waist populations and marine ecosystem dynamics: Navigating the ‘predator pit’ topographies. *Prog Oceanogr*, *68*(271).

Bakun, A., Babcock, E. A., Lluch-Cota, S. E., Santora, C., & Salvadeo, C. J. (2010). Issues of ecosystem-based management of forage fisheries in “open” non-stationary ecosystems: The example of the sardine fishery in the Gulf of California. *Reviews in Fish Biology and Fisheries*, *20*(1), 9–29. https://doi.org/10.1007/s11160-009-9118-1

Beare, D., Burns, F., Jones, E., Peach, K., Portilla, E., Greig, T., McKenzie, E., & Reid, D. (2004). An increase in the abundance of anchovies and sardines in the north-western North Sea since 1995. *Global Change Biology*, *10*(7), 1209–1213. https://doi.org/10.1111/j.1529-8817.2003.00790.x

Beaudoin, C. P., Prepas, E. E., Tonn, W. M., Wassenaar, L. I., & Kotak, B. G. (2001). A stable carbon and nitrogen isotope study of lake food webs in Canada's Boreal Plain. *Freshwater Biology*, *46*(4), 465–477. https://doi.org/10.1046/j.1365-2427.2001.00688.x

Beaugrand, G. (2004). The North Sea regime shift: Evidence, causes, mechanisms and consequences. *Progress in Oceanography*, *60*, 245–262.

Beaugrand, G. (2005). Monitoring pelagic ecosystems using plankton indicators. *ICES Journal of Marine Science*, *62*, 333–338.

Beckerman, A. P., Petchey, O. L., & Warren, P. H. (2006). Foraging biology predicts food web complexity. *Proceedings of the National Academy of Sciences*, *103*(37), 13745–13749. https://doi.org/10.1073/pnas.0603039103

Bedford, J., Ostle, C., Johns, D. G., Atkinson, A., Best, M., Bresnan, E., Machairopoulou, M., Graves, C. A., Devlin, M., Milligan, A., Pitois, S., Mellor, A., Tett, P., & McQuatters-Gollop, A. (2020). Lifeform indicators reveal large-scale shifts in plankton across the North-West European shelf. *Global Change Biology*, *26*(6), 3482–3497. https://doi.org/10.1111/gcb.15066

Behrenfeld, M. J., & Falkowski, P. G. (1997). Photosynthetic rates derived from satellite-based chlorophyll concentration. *Limnology and Oceanography*, *42*(1), 1–20. https://doi.org/10.4319/lo.1997.42.1.0001

Behrenfeld, M. J., O'Malley, R. T., Siegel, D. A., McClain, C. R., Sarmiento, J. L., Feldman, G. C., Milligan, A. J., Falkowski, P. G., Letelier, R. M., & Boss, E. S. (2006). Climate-driven trends in contemporary ocean productivity. *Nature*, *444*(7120), 752–755.

Bentley, J., Lundy, M. G., Howell, D., Beggs, S. E., Bundy, A., Castro, F., Fox, C. J., Heymans, J. J., Lynam, C. P., Pedreschi, D., & Schuchert, P. (2021). Refining fisheries advice with stock-specific ecosystem information. *Frontiers in Marine Science*, *8*, 602072.

Bentley, J., Serpetti, N., Fox, C. J., Heymans, J. J., & Reid, D. G. (2020). Retrospective analysis of the influence of environmental drivers on commercial stocks and fishing opportunities in the Irish Sea. *Fisheries Oceanography*. https://doi.org/10.1111/fog.12486

Bentley, J., Serpetti, N., Fox, C. J., Reid, D. G., & Heymans, J. J. (2019). Modelling the food web in the Irish Sea in the context of a depleted commercial fish community. In *Part 2: ICES Ecopath with Ecosim Key Run*. https://doi.org/10.13140/RG.2.2.15136.12809.

Bentley, J. W., Serpetti, N., & Heymans, J. J. (2017). Investigating the potential impacts of ocean warming on the Norwegian and Barents Seas ecosystem using a time-dynamic food-web model. *Ecological Modelling*, *360*, 94–107. https://doi.org/10.1016/j.ecolmodel.2017.07.002.

Bentorcha, A., Gascuel, D., & Guénette, S. (2017). Using trophic models to assess the impact of fishing in the Bay of Biscay and the Celtic Sea. *Aquat. Living Resour.*, *30*, 7. https://doi.org/10.1051/alr/2017006

Berg, J. (1979). Discussion of methods of investigating the food of fishes, with reference to a preliminary study of the prey of Gobiusculus flavescens (Gobiidae. *Mar Biol*, *50*(263).

Bernreuther, M. (2007). *Investigations on the feeding ecology of Baltic Sea herring (*Clupea harengus *L.) and sprat (*Sprattus sprattus *L.)* [PhD Thesis]. Staats-und Universitätsbibliothek Hamburg Carl von Ossietzky.

Bode, A., Álavarez-Ossorio, M. T., Carrera, P., & Lorenzo, J. (2004). Reconstruction of trophic pathways between plankton ans the North Iberian sardine (Sardina pilchardus) using stable isotopes. *Scientia Marina*, *68*, 165–178.

Bonsall, M. B., & Hassell, M. P. (2007). *Theoretical ecology: Principles and applications* (A. R. May, R. M. & McLean, Ed.). Oxford University Press, 2007. https://books.google.com/books?hl=en{\&}lr={\&}id=BpESDAAAQBAJ{\&}oi=fnd{\&}pg=PR5{\&}ots=aXv3uPyFfh{\&}sig=F4ISZiuvrNIU{_}H7GV0FdiIgN33U

Boyd, R., Roy, S., Sibly, R., Thorpe, R., & Hyder, K. (2018). A general approach to incorporating spatial and temporal variation in individual-based models of fish populations with application to Atlantic mackerel. *Ecological Modelling*, *382*, 9–17. https://doi.org/10.1016/j.ecolmodel.2018.04.015

Boyd, R., Sibly, R., Hyder, K., Walker, N., Thorpe, R., & Roy, S. (2020). Simulating the summer feeding distribution of Northeast Atlantic mackerel with a mechanistic individual-based model. *Progress in Oceanography*, *183*, 102299. https://doi.org/10.1016/j.pocean.2020.102299

Boyd, R., Thorpe, R., Hyder, K., Roy, S., Walker, N., & Sibly, R. (2020). Potential Consequences of Climate and Management Scenarios for the Northeast Atlantic Mackerel Fishery. *Frontiers in Marine Science*, *7*, 639. https://doi.org/10.3389/fmars.2020.00639

Bréchon, A. L., Coombs, S. H., Sims, D. W., & Griffiths, A. M. (2013). Development of a rapid genetic technique for the identification of clupeid larvae in the Western English Channel and investigation of mislabelling in processed fish products. *ICES J Mar Sci*, *70*(399).

Brewin, R. J., Dall'Olmo, G., Pardo, S., van Dongen-Vogels, V., & Boss, E. S. (2016). Underway spectrophotometry along the Atlantic Meridional Transect reveals high performance in satellite chlorophyll retrievals. *Remote Sensing of Environment*, *183*, 82–97.

Brockmann, C., Doerffer, R., Peters, M., Kerstin, S., Embacher, S., & Ruescas, A. (2016). Evolution of the C2RCC neural network for Sentinel 2 and 3 for the retrieval of ocean colour products in normal and extreme optically complex waters. *Living Planet Symposium*, *740*, 54.

Buckland, A., Baker, R., Loneragan, N., & Sheaves, M. (2017). Standardising fish stomach content analysis: The importance of prey condition. *Fisheries Research*, *196*, 126–140. https://doi.org/10.1016/j.fishres.2017.08.003

Butler, C. M., Rudershausen, P. J., & Buckel, J. A. (2010). Feeding ecology of Atlantic bluefin tuna (Thunnus thynnus) in North Carolina: Diet, daily ration, and consumption of Atlantic menhaden (Brevoortia tyrannus. *Fishery Bulletin*, *108*, 56–69.

Campanella, F., & van der Kooij, J. (2021). *Spawning and nursery grounds of forage fish in Welsh and surroundings waters*. Cefas Project Report for RSPB.

Campbell, J. W., & O'Reilly, J. E. (1988). Role of satellites in estimating primary productivity on the northwest Atlantic continental shelf. *Continental Shelf Research*, *8*(2), 179–204.

Capuzzo, E., Wright, S., Bouch, P., Collingridge, K., Creach, V., Pitois, S., Stephens, D., & van der Kooij, J. (2022). Variability in structure and carbon content of plankton communities in autumn in the waters south-west of the UK. *Progress in Oceanography*, *204*, 102805.

Casini, M., Cardinale, M., & Arrhenius, F. (2004). Feeding preferences of herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) in the southern Baltic Sea. *ICES Journal of Marine Science*, *61*(8), 1267–1277. https://doi.org/10.1016/j.icesjms.2003.12.011

Centre for Environment Fisheries and Aquaculture Science. (2019). *Research Vessel Survey Report. RV Cefas Endeavour Survey: C END 15—2019*. Cefas.

Chagaris, D. D., Mahmoudi, B., Walters, C. J., & Allen, M. S. (2015). Simulating the trophic impacts of fishery policy options on the West Florida Shelf using Ecopath with Ecosim. *Marine and Coastal Fisheries*, *7*(1), 44–58.

Chang, N.-B., Imen, S., & Vannah, B. (2015). Remote sensing for monitoring surface water quality status and ecosystem state in relation to the nutrient cycle: A 40-year perspective. *Critical Reviews in Environmental Science and Technology*, *45*(2), 101–166.

Chao, A., Chazdon, R. L., Colwell, R. K., & Shen, T.-J. (2006). Abundance-Based Similarity Indices and Their Estimation When There Are Unseen Species in Samples. *Biometrics*, *62*(2), 361–371. https://doi.org/10.1111/j.1541-0420.2005.00489.x

Chassot, E., Bonhommeau, S., Reygondeau, G., Nieto, K., Polovina, J. J., Huret, M., Dulvy, N. K., & Demarcq, H. (2011). Satellite remote sensing for an ecosystem approach to fisheries management. *ICES Journal of Marine Science*, *68*(4), 651–666. https://doi.org/10.1093/icesjms/fsq195

Checkley, D. M., Alheit, J., Oozeki, Y., & Roy, C. (2009). Climate change and small pelagic fish. In *Climate Change and Small Pelagic Fish*. Cambridge University Press (2009). https://doi.org/10.1017/CBO9780511596681

Cherif, E. K., Mozetič, P., Francé, J., Flander-Putrle, V., Faganeli-Pucer, J., & Vodopivec, M. (2021). Comparison of in-situ chlorophyll-a time series and Sentinel-3 Ocean and land color instrument data in Slovenian National Waters (gulf of Trieste, Adriatic Sea). *Water*, *13*(14), 1903.

Christensen, V., Coll, M., Steenbeek, J., Buszowski, J., Chagaris, D., & Walters, C. J. (2014). Representing variable habitat quality in a spatial food web model. *Ecosystems*, *17*(8), 1397–1412.

Christensen, V., & Pauly, D. (1992). Ecopath II a software for balancing steady state ecosystem models and calculating network characteristics. *Ecological Modelling*, *61*(3–4), 169–185.

Christensen, V., & Walters, C. J. (2004). Ecopath with Ecosim: Methods, capabilities and limitations. *Ecological Modelling*, *172*(2–4), 109–139. https://doi.org/10.1016/j.ecolmodel.2003.09.003

Christensen, V., Walters, C. J., Ahrens, R., Alder, J., Buszowski, J., & Christensen, L. B. (2009). Database-driven models of the world's Large Marine Ecosystems. *Ecological Modelling*, *220*, 1984–1996. https://doi.org/10.1016/j.ecolmodel.2009.04.041.

Christensen, V., Walters, C. J., & Pauly, D. (2005). *Ecopath with Ecosim: A user"s guide, Fisheries Centre*. University of Bristish Columbia.

Christensen, V., Walters, C. J., & Pauly, D. (2008). *Ecopath with Ecosim version 6 user guide. Lenfest Ocean Futures Project 2008*. Fisheries Centre, University of British Columbia.

Coll, M., Libralato, S., Tudela, S., Palomera, I., & Pranovi, F. (2008). Ecosystem Overfishing in the Ocean. *PLoS ONE*, *3*(12), e3881. https://doi.org/10.1371/journal.pone.0003881

Colléter, M., Valls, A., Guitton, J., Gascuel, D., Pauly, D., & Christensen, V. (2015). Global overview of the applications of the Ecopath with Ecosim modeling approach using the EcoBase models repository. *Ecological Modelling*, *302*, 42–53.

Conversi, A., Fonda Umani, T., Peluso, T., Molinero, J. C., Santojanni, A., & Edwards, M. (2010). The Mediterranean Sea regime shift at the end of the 1980s, and intriguing parallelisms with other european basins. *Plos One*, *5*, 1–15.

Conway, D., Coombs, S., Fernández de Puelles, M., & Tranter, P. (1994). Feeding of larval sardine *Sardina pilchardus* (Walbaum) off the north coast of Spain. *Boletin Del Instituto Espanol de Oceanografia*, *10*, 165–175.

Coombs, S., Halliday, N., Conway, D., & Smyth, T. (2010). Sardine (Sardina pilchardus) egg abundance at station L4, western English Channel, 1988−2008. *J Plankton Res*, *32*(693).

Corrales, X., Coll, M., Ofir, E., Piroddi, C., Goren, M., & Edelist, D. (2017). Hindcasting the dynamics of an Eastern Mediterranean marine ecosystem under the impacts of multiple stressors. *Marine Ecology Progress Series*, *580*, 17–36. https://doi.org/10.3354/meps12271.

Corten, A. (2000). A possible adaptation of herring feeding migrations to a change in timing of the *Calanus finmarchicus* season in the eastern North Sea. *ICES Journal of Marine Science*, *57*(4), 1270–2000. https://doi.org/10.1006/jmsc.2000.0812

Corten, A. (2001). Northern distribution of North Sea herring as a response to high water temperatures and/or low food abundance. *Fisheries Research*, *50*(1), 189–204. https://doi.org/10.1016/S0165-7836(00)00251-4

Corten, A. (2013). Recruitment depressions in North Sea herring. *ICES Journal of Marine Science*, *70*(1), 1–15. https://doi.org/10.1093/icesjms/fss187

Cortés, E. (1999). Standardized diet compositions and trophic levels of sharks. *ICES Journal of Marine Science*, *56*(5), 707–717. https://doi.org/10.1006/jmsc.1999.0489

Costello, M. J. (1990). Predator feeding strategy and prey importance: A new graphical analysis. *J Fish Biol*, *36*, 261 263.

Craig, J. K., & Link, J. S. (2023). It is past time to use ecosystem models tactically to support ecosystem-based fisheries management: Case studies using Ecopath with Ecosim in an operational management context. *Fish and Fisheries*, *24*(3), 381–406.

Crawford, R. J. M., Underhill, L. G., Upfold, L., & Dyer, B. M. (2007). An altered carrying capacity of the Benguela upwelling ecosystem for African penguins (Spheniscus demersus. *ICES Journal of Marine Science*, *64*, 570–576.

Cury, P., Bakun, A., Crawford, R. J. M., Jarre, A., Quiñones, R. A., Shannon, L. J., & Verheye, H. M. (2000). Small pelagics in upwelling systems: Patterns of interaction and structural changes in “wasp-waist” ecosystems. *ICES Journal of Marine Science*, *57*(3), 603–618. https://doi.org/10.1006/jmsc.2000.0712

Cury, P., Shannon, L., & Shin, Y. J. (2003). The functioning of marine ecosystems: A fisheries perspective. In M. Sinclair & G. Valdimarsson (Eds.), *Responsible fisheries in the marine ecosystem. FAO, Rome, p 103–123 Daskalov GM*.

Cushing, D. (1990). Plankton production and year class strength in fish populations: An update of the match/mismatch hypothesis. *Adv Mar Biol*, *26*(249).

Darecki, M., Weeks, A., Sagan, S., Kowalczuk, P., & Kaczmarek, S. (2003). Optical characteristics of two contrasting Case 2 waters and their influence on remote sensing algorithms. *Continental Shelf Research*, *23*(3–4), 237–250.

Darlaston, M., & Wynn, R. B. (2012). A record influx of balearic shearwaters in devon and cornwall. *British Birds*, *105*, 37–38.

Daunt, F., Wanless, S., Greenstreet, S. P. R., Jensen, H., Hamer, K. C., & Harris, M. P. (2008). The impact of the sandeel fishery closure on seabird food consumption, distribution, and productivity in the northwestern North Sea. *Canadian Journal of Fisheries and Aquatic Sciences*, *65*, 362–381.

de Mutsert, K., Steenbeek, J., Lewis, K., Buszowski, J., Cowan, J. H., & Christensen, V. (2016). Exploring effects of hypoxia on fish and fisheries in the northern Gulf of Mexico using a dynamic spatially explicit ecosystem model. *Ecological Modelling*, *331*, 142–150. https://doi.org/10.1016/j.ecolmodel.2015.10.013.

Debes, H., Homrum, E., Jacobsen, J. A., Hátún, H., & Danielsen, J. (2012). The feeding ecology of pelagic fish in the southwestern Norwegian Sea–Inter species food competition between Herring (*Clupea harengus*) and mackerel (*Scomber scombrus*). *ICES CM*, *1000*, 07.

Deehr, R. A., Luczkovich, J. J., Hart, K. J., Clough, L. M., Johnson, B. J., & Johnson, J. C. (2014). Using stable isotope analysis to validate effective trophic levels from Ecopath models of areas closed and open to shrimp trawling in Core Sound, NC, USA. *Ecological Modelling*, *282*, 1–17.

Denis, J., Vallet, C., Courcot, L., & V, L. (2016). Feeding strategy of Downs herring larvae (Clupea harengus L.) in the English Channel and North Sea. *J Sea Res*, *115*(33).

Dias, B. S., Frisk, M. G., & Jordaan, A. (2022). Contrasting fishing effort reduction and habitat connectivity as management strategies to promote alewife (Alosa pseudoharengus) recovery using an ecosystem model. *Limnology and Oceanography*, *67*, 5–22.

Dickey-Collas, M., Engelhard, G. H., Rindorf, A., Raab, K., Smout, S., Aarts, G., van Deurs, M., Brunel, T., Hoff, A., Lauerburg, R. A. M., Garthe, S., Haste Andersen, K., Scott, F., van Kooten, T., Beare, D., & Peck, M. A. (2013). Ecosystem-based management objectives for the North Sea: Riding the forage fish rollercoaster. *ICES Journal of Marine Science*, *71*(1), 128–142. https://doi.org/10.1093/icesjms/fst075

Dickmann, M., Möllmann, C., & Voss, R. (2007). Feeding ecology of Central Baltic sprat Sprattus sprattus larvae in relation to zooplankton dynamics: Implications for survival. *Marine Ecology Progress Series*, *342*, 277–289. https://doi.org/10.3354/meps342277

Donlon, C., Berruti, B., Buongiorno, A., Ferreira, M.-H., Féménias, P., Frerick, J., Goryl, P., Klein, U., Laur, H., Mavrocordatos, C., & others. (2012). The global monitoring for environment and security (GMES) sentinel-3 mission. *Remote Sensing of Environment*, *120*, 37–57.

Doray, M., Boyra, G., & others. (2021). ICES Survey Protocols–Manual for acoustic surveys coordinated under ICES Working Group on Acoustic and Egg Surveys for Small Pelagic Fish (WGACEGG). *ICES Techniques in Marine Environmental Sciences*, *64*.

du Buit, M. (1982). Essai d'évaluation de la prédation de quelques téléostéens en Mer Celtique. *ICES Journal of Marine Science*, *40*(1), 37–46. https://doi.org/10.1093/icesjms/40.1.37

du Buit, M. (1992). Alimentation de la cardine, *Lepidorhombus whiffiagonis* en Mer Celtique. *Cahiers de Biologie Marine*, *33*, 501–501.

du Buit, M. (1995). Food and feeding of cod (Gadus morhua L.) in the Celtic Sea. *Fisheries Research*, *22*(3–4), 227–241. https://doi.org/10.1016/0165-7836(94)00322-N

du Buit, M. (1996). Diet of hake (Merluccius merluccius) in the Celtic Sea. *Fisheries Research*, *28*(4), 381–394. https://doi.org/10.1016/S0165-7836(96)00516-4

Duhamel, E., Pawlowski, L., & Garren, F. (2018). In *EVHOE 2018 cruise,Thalassa R/V*. https://doi.org/10.17600/18000518.

Dunne, J. A., Williams, R. J., & Martinez, N. D. (2002). Network structure and biodiversity loss in food webs: Robustness increases with connectance. *Ecology Letters*, *5*(4), 558–567. https://doi.org/10.1046/j.1461-0248.2002.00354.x

Durant, J. M., Hjermann, D. O., Frederiksen, M., Charrassin, J. B., Le Maho, Y., Sabarros, P. S., Crawford, R. J. M., & Stenseth, N. C. (2009). Pros and cons of using seabirds as ecological indicators. *Climate Research*, *39*, 115–129.

Dutkiewicz, S., Hickman, A. E., Jahn, O., Henson, S., Beaulieu, C., & Monier, E. (2019). Ocean colour signature of climate change. *Nature Communications*, *10*(1), 1–13.

Eaton, D. R. (1983). Scad in the North-East Atlantic. Laboratory Leaflet No. 56. In *Ministry of Agriculture, Fisheries and Food, Directorate of Fisheries Research*. UK.

Eero, M., Vinther, M., Haslob, H., Huwer, B., Casini, M., Storr-Paulsen, M., & Köster, F. W. (2012). Spatial management of marine resources can enhance the recovery of predators and avoid local depletion of forage fish. *Conserv Lett*, *5*, 486 492.

Ellis, L., JR, JE, C., PS, R., & S.I. (2002). The marine fauna of the Celtic Sea. In J. D. Nunn (Ed.), *Marine biodiversity in Ireland and adjacent waters. Ulster Museum, Belfast* (p. 45 65).

Ellis, T., & Nash, R. D. M. (1997). Predation by sprat and herring on pelagic fish eggs in a plaice spawning area in the Irish Sea. *Journal of Fish Biology*, *50*(6), 1195–1202. https://doi.org/10.1111/j.1095-8649.1997.tb01647.x

Eloire, D., Somerfield, P. J., Conway, D. V. P., Halsband-Lenk, C., Harris, R., & Bonnet, D. (2010). Temporal variability and community composition of zooplankton at station L4 in the Western Channel: 20 years of sampling. *Journal of Plankton Research*, *32*(5), 657–679. https://doi.org/10.1093/plankt/fbq009

Eme, D., Rufino, M. M., Trenkel, V. M., & Y, V. (2022). Contrasted spatio-temporal changes in the demersal fish assemblages and the dominance of the environment vs fishing pressure, in the Bay of Biscay and Celtic Sea. *Prog Oceanogr*, *204*(102788).

Emmett, R. L., Brodeur, R. D., Miller, T. W., Pool, S. S., Bentley, P. J., Krutzikowsky, G., & McCrae, J. (2005). Pacific sardine (*Sardinops sagax*) abundance, distribution, and ecological relationships in the Pacific Northwest. *California Cooperative Oceanic Fisheries Investigations Report*, *46*, 122.

Engelhard, G. H., Peck, M. A., Rindorf, A., C. Smout, S., van Deurs, M., Raab, K., Andersen, K. H., Garthe, S., Lauerburg, R. A. M., Scott, F., Brunel, T., Aarts, G., van Kooten, T., & Dickey-Collas, M. (2013). Forage fish, their fisheries, and their predators: Who drives whom? *ICES Journal of Marine Science*, *71*(1), 90–104. https://doi.org/10.1093/icesjms/fst087

Eppley, R. W. (1972). Temperature and Phytoplankton Growth in the Sea, Fish. *Bull*, *70*, 1063–1085.

ESA, E. (2019). *Sentinel-3 product notice – OLCI Level-2 ocean colour. EUMETSAT. E.M*.

Essington, T. E. (2007). Evaluating the sensitivity of a trophic mass-balance model (Ecopath) to imprecise data inputs. *Canadian Journal of Fisheries and Aquatic Sciences*, *64*(4), 628–637. https://doi.org/10.1139/f07-042

Essington, T. E., Moriarty, P. E., Froehlich, H. E., Hodgson, E. E., Koehn, L. E., Oken, K. L., Siple, M. C., & Stawitz, C. C. (2015). Fishing amplifies forage fish population collapses. *Proceedings of the National Academy of Sciences*, *112*(21), 6648–6652.

Eyring, V., Bony, S., Meehl, G. A., Senior, C. A., Stevens, B., Stouffer, R. J., & Taylor, K. (2016). Overview of the Coupled Model Intercomparison Project Phase 6 (CMIP6) experimental design and organization, Geosci. *Model Dev*, *9*, 1937-1958,. https://doi.org/10.5194/gmd-9-1937-2016

Falkenhaug, T., & Dalpadado, P. (2014). Diet composition and food selectivity of sprat (*Sprattus sprattus*) in Hardangerfjord, Norway. *Marine Biology Research*, *10*(3), 203–215. https://doi.org/10.1080/17451000.2013.810752

F.A.O., FAO, R. F. L., & G, C. (2018). The state of world fisheries and aquaculture 201—Meeting the sustainable development goals. In D. Mackinlay & K. Shearer (Eds.), *Feeding ecology and nutrition in fish, Symposium Proceedings* (pp. 71–80). American Fisheries Society.

Fauchald, P., Skov, H., M., S.-M., Johns, D., & T, T. (2011). Wasp-Waist Interactions in the North Sea Ecosystem. *PLoS ONE*, *6*(7), 22729. https://doi.org/10.1371/journal.pone.0022729

Ferry, L. A., & Cailliet, G. M. (1996). Sample size sufficiency and data analysis: Are we characterizing and comparing diet properly? In D. Mackinlay & K. Shearer (Eds.), *Feeding ecology and nutrition in fish: Proceedings of the symposium on the feeding* *ecology and nutrition in fish* (pp. 71–80). International Congress on the Biology of Fishes, American Fisheries Society.

Flinkman, J., Aro, E., Vuorinen, I., & Viitasalo, M. (1998). Changes in northern Baltic zooplankton and herring nutrition from 1980s to 1990s: Top-down and bottom-up processes at work. *Marine Ecology Progress Series*, *165*, 127–136. https://doi.org/10.3354/meps165127

Fox, C. J., Taylor, M. I., Van der Kooij, J., Taylor, N., Milligan, S. P., Albaina, A., Pascoal, S., Lallias, D., Maillard, M., & Hunter, E. (2012). Identification of marine fish egg predators using molecular probes. *Marine Ecology Progress Series*, *462*, 205–218. https://doi.org/10.3354/meps09748

Frederiksen, M., Edwards, M., Richardson, A. J., Halliday, N. C., & Wanless, S. (2006). From plankton to top predators: Bottom up control of a marine food web across four trophic levels. *Journal of Animal Ecology*, *75*, 1259–1268.

Frederiksen, M., Wanless, S., Harris, M. P., Rothery, P., & Wilson, L. J. (2004). The role of industrial fisheries and oceanographic change in the decline of North Sea blacklegged kittiwakes. *Journal of Applied Ecology*, *41*, 1129–1139.

Friedland, K. D., Stock, C., Drinkwater, K. F., Link, J. S., Leaf, R. T., Shank, B. V., Rose, J. M., Pilskaln, C. H., & Fogarty, M. J. (2012). Pathways between Primary Production and Fisheries Yields of Large Marine Ecosystems. *PLoS ONE*, *7*(1), e28945. https://doi.org/10.1371/journal.pone.0028945

Froese, R., & Pauly, D. (2009). FishBase. World Wide Web Electronic Publication. *Http://Www. Fishbase. Org*.

Fulton, E. (2010). Approaches to end-to-end ecosystem models. *Journal of Marine Systems*, *81*, 171–183.

Fulton, E. A., Parslow, J. S., Smith, A. D. M., & Johnson, C. R. (2004). Biogeochemical marine ecosystem models II: the effect of physiological detail on model performance.

Ecological Modelling, *173*(4), 371–406. https://doi.org/10.1016/j.ecolmodel.2003.09.024

Fulton, E. A., & Smith, A. D. M. (2004). Lessons learnt from a comparison of three ecosystem models for Port Phillip Bay, Australia. *African Journal of Marine Science*, *26*, 219–243.

Furness, R. (2007). Responses of seabirds to depletion of food fish stocks. *Journal of Ornithology*, *148*, 247–252.

Garrido, S., Ben-Hamadou, R., Oliveira, P. B., Cunha, M. E., Chícharo, M. A., & van der Lingen, C. D. (2008). Diet and feeding intensity of sardine *Sardina pilchardus*: Correlation with satellite-derived chlorophyll data. *Marine Ecology Progress Series*, *354*, 245–256. https://doi.org/10.3354/meps07201

Garrido, S., Marçalo, A., Zwolinski, J., & Van der Lingen, C. D. (2007). Laboratory investigations on the effect of prey size and concentration on the feeding behaviour of *Sardina pilchardus*. *Marine Ecology Progress Series*, *330*, 189–199. https://doi.org/10.3354/meps330189

Gibbs, C. (1979). Chlorophyll B Interference in the Fluorometric Determination of Chlorophyll a and ‘Phaeo-Pigments’. *Mar. Freshw. Res*, *30*(5), 597–606. https://doi.org/10.1071/MF9790597

Gibson, R. N., & Ezzi, I. A. (1992). The relative profitability of particulate- and filter-feeding in the herring, *Clupea harengus* L. *Journal of Fish Biology*, *40*(4), 577–590. https://doi.org/10.1111/j.1095-8649.1992.tb02607.x

Giering, S. L. C., Wells, S. R., Mayers, K. M. J., Schuster, H., Cornwell, L., Fileman, E. S., Atkinson, A., Cook, K. B., Preece, C., & Mayor, D. J. (2019). Seasonal variation of zooplankton community structure and trophic position in the Celtic Sea: A stable isotope and biovolume spectrum approach. *Progress in Oceanography*, *177*, 101943. https://doi.org/10.1016/j.pocean.2018.03.012

Giménez, J., Marçalo, A., Ramírez, F., Verborgh, P., Gauffier, P., Esteban, R., Nicolau, L., González-Ortegón, E., Baldó, F., Vilas, C., Vingada, J., G. Forero, M., & de Stephanis, R. (2017). Diet of bottlenose dolphins (Tursiops truncatus) from the Gulf of Cadiz: Insights from stomach content and stable isotope analyses. *PLOS ONE*, *12*(9), e0184673. https://doi.org/10.1371/journal.pone.0184673

Glazier, D. S. (2012). Temperature affects food-chain length and macroinvertebrate species richness in spring ecosystems. *Freshwater Science*, *31*(2), 575–585. https://doi.org/10.1899/11.058.1

Gohin, F., Saulquin, B., Oger-Jeanneret, H., Lozac'h, L., Lampert, L., & Lefebvre, A. (2008). Towards a Better Assessment of the Ecological Status of Coastal Waters Using Satellite-Derived Chlorophyll-A Concentrations. *Remote Sens. Environ*, *112*(8), 3329–3340. https://doi.org/10.1016/j.rse.2008.02.014

Goldbogen, J. A., Calambokidis, J., Oleson, E., Potvin, J., Pyenson, N. D., Schorr, G., & Shadwick, R. E. (2011). Mechanics, hydrodynamics and energetics of blue whale lunge feeding: Efficiency dependence on krill density. *Journal of Experimental Biology*, *214*(1), 131–146.

Gravel, D., Canard, E., Guichard, F., & Mouquet, N. (2011). Persistence Increases with Diversity and Connectance in Trophic Metacommunities. *PLOS ONE*, *6*(5), 1–9. https://doi.org/10.1371/journal.pone.0019374

Grüss, A., Babcock, E. A., Sagarese, S. R., Drexler, M., Chagaris, D. D., Ainsworth, C. H., Penta, B., DeRada, S., & Sutton, T. T. (2016). Improving the spatial allocation of functional group biomasses in spatially-explicit ecosystem models: Insights from three Gulf of Mexico models. *Bulletin of Marine Science*, *92*(4), 473–496.

Grüss, A., Chagaris, D. D., Babcock, E. A., & Tarnecki, J. H. (2018). Assisting ecosystem-based fisheries management efforts using a comprehensive survey database, a large environmental database, and generalized additive models. *Trans. Am. Fish. Soc*, *10*, 40–70. https://doi.org/10.1002/mcf2.10002

Grüss, A., Rose, K. A., Justiæ, D., & Wang, L. (2020). Making the most of available monitoring data: A grid-summarization method to allow for the combined use of monitoring data collected at random and fixed sampling stations. *Fish. Res*, *229*(105623). https://doi.org/10.1016/j.fishres.2020.105623

Guénette, S., & Gascuel, D. (2012). Shifting baselines in European fisheries: The case of the Celtic Sea and Bay of Biscay. *Ocean & Coastal Management*, *70*, 10–21.

Guldberg, O. H., & Bruno, J. F. (2010). The Impact of Climate Change on the World‟s Marine Ecosystems. *Science*, *328*, 1523–1528.

Han, D., Zhang, C., Xue, Y., Xu, B., Ren, Y., & Chen, Y. (2020). Impacts of sample size for stomach content analysis on the estimation of ecosystem indices. *Acta Oceanologica Sinica*, *39*(8), 53–61. https://doi.org/10.1007/s13131-020-1633-x

Hannesson, R., Herrick, S., & Field, J. (2009). Ecological and economic considerations in the conservation and management of the Pacific sardine (Sardinops sagax. *Canadian Journal of Fisheries and Aquatic Sciences*, *66*, 859–868.

Hardy, A. C. (1924). The herring in relation to its animate environment. Part I. The food and feeding habits of the herring with special reference to the east coast of England. *Ministry of Agriculture and Fisheries, Fisheries Investigations, Series II*, *7*, 1–53.

Harshada, D., Raman, M., & Jayappa, K. (2021). Evaluation of the operational Chlorophyll-a product from global ocean colour sensors in the coastal waters, south-eastern Arabian Sea. *The Egyptian Journal of Remote Sensing and Space Science*, *24*(3), 769–786.

Harvey, E. T., Walve, J., Andersson, A., Karlson, B., & Kratzer, S. (2019). The Effect of Optical Properties on Secchi Depth and Implications for Eutrophication Management. *Front. Mar. Sci*, *5*, 496. https://doi.org/10.3389/fmars.2018.00496

Hawkins, S. J., Southward, A. J., & Genner, M. J. (2003). Detection of environmental change in a marine ecosystem—Evidence from the western English Channel. *Science of The Total Environment*, *310*(1), 245–256. https://doi.org/10.1016/S0048-9697(02)00645-9

Helgason, T., CM, H. G.-I., & 1979, U. (1979). VPA-analysis with special interaction due to predation. *Orbit.Dtu.Dk*. http://orbit.dtu.dk/en/publications/vpaanalysis-with-special-interaction-due-to-predation(c952a34d-5094-44f8-a1ce-68ce90ab788a).html

Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023). Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. *Nature Climate Change*, 1–8. https://doi.org/10.1038/s41558-023-01630-7

Hernvann, P. Y., Gascuel, D., Kopp, D., Robert, M., & Rivot, E. (2022). EcoDiet: A hierarchical Bayesian model to combine stomach, biotracer, and literature data into diet matrix estimation. *Ecological Applications*, *32*(2), 2521.

Hernvann, P.-Y., & Gascuel, D. (2020). Exploring the impacts of fishing and environment on the Celtic Sea ecosystem since 1950. *Fisheries Research*, *225*(105472).

Hernvann, P.-Y., Gascuel, D., Grüss, A., Druon, J.-N., Kopp, D., Perez, I., Piroddi, C., & Robert, M. (2020). The Celtic Sea Through Time and Space: Ecosystem Modeling to Unravel Fishing and Climate Change Impacts on Food-Web Structure and Dynamics. *Front Mar Sci*, *7*.

Heymans, J. J., Link, J. S., Mackinson, S., Steenbeek, J., Walters, C., & Christensen, V. (2016). Best practice in Ecopath with Ecosim food-web models for ecosystem-based management. *Ecological Modelling*, *331*, 173–184. https://doi.org/10.1016/J.ECOLMODEL.2015.12.007

Heymans, J. J., Sumaila, U. R., & Christensen, V. (2009). Policy options for the northern Benguela ecosystem using a multispecies, multifleet ecosystem model. *Progress in Oceanography*, *83*(1–4), 417–425.

Heymans, J. J., & Tomczak, M. T. (2016). Regime shifts in the Northern Benguela ecosystem: Challenges for management. *Ecological Modelling*, *331*, 151–159.

Hijmans, R. J., van Etten, J., Cheng, J., Mattiuzzi, M., Sumner, M., Greenberg, J. A., Lamigueiro, O. P., Bevan, A., Racine, E. B., Shortridge, A., others, & ESA. (2021). Raster: Geographic analysis and modeling with raster data. R package version 3.4-

13. *R Package*, *3.4-13*. https://sentinels.copernicus.eu/web/sentinel/user-guides/sentinel-3-olci/resolutions/radiometric

Hillgruber, N., & Kloppmann, M. (2001). Small scale patterns in distribution and feeding of Atlantic mackerel (Scomber scombrus L.) larvae in the Celtic Sea with special regard to intra-cohort cannibalism. *Helgoland Mar Res*, *55*, 135–149.

Holt, R. D. (1987). On the relation between niche overlap and competition: The effect of incommensurable niche dimensions. *Oikos*, *48*, 110–114.

Horton, T. W., Block, B. A., Davies, R., Hawkes, L. A., Jones, D., Jones, H., Leeves, K., Maoiléidigh, N. Ó., Righton, D., van der Kooij, J., Wall, D., & Witt, M. J. (2021). Evidence of increased occurrence of Atlantic bluefin tuna in territorial waters of the United Kingdom and Ireland. *ICES Journal of Marine Science*, *78*(5), 1672–1683. https://doi.org/10.1093/icesjms/fsab039

Houde, E. D. (2008). Emerging from Hjort's shadow. *Journal of Northwest Atlantic Fishery Science*, *41*.

Hunter, M. D., & Price, P. W. (1992). Playing chutes and ladders: Heterogeneity and the relative roles of bottom-up and topdown forces in natural communities. *Ecology*, *73*, 724–732.

Huret, M., Lebigre, C., Iriondo, M., Montes, I., & Estonba, A. (2020). Genetic population structure of anchovy (\texitEngraulis encrasicolus) in North-western Europe and variability in the seasonal distribution of the stocks. *Fisheries Research*, *229*, 105619. https://doi.org/10.1016/j.fishres.2020.105619

Hutchings, J. A. (2000). Collapse and recovery of marine fishes. *Nature*, *406*(6798), 882–885.

Hynes, H. B. N. (1950). The Food of Fresh-Water Sticklebacks (Gasterosteus aculeatus and Pygosteus pungitius), with a Review of Methods Used in Studies of the Food of Fishes. *The Journal of Animal Ecology*, *19*(1), 36. https://doi.org/10.2307/1570

ICES. (2004). Information and advice about appropriate ecoregions for the implementation of an ecosystem approach in European waters. *Report of the ICES Advisory Committee on Fishery Management and Advisory Committee on Ecosystems*, *1*(2), 115–131.

ICES. (2007). *Report of the Working Group for Regional Ecosystem Description (WGRED)* (p. 153).

ICES. (2008). Celtic Sea and West of Scotland. In *ICES, editor. Advice book 5* (p. 12).

ICES. (2010). Report of the Herring Assessment Working Group South of 62°N (HAWG. In *ICES Advisory Committee; ICES HQ*.

ICES. (2012). *Report of the Working Group of International Pelagic Surveys (WGIPS*. ICES HQ.

ICES. (2016). *Report of the Working Group on Southern Horse Mackerel, Anchovy and Sardine (WGHANSA)* (p. 531).

ICES. (2020). *ICES Advice on fishing opportunities, catch, and effort Celtic Seas ecoregion Herring (*Clupea harengus*) in divisions 7.a South of 52°30'N, 7.g-h, and 7.j-k (Irish Sea, Celtic Sea, and southwest of Ireland)*. ICES. https://doi.org/10.17895/ices.advice.5927

ICES. (2022). Sprat (Sprattus sprattus) in divisions 7.d and 7.e (English Channel. In *Report of the ICES Advisory Committee*. spr.27.7de

IMT. (2019). IMT Neural Net. *Https://Sentinels.Copernicus.Eu/Web/Sentinel/Technical-Guides/Sentinel-3-Olci/Level-2/Imt-Neural-Net*.

International Ocean-Colour Coordinating Group [IOCCG]. (2000). *Reports of the International Ocean-Colour Coordinating Group* (3; pp. 1–140).

Ioannou, I., Foster, R., Gilerson, A., Gross, B., Moshary, F., & Ahmed, S. (2013). Neural network approach for the derivation of chlorophyll concentration from ocean color. In *Ocean Sensing and Monitoring V* (Vol. 8724). SPIE.

IOCCG. (2010). *Atmospheric Correction for Remotely-Sensed Ocean-Colour Products (Reports of the International Ocean-Colour Coordinating Group, No. 10)* [Report].

International Ocean Colour Coordinating Group (IOCCG). https://doi.org/10.25607/OBP-101

Irigoien, X., Klevjer, T. A., Røstad, A., Martinez, U., Boyra, G., Acuña, J. L., Bode, A., Echevarria, F., Gonzalez-Gordillo, J. I., Hernandez-Leon, S., Agusti, S., Aksnes, D. L., Duarte, C. M., & Kaartvedt, S. (2014). Large mesopelagic fishes biomass and trophic efficiency in the open ocean. *Nature Communications*, *5*(1), 3271. https://doi.org/10.1038/ncomms4271

Jahncke, J., Checkley, D. M., & Hunt, G. L. (2004). Trends in carbon flux to seabirds in the Peruvian upwelling system: Effects of wind and fisheries on population regulation. *Fisheries Oceanography*, *13*, 208–223.

Jansen, T., Kristensen, K., Kooij, J., & S, P. (2015). Nursery areas and recruitment variation of Northeast Atlantic mackerel (Scomber scombrus. *ICES J Mar Sci*, *72*, 1779–1789.

Jennings, S., Pinnegar, J., Polunin, N., & Warr, K. (2002). Linking size-based and trophic analyses of benthic community structure. *Marine Ecology Progress Series*, *226*, 77–85. https://doi.org/10.3354/meps226077

Johns, D. (2006). The plankton ecology of the SEA 8 area. *Sir Alistair Hardy Foundation for Ocean Science, Plymouth*. https://assets.publishing.service.gov.uk/government/

Johnson, G. A. (2006). *Multispecies interactions in a fishery ecosystem and implications for fisheries management: The impacts of the estuarine shrimp trawl fishery in North Carolina*. The University of North Carolina at Chapel Hill.

Joint, I., & Groom, S. B. (2000). Estimation of phytoplankton production from space: Current status and future potential of satellite remote sensing. *Journal of Experimental Marine Biology and Ecology*, *250*(1–2), 233–255.

Jones, A. R., Wynn, R. B., Yésou, P., Thebault, L., COLLINS, P., Suberg, L., Lewis, K. M., & Brereton, T. M. (2014). Using integrated land- and boat-based surveys to inform conservation of the critically endangered balearic shearwater. *Endangered Species Research*, *25*, 1–18.

Kanstinger, P., Beher, J., Grenzdörffer, G., Hammer, C., Huebert, K. B., Stepputis, D., & Peck, M. A. (2018). What is left? Macrophyte meadows and Atlantic herring (Clupea harengus) spawning sites in the Greifswalder Bodden, Baltic Sea. *Estuarine, Coastal and Shelf Science*, *201*, 72–81. https://doi.org/10.1016/j.ecss.2016.03.004

Kaschner, K., Karpouzi, V., Watson, R., & Pauly, D. (2006). Forage fish consumption by marine mammals and seabirds. *On the Multiple Uses of Forage Fish: From Ecosystems to Markets. Fisheries Centre Research Reports*, *14*(3), 33–46.

Kaschner, K., Kesner-Reyes, K., Garilao, C., Segschneider, J., Rius-Barile, J., Rees, T., & Froese, R. (2019). AquaMaps: Predicted range maps for aquatic species. *World Wide Web Electronic Publication*.

Kassambara, A., & Mundt, F. (2020). factoextra: Extract and visualize the results of multivariate data analyses. *R Package Version 1.0.7*. https://cran.r-project.org/web/packages/

Keast, A. (1978). Feeding interrelations between age-groups of pumpkinseed (Lepomis gibbosus) and comparisons with bluegill (L. macrochirus). *Journal of the Fisheries Board of Canada*, *35*(1), 12–27.

Kempf, J., Breen, P., Rogan, E., & Reid, D. G. (2022). Trends in the abundance of Celtic Sea demersal fish-identifying the relative importance of fishing and environmental drivers. *Frontiers in Marine Science*.

Kennington, K., & Rowlands, W. L. (2006). SEA area 6 technical report—Plankton ecology of the Irish Sea. Offshore Energy Strategic Environmental Assessment—SEA6 Irish Sea. *Department of Trade and Industry, London*. https://assets.publishing.service.gov.uk/government/uploads/system/uploads/attachment_data/file/197299/

Kinzey, D., & Punt, A. E. (2008). Multispecies and single-species models of fish population dynamics: Comparing parameter estimates. *Natural Resource Modeling*, *22*(1), 67–104. https://doi.org/10.1111/j.1939-7445.2008.00030.x

Kratzer, S., Harvey, E. T., & Canuti, E. (2022). International intercomparison of in situ chlorophyll-a measurements for data quality assurance of the Swedish Monitoring Program. *Frontiers in Remote Sensing*, *3*, 866712.

Krebs, C. J. (1999). *Ecological Methodology* (2nd ed.). Addison-Welsey Education Publishers, Inc., Menlo Park, CA, USA (1999).

Krebs, C. J. (2009). *Ecology* (6th ed.). Pearson Benjamin Cummings.

Kvaavik, C., Óskarsson, G. J., Daníelsdóttir, A. K., & Marteinsdóttir, G. (2019). Diet and feeding strategy of Northeast Atlantic mackerel (*Scombrus scomber*) in Icelandic waters. *PLOS ONE*, *14*(12), 1–22. https://doi.org/10.1371/journal.pone.0225552

Lamb, P. D., Hunter, E., Pinnegar, J. K., van der Kooij, J., Creer, S., & Taylor, M. I. (2019). Cryptic diets of forage fish: Jellyfish consumption observed in the Celtic Sea and western English Channel. *Journal of Fish Biology*, *94*(6), 1026–1032. https://doi.org/10.1111/jfb.13926

Langøy, H., Nøttestad, L., Skaret, G., Broms, C., & Fernö, A. (2012). Overlap in distribution and diets of Atlantic mackerel (*Scomber scombrus*), Norwegian spring-spawning herring (*Clupea harengus*) and blue whiting (*Micromesistius poutassou*) in the Norwegian Sea during late summer. *Marine Biology Research*, *8*(5–6), 442–460. https://doi.org/10.1080/17451000.2011.642803

Lauria, V. (2012). *Impacts of Climate Change and Fisheries on the Celtic Sea Ecosystem* [(PhD thesis).]. Plymouth University, School of Science and Technology, Faculty of Marine Science and Engineering, UK.

Lauria, V., Attrill, M. J., Pinnegar, J. K., Brown, A., Edwards, M., & Votier, S. C. (2012). Influence of Climate Change and Trophic Coupling across Four Trophic Levels in the Celtic Sea. *PLOS ONE*, *7*(10), 1–11. https://doi.org/10.1371/journal.pone.0047408

Lauria, V., Posen, P., & Mackinson, S. (2016). *An Ecopath with Ecosim and Ecospace for the Celtic Sea*. CEFAS.

Lee, Z., & Carder, K. L. (2002). Effect of spectral band numbers on the retrieval of water column and bottom properties from ocean color data. *Applied Optics*, *41*(12), 2191. https://doi.org/10.1364/ao.41.002191

Lee, Z., Carder, K. L., & Arnone, R. A. (2002). Deriving inherent optical properties from water color: A multiband quasi-analytical algorithm for optically deep waters. *Applied Optics*, *41*(27), 5755–5772. https://doi.org/10.1364/AO.41.005755

Legendre, P., & Legendre, L. (1998). *Numerical ecology* (3rd ed.). Elsevier.

Leggett, W. C., & Deblois, E. (1994). Recruitment in marine fishes: Is it regulated by starvation and predation in the egg and larval stages? *Netherlands Journal of Sea Research*, *32*(2), 119–134. https://doi.org/10.1016/0077-7579(94)90036-1

Lewy, P., & Vinther, M. (2004). *A stochastic age-length-structured multispecies model applied to North Sea stocks. ICES CM 2004/FF:20*.

Li, J., Jamet, C., Zhu, J., Han, B., Li, T., Yang, A., Guo, K., & Jia, D. (2019). Error budget in the validation of radiometric products derived from OLCI around the China Sea from open Ocean to Coastal Waters Compared with MODIS and VIIRS. *Remote Sensing*, *11*(20), 2400.

Libralato, S., Pranovi, F., Stergiou, K., & Link, J. (2014). Trophodynamics in marine ecology: 70 years after Lindeman. *Marine Ecology Progress Series*, *512*, 1–7. https://doi.org/10.3354/meps11033

Lindeman, R. L. (1942). The Trophic-Dynamic Aspect of Ecology. *Ecology*, *23*(4), 399–417. https://doi.org/10.2307/1930126

Link, J. S. (2010). Adding rigor to ecological network models by evaluating a set of pre-balance diagnostics: A plea for PREBAL. *Ecological Modelling*, *221*, 1580–1591. https://doi.org/10.1016/j.ecolmodel.2010.03.012.

Lloret, J., Palomera, I., Salat, J., & Sole, I. (2004). Impact of freshwater input and wind on landings of anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) in shelf waters surrounding the Ebre (Ebro) River delta (north-western Mediterranean).

Fisheries Oceanography, *13*(2), 102–110. https://doi.org/10.1046/j.1365-2419.2003.00279.x

Lockwood, S. J., & Shepherd, J. G. (1984). An assessment of the Western mackerel stock. *ICES Journal of Marine Science*, *41*(2), 167–180. https://doi.org/10.1093/icesjms/41.2.167

Lodish, H., Berk, A., Zipursky, S. L., Matsudaira, P., Baltimore, D., & Darnell, J. (2005). Photosynthetic stages and light-absorbing pigments. In *Molecular Cell Biology. 5th edition* (pp. 331–336). WH Freeman and Co.

Logan, J. M., Rodriguez-Marin, E., & Goni, N. (2011). Diet of young Atlantic bluefin tuna (Thunnus thynnus) in eastern and western Atlantic foraging grounds. *Marine Biology*, *158*, 73–85.

Longhurst, A., Sathyendranath, S., Platt, T., & Caverhill, C. (1995). An estimate of global primary production in the ocean from satellite radiometer data. *Journal of Plankton Research*, *17*(6), 1245–1271. https://doi.org/10.1093/plankt/17.6.1245

Lynam, C. P., Halliday, N. C., Hoffle, H., Wright, P. J., Damme, C. J. G., Edwards, M., & Pitois, S. (2013). Spatial patterns and trends in abundance of larval sandeels in the North Sea: 1950–2005. *ICES Journal of Marine Science*. https://doi.org/10.1093/icesjms/fst006

Macer, C. T. (1966). Sand eels (Ammodytidae) in the south-western North Sea; their biology and fishery. *MAFF Fish. Investig. Ser*, *24*(6), 1–55.

Magnussen, E. (2011). Food and feeding habits of cod (Gadus morhua) on the Faroe Bank. *ICES Journal of Marine Science*, *68*, 1909–1917.

Mahe, K., Amara, R., Bryckaert, T., Kacher, M., & Brylinski, J. M. (2007). Ontogenetic and spatial variation in the diet of hake (*Merluccius merluccius*) in the Bay of Biscay and the Celtic Sea. *ICES Journal of Marine Science*, *64*(6), 1210–1219. https://doi.org/10.1093/icesjms/fsm100

Maritorena, S., Siegel, D. A., & Peterson, A. R. (2002). Optimization of a semianalytical ocean color model for global-scale applications. *Applied Optics*, *41*(15), 2705–2714. https://doi.org/10.1364/AO.41.002705

Martinez, E., Antoine, D., D'Ortenzio, F., & Gentili, B. (2009). Climate-driven basin-scale decadal oscillations of oceanic phytoplankton. *Science*, *326*(5957), 1253–1256.

Martino, E. J., & Houde, E. D. (2010). Recruitment of striped bass in Chesapeake Bay: Spatial and temporal environmental variability and availability of zooplankton prey. *Marine Ecology Progress Series*, *409*, 213–228. https://doi.org/10.3354/meps08586

Matsushita, B., Yang, W., Chang, P., Yang, F., & Fukushima, T. (2012). A simple method for distinguishing global Case-1 and Case-2 waters using SeaWiFS measurements. *ISPRS Journal of Photogrammetry and Remote Sensing*, *69*, 74–87. https://doi.org/10.1016/j.isprsjprs.2012.02.008

Mavor, R. A., Parsons, M., Heubeck, M., & Schmitt, S. (2005). Seabird numbers and breeding success in Britain and Ireland, 2004. *UK Nature Conservation Rep*, *29*.

McKee, D., Cunningham, A., & Dudek, A. (2007). Optical water type discrimination and tuning remote sensing band-ratio algorithms: Application to retrieval of chlorophyll and Kd (490) in the Irish and Celtic Seas. *Estuarine, Coastal and Shelf Science*, *73*(3–4), 827–834.

Meister, G., & Franz, B. A. (2014). Corrections to the MODIS Aqua calibration derived from MODIS Aqua ocean color products. *IEEE Transactions on Geoscience and Remote Sensing*, *52*(10), 6534–6541.

Meister, G., Franz, B. A., Kwiatkowska, E. J., & McClain, C. R. (2011). Corrections to the calibration of MODIS Aqua ocean color bands derived from SeaWiFS data. *IEEE Transactions on Geoscience and Remote Sensing*, *50*(1), 310–319.

Miller, R. L., & McKee, B. A. (2004). Using MODIS Terra 250 m imagery to map concentrations of total suspended matter in coastal waters. *Remote Sensing of Environment*, *93*(1), 259–266. https://doi.org/10.1016/j.rse.2004.07.012

Miyamoto, K. (1997). Renewable biological systems for alternative sustainable energy production. *FAO Agricultural Services Bulletin*, *128*. Scopus.

Mobley, C. (1994). *Light and Water: Radiative Transfer in Natural Waters*. Academic Press.

Möllmann, C., Kornilovs, G., Fetter, M., & Köster, F. W. (2004). Feeding ecology of central Baltic Sea herring and sprat. *Journal of Fish Biology*, *65*(6), 1563–1581. https://doi.org/10.1111/j.0022-1112.2004.00566.x

Montero, L. C., Christensen, V., & Hernández, J. J. C. (2021). Simulating trophic impacts of fishing scenarios on two oceanic islands using Ecopath with Ecosim. *Marine Environmental Research*, *169*, 105341.

Moore, C., Davie, S., Robert, M., Pawlowski, L., Dolder, P., & Lordan, C. (2019). Defining métier for the Celtic Sea mixed fisheries: A multiannual international study of typology. *Fisheries Research*, *219*, 105310.

Morel, A., & Berthon, J. F. (1989). Surface pigments, algal biomass profiles, and potential production of the euphotic layer: Relationships reinvestigated in view of remote-sensing applications. *Limnology and Oceanography*, *34*(8), 1545–1562.

Morote, E., Olivar, M. P., Villate, F., & Uriarte, I. (2010). A comparison of anchovy (Engraulis encrasicolus) and sardine (Sardina pilchardus) larvae feeding in the Northwest Mediterranean: Influence of prey availability and ontogeny. *ICES Journal of Marine Science*, *67*(5), 897–908. https://doi.org/10.1093/icesjms/fsp302

Moutzouris-Sidiris, I., & Topouzelis, K. (2021). Assessment of Chlorophyll-a concentration from Sentinel-3 satellite images at the Mediterranean Sea using CMEMS open source in situ data. *Open Geosciences*, *13*(1), 85–97.

Mueller, J. L., Davis, C., Arnone, R., Frouin, R., Carder, K., Lee, Z., Steward, R., Hooker, S., Mobley, C. D., & McLean, S. (2003). Above-water radiance and remote sensing reflectance measurement and analysis protocols. *Radiometric Measurements and Data Analysis, Ocean Optics Protocols For Satellite Ocean Color Sensor, Validation, Revision*, *4*, 21–30.

Munuera-Fernández, I., & González-Quirós, R. (2006). Analysis of feeding of *Sardina pilchardus* (Walbaum, 1792) larval stages in the central Cantabrian Sea. *Scientia Marina*, *70*(S1), 131–139.

Muus, B. J., & Nielsen, J. G. (1999). Sea fish. In *Scandinavian Fishing Year Book, Hedehusene, Denmark*. Scandinavian Fishing Year Book–Hedehusene.

Neeley, A. R., Mannino, A., & others. (2018). *Ocean Optics and Biogeochemistry Protocols for Satellite Ocean Colour Sensor Validation; Volume 1.0. Inherent Optical Property Measurements and Protocols: Absorption Coefficient.* International Ocean Colour Coordinating Group (IOCCG).

Nikolioudakis, N., Isari, S., & Somarakis, S. (2014). Trophodynamics of anchovy in a non-upwelling system: Direct comparison with sardine. *Marine Ecology Progress Series*, *500*, 215–229. https://doi.org/10.3354/meps10604

Nissling, A. (2004). Effects of temperature on egg and larval survival of cod (Gadus morhua) and sprat (Sprattus sprattus) in the Baltic Sea—Implications for stock development. In *Biology of the Baltic Sea* (pp. 115–123). Springer. https://doi.org/10.1007/978-94-017-0920-0_11

Novakowski, G. C., Hahn, N. S., & Fugi, R. (2008). Diet seasonality and food overlap of the fish assemblage in a pantanal pond. *Neotropical Ichthyology*, *6*(4), 567–576.

Odum, E. P. (1969). The strategy of ecosystem development. *Science*, *164*, 262–270.

Olafsdottir, A. H., Slotte, A., Jacobsen, J. A., Oskarsson, G. J., Utne, K. R., & Nøttestad, L. (2016). Changes in weight-at-length and size-at-age of mature Northeast Atlantic mackerel (Scomber scombrus) from 1984 to 2013: Effects of mackerel stock size and herring (Clupea harengus) stock size. *ICES Journal of Marine Science*, *73*(4), 1255–1265.

Olin, A. B., Banas, N. S., Johns, D. G., Heath, M. R., Wright, P. J., & Nager, R. G. (2022). Spatio-temporal variation in the zooplankton prey of lesser sandeels: Species and community trait patterns from the Continuous Plankton Recorder. *ICES Journal of Marine Science*, *79*(5), 1649–1661. https://doi.org/10.1093/icesjms/fsac101

O'Reilly, J. E., Maritorena, S., Mitchell, B. G., Siegel, D. A., Carder, K. L., Garver, S. A., Kahru, M., & McClain, C. (1998). Ocean color chlorophyll algorithms for SeaWiFS. *Journal of Geophysical Research: Oceans*, *103*(C11), 24937–24953.

Óskarsson, G. J., Gudmundsdottir, A., Sveinbjörnsson, S., & Sigurðsson, Þ. (2016). Feeding ecology of mackerel and dietary overlap with herring in Icelandic waters. *Marine Biology Research*, *12*(1), 16–29. https://doi.org/10.1080/17451000.2015.1073327

OSPAR. (2000). *OSPAR Commission for the Protection of the Marine Environment of the North-East Atlantic Quality Status Report 2000 Region III Celtic Seas*. http://www.ospar.org

Österblom, H., Hansson, S., Larsson, U., Hjerne, O., Wulff, F., Elmgren, R., & Folke, C. (2007). *Human-induced trophic cascades and ecological regime shifts in the Baltic Sea*. https://doi.org/10.1007/s10021-007-9069-0.

Ottersen, G., Alheit, J., Drinkwater, K., Friedland, K., Hagen, E., & Stenseth, N. (2004). The response of fish populations to ocean climate fluctuations. In *Marine Ecosystems and climate variation* (p. 231).

Oven, L. S., Shevchenko, N. F., & Volodin, S. V. (1995). Size-age composition and diet of whiting, Merlangus merlangus euxinus (Gadidae), in different areas of the Black Sea differing in levels of pollution. *J. Ichthyol*, *35*(9), 113–122.

Pahlevan, N., Smith, B., Schalles, J., Binding, C., Cao, Z., Ma, R., Alikas, K., Kangro, K., Gurlin, D., Hà, N., & others. (2020). Seamless retrievals of chlorophyll-a from Sentinel-2 (MSI) and Sentinel-3 (OLCI) in inland and coastal waters: A machine-learning approach. *Remote Sensing of Environment*, *240*, 111604.

Palomares, M. L. D., Froese, R., Derrick, B., Nöel, S.-L., Tsui, G., Woroniak, J., & Pauly, D. (2018). *A preliminary global assessment of the status of exploited marine fish and* *invertebrate populations. A report prepared by the Sea Around Us for OCEANA*. The University of British Columbia.

Pasztaleniec, A., & Poniewozik, M. (2010). Phytoplankton Based Assessment of the Ecological Status of Four Shallow Lakes (Eastern Poland) According to Water Framework Directive—A Comparison of Approaches. *Limnologica - Ecol. Manag. Inland Waters*, *40*(3), 251–259. https://doi.org/10.1016/j.limno.2009.07.001

Patel, R., Roy, S., Capuzzo, E., & Kooij, J. van der. (2023). Seasonality of diet overlap among small pelagic fish in the waters southwest of the UK. *Marine Ecology Progress Series*, *708*, 101–123. https://doi.org/10.3354/meps14260

Patti, B., Torri, M., & Cuttitta, A. (2020). General surface circulation controls the interannual fluctuations of anchovy stock biomass in the Central Mediterranean Sea. *Scientific Reports*, *10*(1), 1–14. https://doi.org/10.1038/s41598-020-58028-0

Pauly, D. (1980). On the interrelationships between natural mortality, growth parameters and mean environmental temperature in 175 fish stock. *Journal Du Conseil International Exploration de Mer*, *39*, 175–192.

Pauly, D. (1998). Diet composition and trophic levels of marine mammals. *ICES Journal of Marine Science*, *55*(3), 467–481. https://doi.org/10.1006/jmsc.1997.0280

Pauly, D., & Christensen, V. (1995). Primary production required to sustain global fisheries. *Nature*, *374*(6519), 255–257. https://doi.org/10.1038/374255a0

Pauly, D., & Christensen, V. (2000). *Trophic Levels of Fishes* (p. 181). ICLARM.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., & Torres, F. (1998). Fishing down marine food webs. *Science (New York, N.Y.)*, *279*(5352), 860–863. https://doi.org/10.1126/SCIENCE.279.5352.860

Pauly, D., Christensen, V., & Sambilay, V. (1990). Some features of fish food consumption estimates used by ecosystem modellers. *ICES CM*, *17*, 8.

Pauly, D., Christensen, V., & Walters, C. (2000). Ecopath, Ecosim, and Ecospace as tools for evaluating ecosystem impact of fisheries. *ICES Journal of Marine Science*, *57*(3), 697–706. https://doi.org/10.1006/jmsc.2000.0726

Pauly, D., & Sa-a, P. (2000). *Estimating Trophic Levels from Individual Food Items* (p. 185). ICLARM.

Pauly, D., Watson, R., & Alder, J. (2005). Global trends in world fisheries: Impacts on marine ecosystems and food security. *Philosophical Transaction of the Royal Society*, *360*, 5–12.

Pauly, D., Zeller, D., & Palomares, M. L. D. (Eds.). (2020). *Sea Around Us Concepts, Design and Data*. seaaroundus.org

Peck, M. A., Alheit, J., Bertrand, A., & IA, C. (2021). Small pelagic fish in the new millennium: A bottom-up view of global research effort. *Prog Oceanogr*, *191*(102494).

Pennino, M. G., Coll, M., Albo-Puigserver, M., & E, F.-C. (2020). Current and future influence of environmental factors on small pelagic fish distributions in the Northwestern Mediterranean Sea. *Front Mar Sci*, *7*, 622.

Petitgas, P., Rijnsdorp, A. D., Dickey-Collas, M., Engelhard, G. H., Peck, M. A., Pinnegar, J. K., Drinkwater, K., Huret, M., & Nash, R. D. M. (2012). Impacts of climate change on the complex life cycles of fish. *Fisheries Oceanography*, *22*(2), 121–139. https://doi.org/10.1111/fog.12010

Petrik, C. M., Luo, J. Y., Heneghan, R. F., Everett, J. D., Harrison, C. S., & Richardson, A. J. (2022). Assessment and Constraint of Mesozooplankton in CMIP6 Earth System Models. *Global Biogeochemical Cycles*, *36*(11), e2022GB007367. https://doi.org/10.1029/2022GB007367

Phillips, J. A., Banks, A. N., Bolton, M., Brereton, T., Cazenave, P., Gillies, N., Padget, O., van der Kooij, J., Waggitt, J., & Guilford, T. (2021). Consistent concentrations of critically endangered Balearic shearwaters in UK waters revealed by at-sea surveys. *Ecology and Evolution*, *11*(4), 1544–1557. https://doi.org/10.1002/ece3.7059

Pianka, E. R. (1973). The Structure of Lizard Communities. *Annual Review of Ecology and Systematics*, *4*(1), 53–74. https://doi.org/10.1146/annurev.es.04.110173.000413

Piatt, J. F., & Methven, D. A. (1992). Threshold foraging behavior of baleen whales. *Marine Ecology Progress Series*, *84*, 205–210.

Piatt, J. F., Methven, D. A., Burger, A. E., McLagan, R. L., Mercer, V., & Creelman, E. (1989). Baleen whales and their prey in a coastal environment. *Canadian Journal of Zoology*, *67*(6), 1523–1530. https://doi.org/10.1139/z89-217

Pikitch, E. K., Rountos, K. J., Essington, T. E., Santora, C., Pauly, D., Watson, R., Sumaila, U. R., Boersma, P. D., Boyd, I. L., Conover, D. O., & Cury, P. (2014). The global contribution of forage fish to marine fisheries and ecosystems. *Fish and Fisheries*, *15*(1), 43–64.

Pingree, R. D., Holligan, P. M., Mardell, G. T., & Head, R. N. (1976). The influence of physical stability on spring, summer and autumn phytoplankton blooms in the Celtic sea. *Journal of the Marine Biological Association UK*, *56*, 845–873.

Pingree, R. D., Pugh, P. R., Holligan, P. M., & Forster, G. R. (1975). Summer phytoplankton blooms and red tides along tidal fronts in the approaches to the English Channel. *Nature*, *258*, 672–677. https://doi.org/10.1038/258672a0.

Pinnegar, J. K. (2014). *DAPSTOM — an integrated database & portal for fish stomach records*. Centre for Environment, Fisheries & Aquaculture Science.

Pinnegar, J. K., Goñi, N., Trenkel, V. M., Arrizabalaga, H., Melle, W., Keating, J., & Óskarsson, G. (2015). A new compilation of stomach content data for commercially important pelagic fish species in the northeast Atlantic. *Earth System Science Data*, *7*(1), 19–28. https://doi.org/10.5194/essd-7-19-2015

Pinnegar, J. K., Jennings, S., O'Brien, C. M., & Polunin, N. V. C. (2002). Long-term changes in the trophic level of the Celtic Sea fish community and fish market price distribution. *Journal of Applied Ecology*, *39*(3), 377–390. https://doi.org/10.1046/j.1365-2664.2002.00723.x

Pinnegar, J. K., Trenkel, V. M., Tidd, A. N., Dawson, W. A., & du buit, M. H. (2003). Does diet in Celtic Sea fishes reflect prey availability? *Journal of Fish Biology*, *63*(s1), 197–212. https://doi.org/10.1111/j.1095-8649.2003.00204.x

Pitois, S. G., & Fox, C. J. (2006). Long-term changes in zooplankton biomass concentration and mean size over the Northwest European shelf inferred from Continuous Plankton Recorder data. *ICES J Mar Sci*, *63*(785).

Pitois, S. G., Graves, C. A., Close, H., Lynam, C., Scott, J., Tilbury, J., Kooij, J. van der, & Culverhouse, P. (2021). A first approach to build and test the Copepod Mean Size and Total Abundance (CMSTA) ecological indicator using *in-situ* size measurements from the Plankton Imager (PI). *Ecological Indicators*, *123*, 107307. https://doi.org/10.1016/j.ecolind.2020.107307

Planque, B., & Fromentin, J. (1996). Calanus and environment in the eastern North Atlantic. I. Spatial and temporal patterns of C. finmarchicus and C. helgolandicus. *Marine Ecology Progress Series*, *134*, 101–109. https://doi.org/10.3354/meps134101

Planque, B., Fromentin, J. M., Cury, P., Drinkwater, K. F., Jennings, S., Perry, R. I., & Kifany, S. (2010). How does fishing alter marine populations and ecosystems sensitivity to climate? *Journal of Marine Systems*, *79*, 403–417.

Platt, T., & Sathyendranath, S. (1988). Oceanic Primary Production: Estimation by Remote Sensing at Local and Regional Scales. *Science*, *241*, 1613–1620.

Platt, T., & Sathyendranath, S. (1993). Estimators of Primary Production for Interpretation of Remotely Sensed Data on Ocean Color. *J. Geophys. Res*, *98*, 561–576.

Pleizier, N. K., Campana, S. E., Schaller, R. J., Wilson, S. G., & Block, B. A. (2012). Atlantic bluefin tuna (Thunnus thynnus) diet in the Gulf of St. Lawrence and on the eastern Scotian Shelf. *Journal of Northwest Atlantic Fishery Science*, *44*.

Plirú, A., van der Kooij, J., Engelhard, G. H., Fox, C. J., Milligan, S. P., & Hunter, E. (2012). Sprat feeding behaviour, selective predation, and impact on plaice egg mortality. *ICES Journal of Marine Science*, *69*(6), 1019–1029. https://doi.org/10.1093/icesjms/fss081

Plounevez, S., & Champalbert, G. (2000). Diet, feeding behaviour and trophic activity of the anchovy (Engraulis encrasicolus L.) in the Gulf of Lions (Mediterranean Sea. *Oceanografica Acta*, *23*(2), 175–192.

Polovina, J. J. (1984). Model of a coral reef ecosystem—I. The ECOPATH model and its application to French Frigate Shoals. *Coral Reefs*, *3*(1), 1–11. https://doi.org/10.1007/BF00306135

Pope, J. (1979). *A modified cohort analysis in which constant natural mortality is replaced by estimates of predation levels*.

Potier, M. (2021). *Investigating temporal and spatial impacts of mixed fisheries fleets on the Celtic Sea ecosystem in the frame of climate change through trophic modeling* [Masters Thesis, L'Institut Agro Rennes-Angers]. https://halieutique.institut-agro-rennes-angers.fr/files/fichiers/memoires/202118.pdf

Prokopchuk, I., & Sentyabov, E. (2006). Diets of herring, mackerel, and blue whiting in the Norwegian Sea in relation to *Calanus finmarchicus* distribution and temperature conditions. *ICES Journal of Marine Science*, *63*(1), 117–127. https://doi.org/10.1016/j.icesjms.2005.08.005

R Core Team. (2020). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Raab, K. (2013). *The European anchovy (*Engraulis encrasicolus*) increase in the North Sea* [PhD Thesis]. Wageningen University & Research.

Raab, K., Nagelkerke, L. A. J., Boerée, C., Rijnsdorp, A. D., Temming, A., & Dickey-Collas, M. (2011). Anchovy Engraulis encrasicolus diet in the North and Baltic Seas. *Journal of Sea Research*, *65*(1), 131–140. https://doi.org/10.1016/J.SEARES.2010.09.002

Raab, K., Nagelkerke, L., Boerée, C., Rijnsdorp, A., Temming, A., & Dickey-Collas, M. (2012). Dietary overlap between the potential competitors herring, sprat and anchovy in the North Sea. *Marine Ecology Progress Series*, *470*, 101–111. https://doi.org/10.3354/meps09919

Ratcliffe, F. C., Uren Webster, T. M., Leaniz, C., & Consuegra, S. (2021). A drop in the ocean: Monitoring fish communities in spawning areas using environmental DNA. *Environmental DNA*, *3*(1), 43–54.

Rault, J., Le Bris, H., Robert, M., Pawlowski, L., Denamiel, M., & Kopp, D. (2017). Diets and trophic niches of the main commercial fish species from the Celtic Sea. *Journal of Fish Biology*, *91*(5), 1449–1474. https://doi.org/10.1111/jfb.13470

Reid, P. C., Battle, E. J. V., Batten, S. D., & Brander, K. M. (2000). Impacts of fisheries on plankton community structure. *ICES J Mar Sci*, *57*, 495–502.

Reygondeau, G., Molinero, J. C., Coombs, S., MacKenzie, B. R., & Bonnet, D. (2015). Progressive changes in the Western English Channel foster a reorganization in the plankton food web. *Progress in Oceanography*, *137*, 524–532. https://doi.org/10.1016/j.pocean.2015.04.025

Rice, A. L. (1963). The food of the Irish sea herring in 1961 and 1962. *J. Cons. Int. Explor. Mer*, *28*, 188–200.

Rice, J. (1995). Food web theory, marine food webs, and what climate change may do to northern marine fish populations. *Climate Change and Northern Fish Populations*.

Richardson, D. E., Hare, J. A., Fogarty, M. J., & Link, J. S. (2011). Role of egg predation by haddock in the decline of an Atlantic herring population. *Proceedings of the National Academy of Sciences*, *108*(33), 13606–13611. https://doi.org/10.1073/pnas.1015400108

Rooney, N., McCann, K., Gellner, G., & Moore, J. C. (2006). Structural asymmetry and the stability of diverse food webs. *Nature*, *442*(7100), 265–269. https://doi.org/10.1038/nature04887

Rowlands, W. L., Dickey-Collas, M., Geffen, A. J., & Nash, R. D. (2008). Diet overlap and prey selection through metamorphosis in Irish Sea cod (Gadus morhua), haddock (Melanogrammus aeglefinus), and whiting (Merlangius merlangus). *Canadian Journal of Fisheries and Aquatic Sciences*, *65*(7), 1297–1306.

Roy, S., Sathyendranath, S., Bouman, H., & Platt, T. (2013). The global distribution of phytoplankton size spectrum and size classes from their light-absorption spectra derived from satellite data. *Remote Sensing of Environment*, *139*, 185–197. https://doi.org/10.1016/j.rse.2013.08.004

Ruiz-Castillo, E., Sharples, J., Hopkins, J., & Woodward, M. (2019). Seasonality in the cross-shelf physical structure of a temperate shelf sea and the implications for nitrate supply. *Progress in Oceanography*, *177*, 101985. https://doi.org/10.1016/j.pocean.2018.07.006

Ryan, C., Berrow, S. D., McHugh, B., O'Donnell, C., Trueman, C. N., & O'Connor, I. (2014). Prey preferences of sympatric fin (Balaenoptera physalus) and humpback (Megaptera novaeangliae) whales revealed by stable isotope mixing models. *Marine Mammal Science*, *30*(1), 242–258. https://doi.org/10.1111/mms.12034

Ryther, J. H. (1969). Photosynthesis and fish production in the sea. *Science (New York, N.Y.)*, *166*(3901), 72–76. https://doi.org/10.1126/SCIENCE.166.3901.72

Ryther, J. H., & Yentsch, C. S. (1957). The estimation of phytoplankton production in the ocean from chlorophyll and light data 1. *Limnology and Oceanography*, *2*(3), 281–286.

Scharf, F. S., Juanes, F., & Rountree, R. A. (2000). Predator size-prey size relationships of marine fish predators: Interspecific variation and effects of ontogeny and body size on trophic-niche breadth. *Mar Ecol Prog Ser*, *208*(229).

Schoener, T. W. (1970). Nonsynchronous Spatial Overlap of Lizards in Patchy Habitats. *Ecology*, *51*(3), 408–418. https://doi.org/10.2307/1935376

Scott, E., Serpetti, N., Steenbeek, J., & Heymans, J. J. (2016). A Stepwise Fitting Procedure for automated fitting of Ecopath with Ecosim models. *SoftwareX*, *5*, 25–30. https://doi.org/10.1016/j.softx.2016.02.002.

Scott, F., Blanchard, J. L., & Andersen, K. H. (2014). mizer: An R package for multispecies, trait-based and community size spectrum ecological modelling. *Methods in Ecology and Evolution*, *5*(10), 1121–1125.

Scott, J., Pitois, S., Close, H., Almeida, N., Culverhouse, P., Tilbury, J., & Malin, G. (2021). *In situ* automated imaging, using the Plankton Imager, captures temporal variations in mesozooplankton using the Celtic Sea as a case study. *Journal of Plankton Research*, *43*(2), 300–313. https://doi.org/10.1093/plankt/fbab018

Scott, J., Pitois, S., Creach, V., Malin, G., Culverhouse, P., & Tilbury, J. (2023). Resolution changes relationships: Optimizing sampling design using small scale zooplankton data. *Progress in Oceanography*, *210*, 102946. https://doi.org/10.1016/j.pocean.2022.102946

Segers, F. H. I. D., Dickey-Collas, M., & Rijnsdorp, A. D. (2007). Prey selection by North Sea herring (Clupea harengus), with special reference to fish eggs. *ICES Journal of Marine Science*, *64*(1), 60–68. https://doi.org/10.1093/icesjms/fsl002

Serpetti, N., Baudron, A. R., Burrows, M. T., Payne, B. L., Helaouët, P., & Fernandes, P. G. (2017). Impact of ocean warming on sustainable fisheries management informs the Ecosystem Approach to Fisheries. *Scientific Reports*, *7*. https://doi.org/10.1038/s41598-017-13220-7.

Shephard, S., Rindorf, A., Dickey-Collas, M., Hintzen, N. T., Farnsworth, K., & Reid, D. G. (2014). Assessing the state of pelagic fish communities within an ecosystem approach and the European Marine Strategy Framework Directive. *ICES J Mar Sci*, *71*(1572).

Shin, Y. J., & Cury, P. (2001). Exploring fish community dynamics through size-dependent trophic interactions using a spatialized individual-based model. *Aquat Living Resour*, *14*, 65 80.

Siegel, D. A., Buesseler, K. O., Doney, S. C., Sailley, S. F., Behrenfeld, M. J., & Boyd, P. W. (2014). Global assessment of ocean carbon export by combining satellite observations and food-web models. *Global Biogeochemical Cycles*, *28*(3), 181–196. https://doi.org/10.1002/2013GB004743

Sikora, W. B., Heard, R. W., & Dahlberg, M. D. (1972). The Occurrence and Food Habits of Two Species of Hake, \texitUrophycis regius and \texitU. floridanus in Georgia Estuaries. *Transactions of the American Fisheries Society*, *101*(3), 513–525. https://doi.org/10.1577/1548-8659(1972)101<513:TOAFHO>2.0.CO;2

Siple, M. C., Essington, T. E., Plagányi, E., & É. (2019). Forage fish fisheries management requires a tailored approach to balance trade-offs. *Fish and Fisheries*, *20*(1), 110–124.

Smith, T. M., & Smith, R. L. (2009). *Elements of Ecology* (7th ed.). Pearson Benjamin Cummings.

Smith-Vaniz, W. F. (1986). *Carangidae. In Fishes of the north-eastern Atlantic and the Mediterranean* (P. J. P. Whitehead, M.-L. Bauchot, J.-C. Hureau, J. Nielsen, & E. Tortonese, Eds.; Issue 2). UNESCO.

Smyth, T. J., Fishwick, J. R., Al-Moosawi, L., Cummings, D. G., Harris, C., Kitidis, V., Rees, A., Martinez-Vicente, V., & Woodward, E. M. (2010). A broad spatio-temporal view of the Western English Channel observatory. *Journal of Plankton Research*, *32*(5), 585–601.

Son, S., & Wang, M. (2012). Water properties in Chesapeake Bay from MODIS-Aqua measurements. *Remote Sensing of Environment*, *123*, 163–174. https://doi.org/10.1016/j.rse.2012.03.009

Sørensen, K., Grung, M., & Röttgers, R. (2007). An intercomparison of in vitro chlorophyll a determinations for MERIS level 2 data validation. *International Journal of Remote Sensing*, *28*(3–4), 537–554.

Soudijn, F. H., Daniël van Denderen, P., Heino, M., Dieckmann, U., & de Roos, A. M. (2021). Harvesting forage fish can prevent fishing-induced population collapses of large piscivorous fish. *Proceedings of the National Academy of Sciences*, *118*(6), e1917079118. https://doi.org/10.1073/pnas.1917079118

Southward, A. J., Boalch, G. T., & Maddock, L. (1988). Fluctuations in the herring and pilchard fisheries of Devon and Cornwall linked to change in climate since the 16th century. *Journal of the Marine Biological Association of the United Kingdom*, *68*(3), 423–445.

Southward, A. J., Hawkins, S. J., & Burrows, M. T. (1995). Seventy years' observations of changes in distribution and abundance of zooplankton and intertidal organisms in the western English Channel in relation to rising sea temperature. *Journal of Thermal Biology*, *20*(1), 127–155. https://doi.org/10.1016/0306-4565(94)00043-I

Sreekanth, G. B., Chakraborty, S. K., Jaiswar, A. K., Zacharia, P. U., & Mohamed, K. S. (2021). *Modeling the impacts of fishing regulations in a tropical Indian estuary using Ecopath with Ecosim approach* (pp. 1–19). Development and Sustainability.

STECF. (2020). *FDI Fisheries Dependent Information [Database*. STECF.

Stergiou, K. I., & Karpouzi, V. S. (2001). Feeding habits and trophic levels of Mediterranean fish. *Reviews in Fish Biology and Fisheries*, *11*(3), 217–254. https://doi.org/10.1023/A:1020556722822

Stienen, E. (2006). *Living with gulls: Trading off food and predation in the Sandwich Tern Sterna sandvicensis* [PhD Thesis,]. University of Groningen.

Stock, C. A., John, J. G., Rykaczewski, R. R., Asch, R. G., Cheung, W. W. L., Dunne, J. P., Friedland, K. D., Lam, V. W. Y., Sarmiento, J. L., & Watson, R. A. (2017). Reconciling fisheries catch and ocean productivity. *Proceedings of the National Academy of Sciences*, *114*(8), E1441–E1449. https://doi.org/10.1073/pnas.1610238114

Stokstad, E. (2006). Global Loss of Biodiversity Harming Ocean Bounty. *Science*, *314*, 745.

Talling, J. (1971). The underwater light climate as a controlling factor in the production ecology of freshwater phytoplankton: With 14 figures in the text and on 1 folder. In *Internationale Vereinigung für Theoretische und Angewandte Limnologie: Mitteilungen* (1; Vol. 19, pp. 214–243). Taylor & Francis.

Temple, A. J., Kiszka, J. J., Stead, S. M., Wambiji, N., Brito, A., Poonian, C. N., Amir, O. A., Jiddawi, N., Fennessy, S. T., Pérez-Jorge, S., & Berggren, P. (2018). Marine megafauna interactions with small-scale fisheries in the southwestern Indian Ocean: A review of status and challenges for research and management. *Reviews in Fish Biology and Fisheries*, *28*, 89–115.

Théro, H., Rivot, E., Robert, M., Guitton, J., Kopp, D., & Gascuel, D. (2020). *EcoDiet. R package version 1.0.0.0.* [R]. 10.5281/zenodo.4081537

Thompson, D., Furness, R., & Lewis, S. (1995). Diets and long term changes in δ15N and δ13C values in Northern Fulmar Fulmarus glacialis from two northeast Atlantic colonies. *Marine Ecology Progress Series*, *125*, 3–11.

Tilstone, G. H., Pardo, S., Dall'Olmo, G., Brewin, R. J. W., Nencioli, F., Dessailly, D., Kwiatkowska, E., Casal, T., & Donlon, C. (2021). Performance of Ocean Colour Chlorophyll a algorithms for Sentinel-3 OLCI, MODIS-Aqua and Suomi-VIIRS in open-ocean waters of the Atlantic. *Remote Sensing of Environment*, *260*, 112444. https://doi.org/10.1016/j.rse.2021.112444

Tilstone, G., Mallor-Hoya, S., Gohin, F., Couto, A. B., Sá, C., Goela, P., Cristina, S., Airs, R., Icely, J., Zühlke, M., & others. (2017). Which ocean colour algorithm for MERIS in North West European waters? *Remote Sensing of Environment*, *189*, 132–151.

Toming, K., Kutser, T., Uiboupin, R., Arikas, A., Vahter, K., & Paavel, B. (2017). Mapping Water Quality Parameters with Sentinel-3 Ocean and Land Colour Instrument imagery in the Baltic Sea. *Remote Sensing*, *9*(10), 1070. https://doi.org/10.3390/rs9101070

Trenkel, V., Pinnegar, J., Dawson, W., du Buit, M., & Tidd, A. (2005). Spatial and temporal structure of predator-prey relationships in the Celtic Sea fish community. *Marine Ecology Progress Series*, *299*, 257–268. https://doi.org/10.3354/meps299257

Trites, A. W., Christensen, V., & Pauly', D. (1997). Competition Between Fisheries and Marine Mammals for Prey and Primary Production in the Pacific Ocean. In *J. Northw. Atl. Fish. Sci* (Vol. 22, pp. 173–187).

Tsou, T. S., & Collie, J. S. (2001). Predation-mediated recruitment in the Georges Bank fish community. *ICES Journal of Marine Science*, *58*(5), 994–1001. https://doi.org/10.1006/jmsc.2001.1088

Tudela, S., & Palomera, I. (1997). Trophic ecology of European anchovy Engraulis encrasicolus in the Catalan Sea (Northwest Mediterranean. *Marine Ecology Progress Series*, *160*, 121–134.

Ulanovicz, R. E., & Puccia, C. J. (1990). Mixed trophic impacts in ecosystems. *Coenoses*, *5*, 7–16.

Uncles, R. J. (2010). Physical properties and processes in the Bristol Channel and Severn Estuary. *Marine Pollution Bulletin*, *61*(1), 5–20. https://doi.org/10.1016/j.marpolbul.2009.12.010

Utne, K. R., Huse, G., Ottersen, G., Holst, J. C., Zabavnikov, V., Jacobsen, J. A., Óskarsson, G. J., & Nøttestad, L. (2012). Horizontal distribution and overlap of planktivorous fish stocks in the Norwegian Sea during summers 1995–2006. *Marine Biology Research*, *8*(5–6), 420–441. https://doi.org/10.1080/17451000.2011.640937

Valdes, E. S., Shelton, P. A., Armstrong, M. J., & Field, J. G. (1987). Cannibalism in South African anchovy: Egg mortality and egg consumption rates. *South African Journal of Marine Science*, *5*, 613–622.

van der Kooij, J., Fässler, S. M. M., Stephens, D., Readdy, L., Scott, B. E., & Roel, B. A. (2015). Opportunistically recorded acoustic data support Northeast Atlantic mackerel expansion theory. *ICES Journal of Marine Science*, *73*(4), 1115–1126. https://doi.org/10.1093/icesjms/fsv243

van der Lingen, C. D., Bertrand, A., Bode, A., Brodeur, R., Cubillos, L. A., Espinoza, P., Friedland, K., Garrido, S., Irigoien, X., Miller, T., Möllmann, C., Tanaka, H., & Temming, A. (2009). Trophic dynamics. In *Climate Change and Small Pelagic Fish* (pp. 112–157). Cambridge University Press. https://doi.org/10.1017/CBO9780511596681.009

Van Der Lingen, C. D., Hutchings, L., & Field, J. G. (2006). Comparative trophodynamics of anchovy Engraulis encrasicolus and sardine Sardinops sagax in the southern Benguela: Are species alternations between small pelagic fish trophodynamically mediated? In *African Journal of Marine Science* (Vol. 28, Issues 3–4, pp. 465–477). National Inquiry Services Centre Ltd. https://doi.org/10.2989/18142320609504199

Van Ginderdeuren, K., Vandendriessche, S., Prössler, Y., Matola, H., Vincx, M., & Hostens, K. (2013). Selective feeding by pelagic fish in the Belgian part of the North Sea. *ICES Journal of Marine Science*, *71*(4), 808–820. https://doi.org/10.1093/icesjms/fst183

van Heukelem, C. S., L. ,. Thomas. (2005). *In. Hooker S.B. et al. Second SeaWiFS HPLC analysis round-robin experiment (SeaHARRE-2)*. National Aeronautics and Space Administration, Goddard Space Flight Center.

van Rossum, G., & Drake, F. L. (2009). *Python 3 Reference Manual* (3.8) [Computer software]. CreateSpace.

Verity, P. G., & Smetacek, V. (1996). Organism life cycles, predation, and the structure of marine pelagic ecosystems. *Marine Ecology Progress Series*, *130*, 277–293.

Volkenandt, M., O’Connor, I., Guarini, J.-M., Berrow, S., & O’Donnell, C. (2016). Fine-scale spatial association between baleen whales and forage fish in the Celtic Sea. *Canadian Journal of Fisheries and Aquatic Sciences*, *73*(2), 197–204. https://doi.org/10.1139/cjfas-2015-0073

Voss, R., Dickmann, M., & Schmidt, J. O. (2009). Feeding ecology of sprat (*Sprattus sprattus* L.) and sardine (*Sardina pilchardus* W.) larvae in the German Bight, North Sea. *Oceanologia*, *51*(1), 117–138.

Votier, S. C., Furness, R. W., Bearhop, S., Crane, J. E., Caldow, R. W. G., Catry, P., Ensor, K., Hamer, K. C., Hudson, A. V., Kalmbach, E., Klomp, N. I., Pfeiffer, S., Phillips, R. A., Prieto, I., & Thompson, D. R. (2004). Changes in fisheries discards rates and seabird communities. *Nature*, *427*, 727–730.

Wallace, P. D., & Pleasants, C. A. (1972). The distribution of eggs and larvae of some pelagic fish species in the English Channel and adjacent waters in 1967 and 1968. In *ICES CM1972/J:8*.

Walter, J. F., & Austin, H. M. (2003). Diet composition of large striped bass (Morone saxatilis) in Chesapeake Bay. *Fishery Bulletin*, *101*, 414–423.

Walters, C., Christensen, V., & Pauly, D. (1997). Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. *Reviews in Fish Biology and Fisheries*, *7*(2), 139–172. https://doi.org/10.1023/A:1018479526149

Walters, C., Pauly, D., & Christensen, V. (1999). Ecospace: Prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. *Ecosystems*, *2*(6), 539–554. https://doi.org/10.1007/s100219900101

Wang, M. (2007). Remote sensing of the ocean contributions from ultraviolet to near-infrared using the shortwave infrared bands: Simulations. *Applied Optics*, *46*(9), 1535–1547.

Wang, Y., Li, S. Y., Duan, L. J., & Liu, Y. (2012). Fishery policy exploration in the Pearl River Estuary based on an Ecosim model. *Ecological Modelling*, *230*, 34–43.

Wanless, S., Harris, M. P., Redman, P., & Speakman, J. R. (2005). Low energy values of fish as a probable cause of a major seabird breeding failure in the North Sea. *Marine Ecology Progress Series*, *294*, 1–8.

Ware, D. (2000). *Aquatic ecosystems: Properties and models* (P. T. Harrison PJ, Ed.; 2nd ed.). Blackwell Science, Oxford.

Ware, D., & Thomson, R. (2005). Bottom-up ecosystem trophic dynamics determine fish production in the northeast pacific. *Science*, *308*(5726), 1280–1284. https://doi.org/10.1126/science.1109049

Welschmeyer, N. A. (1994). Fluorometric Analysis of Chlorophyll a in the Presence of Chlorophyll B and Pheopigments. *Limnol. Oceanogr*, *39*(8), 1985–1992. https://doi.org/10.4319/lo.1994.39.8.1985

Werdell, P. J., & Bailey, S. W. (2005). An improved in-situ bio-optical data set for ocean color algorithm development and satellite data product validation. *Remote Sensing of Environment*, *98*(1), 122–140.

Wernand, M. R., van der Woerd, H. J., & Gieskes, W. W. (2013). Trends in ocean colour and chlorophyll concentration from 1889 to 2000, worldwide. *PLOS One*, *8*(6), e63766.

Whitehead, P. J. P. (1985). FAO Species Catalogue. *FAO Fish. Synop*, *7*(7/1), 1–303.

Widdicombe, C. E., Eloire, D., Harbour, D., Harris, R. P., & Somerfield, P. J. (2010). Long-term phytoplankton community dynamics in the Western English Channel. *Journal of Plankton Research*, *32*(5), 643–655. https://doi.org/10.1093/plankt/fbp127

Więcaszek, B., Sobecka, E., Keszka, S., Stepanowska, K., Dudko, S., Biernaczyk, M., & Wrzecionkowski, K. (2015). Studies on endangered and rare non-commercial fish species recorded in the Pomeranian Bay (southern Baltic Sea) in 2010–2013. *Helgoland Marine Research*, *69*, 411–416.

Wilson, C. J., Murphy, H. M., Bourne, C., Pepin, P., & Robert, D. (2018). Feeding ecology of autumn-spawned Atlantic herring (Clupea harengus) larvae in Trinity Bay, Newfoundland: Is recruitment linked to main prey availability? *Journal of Plankton Research*, *40*(3), 255–268. https://doi.org/10.1093/plankt/fby003

Winberg, G. G. (1956). *Rate of Metabolism and Food Requirements of Fishes: New Information on Metabolic Rate in Fishes*. Fisheries Research Board of Canada.

Winemiller, K. O. (1990). Spatial and temporal variation in tropical fish trophic networks. *Ecol Monogr*, *60*(331).

Wolda, H. (1981). Similarity Indices, Sample Size and Diversity. *Oecologia*, *50*(3), 296–302.

Wright, S. W., & Jeffrey, S. W. (2006). Pigment Markers for Phytoplankton Production. In J. K. Volkman (Ed.), *Marine Organic Matter: Biomarkers, Isotopes and DNA* (pp. 71–104). Springer. https://doi.org/10.1007/698_2_003

Wynn, R. B., & Yésou, P. (2007). The changing status of Balearic Shearwater in northwest European waters. *British Birds*, *100*, 392–406.

Young, I. R., Zieger, S., & Babanin, A. V. (2011). Global trends in wind speed and wave height. *Science*, *332*(6028), 451–455. https://doi.org/10.1126/science.1197219

Zhang, J. (2016). *spaa: SPecies Association Analysis*. https://CRAN.R-project.org/package=spaa

Zhang, M., Tang, J., Dong, Q., Song, Q., & Ding, J. (2010). Retrieval of total suspended matter concentration in the Yellow and East China Seas from MODIS imagery. *Remote Sensing of Environment*, *114*(2), 392–403. https://doi.org/10.1016/j.rse.2009.09.016

Zieger, S., Vinoth, J., & Young, I. R. (2009). Joint Calibration of Multiplatform Altimeter Measurements of Wind Speed and Wave Height over the Past 20 Years. *Journal of Atmospheric and Oceanic Technology*, *26*(12), 2549–2564. https://doi.org/10.1175/2009JTECHA1303.1

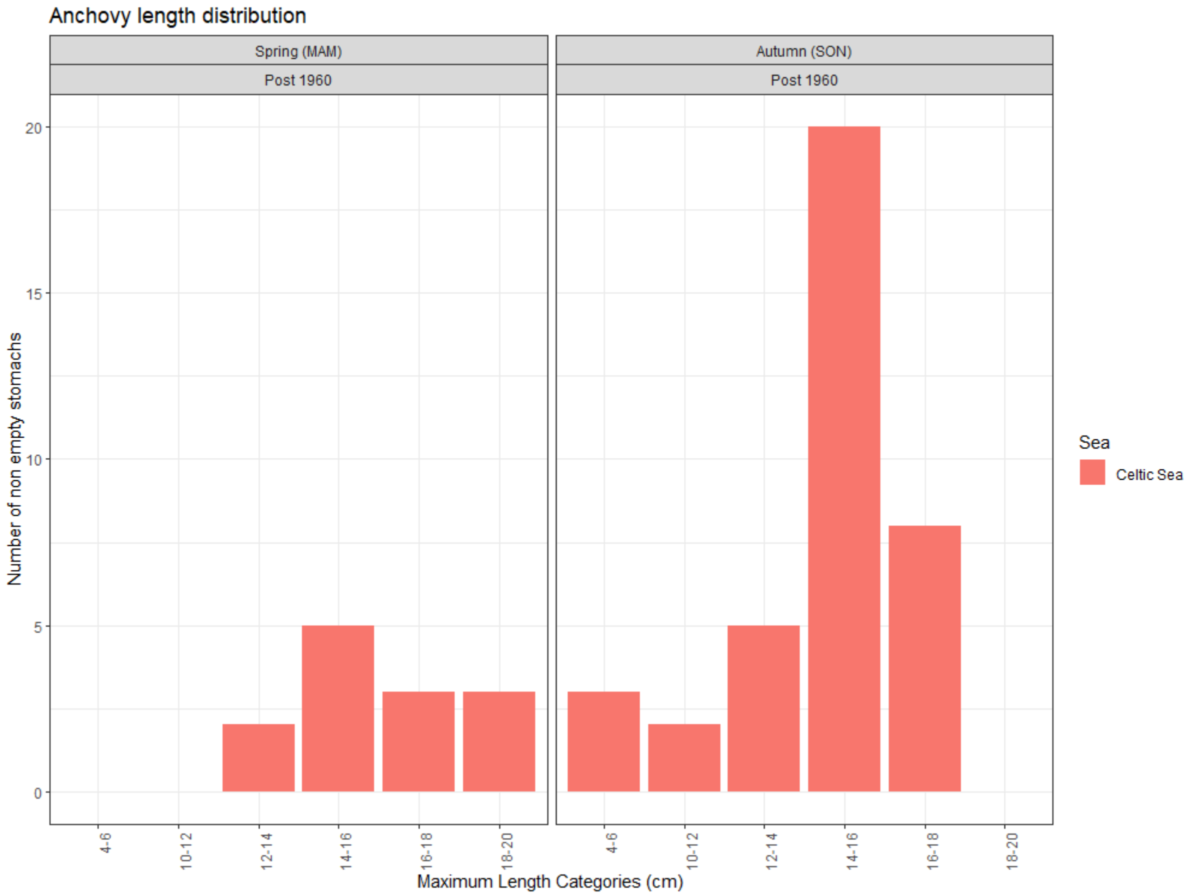
Appendices

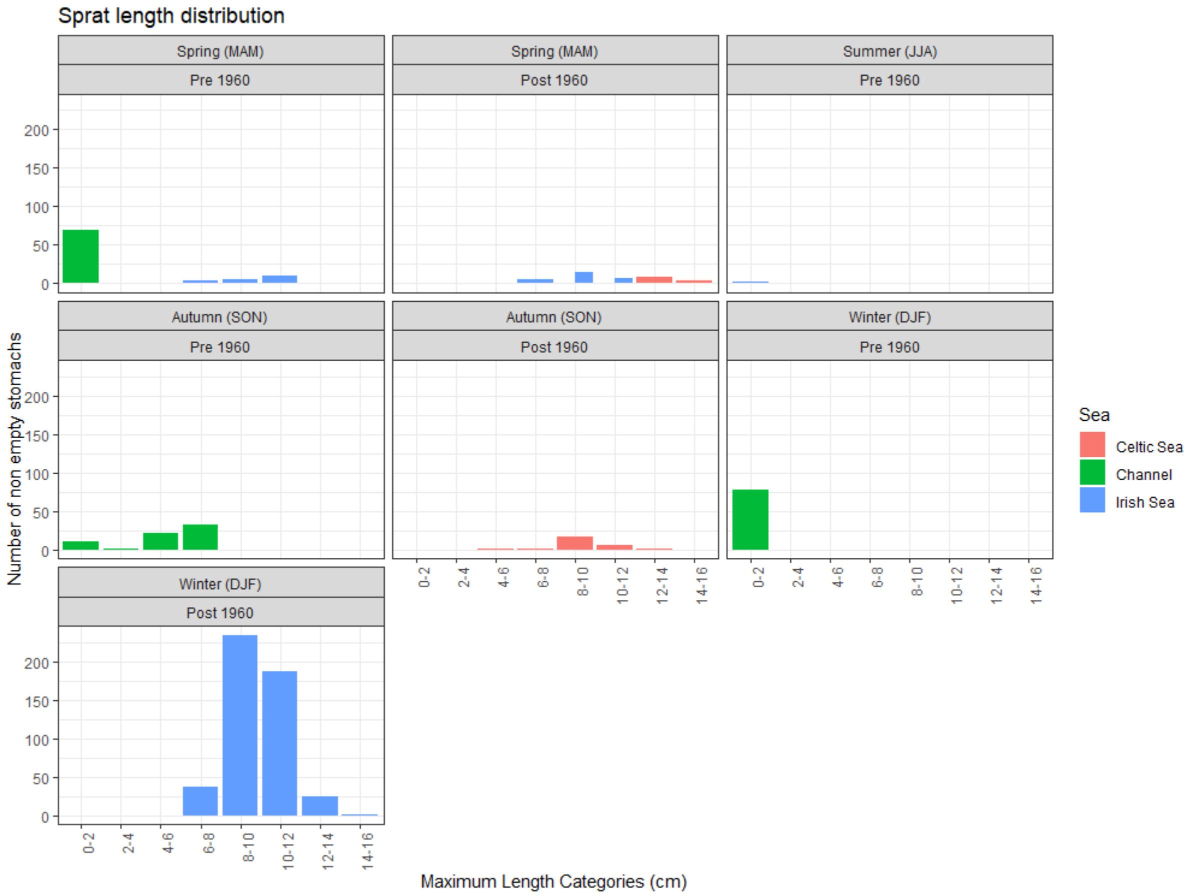
Appendix A

Table A 1 - Empty stomach by season and species in the Celtic Seas ecoregion. Seasons were defined by Spring (March – May); Summer (June – August); Autumn (September – October); December (December – February).

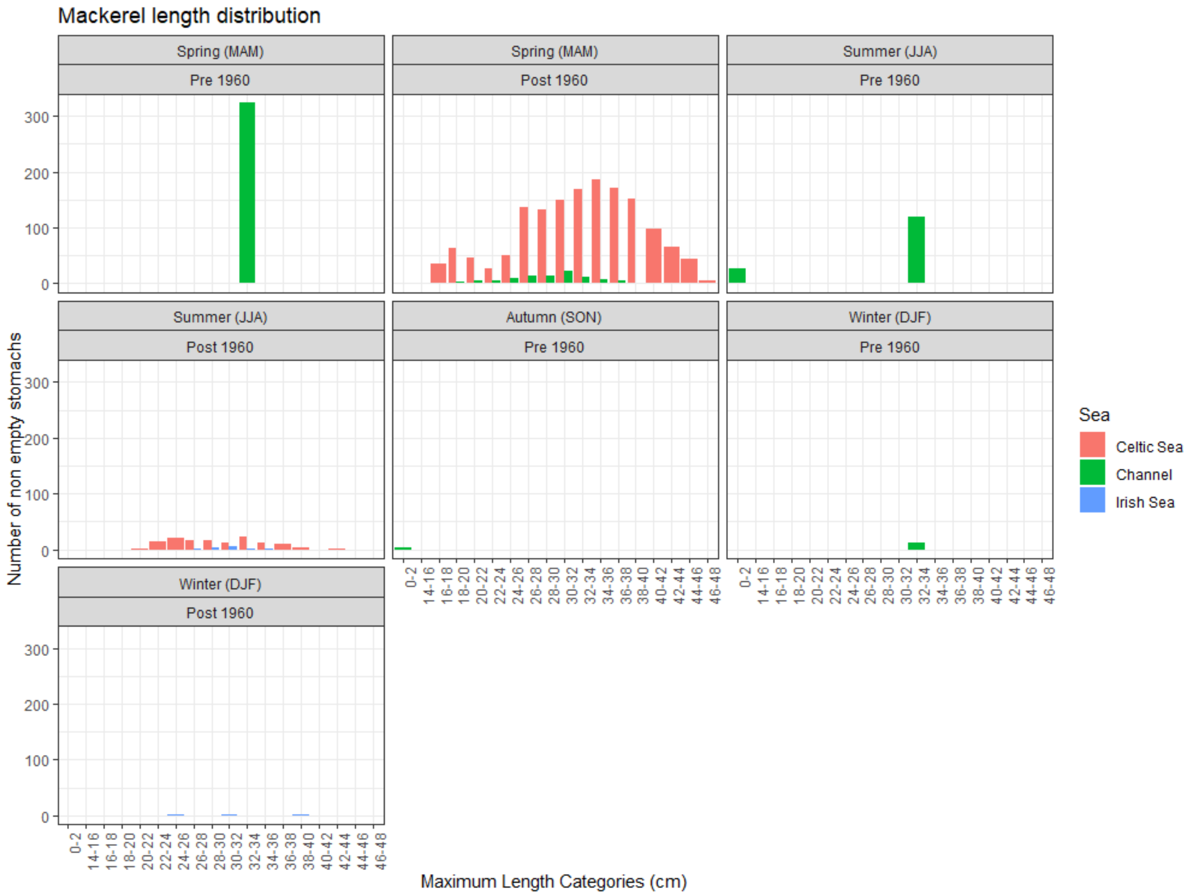
Species	**Spring (MAM)**	**Summer (JJA)**	**Autumn (SON)**	**Winter (DJF)**	**Unknown**
Anchovy	7		2		
Herring	31	0	197	676	
Herring larvae	49		17	1393	0
Horse mackerel	364		2	17	2
Horse mackerel larvae		0	0		18
Mackerel	804	2		0	
Mackerel larvae		5	0		70
Sardine	37	0	0		
Sardine larvae		104	11		230
Sprat	36	1	4	518	
Sprat larvae	114	12	6	59	6

Figure A 1 - Length distribution of species binned in 2cm groups. Seasons were defined by Spring (March – May); Summer (June – August); Autumn (September – October); December (December – February). NA represents unknown season.


Anchovy length distribution
Spring (MAM)
Post 1960
Autumn (SON)
Post 1960
Number of non empty stomachs
0
5
10
15
20
4-6
10-12
12-14
14-16
16-18
18-20
Maximum Length Categories (cm)
Sea
Celtic Sea


Sprat length distribution
Spring (MAM)
Pre 1960
Spring (MAM)
Post 1960
Summer (JJA)
Pre 1960
Autumn (SON)
Pre 1960
Autumn (SON)
Post 1960
Winter (DJF)
Pre 1960
Winter (DJF)
Post 1960
Number of non empty stomachs
0
50
100
150
200
0-2
2-4
4-6
6-8
8-10
10-12
12-14
14-16
Maximum Length Categories (cm)
Sea
🟥 Celtic Sea
🟩 Channel
🟦 Irish Sea


Sardine length distribution
Spring (MAM)
Post 1960
Summer (JJA)
Pre 1960
Autumn (SON)
Pre 1960
Autumn (SON)
Post 1960
Number of non empty stomachs
0
25
50
75
100
2-4
6-8
8-10
10-12
12-14
14-16
16-18
18-20
20-22
22-24
24-26
Maximum Length Categories (cm)
Sea
🟥 Celtic Sea
🟦 Channel


Mackerel length distribution
Spring (MAM)
Pre 1960
Spring (MAM)
Post 1960
Summer (JJA)
Pre 1960
Summer (JJA)
Post 1960
Autumn (SON)
Pre 1960
Winter (DJF)
Pre 1960
Winter (DJF)
Post 1960
0
100
200
300
0-2
14-16
16-18
18-20
20-22
22-24
24-26
26-28
28-30
30-32
32-34
34-36
36-38
38-40
40-42
42-44
44-46
46-48
Number of non empty stomachs
Maximum Length Categories (cm)
Sea
Celtic Sea
Channel
Irish Sea


Horse mackerel length distribution
Spring (MAM)
Post 1960
Summer (JJA)
Pre 1960
Autumn (SON)
Pre 1960
Autumn (SON)
Post 1960
Winter (DJF)
Post 1960
0
5
10
15
0-2
2-4
4-6
6-8
8-10
10-12
12-14
14-16
16-18
18-20
20-22
22-24
24-26
26-28
28-30
30-32
32-34
34-36
Number of non empty stomachs
Maximum Length Categories (cm)
Sea
Celtic Sea
Channel
Irish Sea

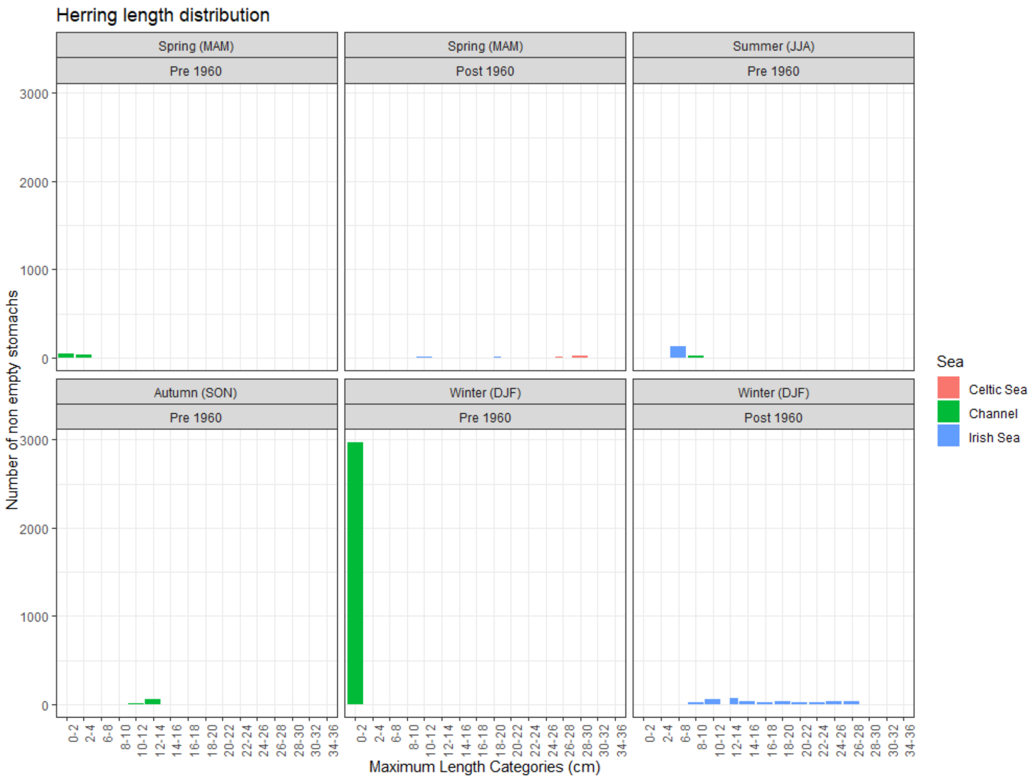


Figure A 2 - Length distribution of non-empty stomachs split by sea and season and pre-, post-1960. Seasons were defined by Spring (March – May); Summer (June – August); Autumn (September – October); December (December – February).

Table A 2 - Trophic levels assigned to each prey group.

Prey Group	Trophic Level	Reference/Justification
Amphipod	3	Hyperiidae - Lebour (1922) & Kaestner (1967)
Appendicularia	2.1	Based on the table from Jiming (1982) - Davis (1955)
Bivalve	2.1	Mollusca taken from Cortes (1999)
Chaetognath	3.5	Based on Sagitta from Jiming (1982) - Lebour (1922), Lebour (1924)
Cirripedes	2.1	Based on Barnacle nauplii from Jiming (1982) - Raymont (1963)
Cladocera	2.1	Based on the table from Jiming (1982) - Raymont (1963)
Copepod - Calanoida	2.22	Averaged from Jiming (1982) - Lebour (1922), Raymont (1963), Marshall & Orr (1972), Kaestner (1967)
Copepod - Cyclopoida	2.1	Based on Oithona sp from Jiming (1982) - Lebour (1922)

Copepod - Harpacticoida	2.1	Based on diet from Buffan-Dubau (1996), a particular species of harpacticoids eat purple phototrophic bacteria and phytoplankton (diatoms). Some species however do not just eat primary producers hence the justification for 2.1
Copepod eggs	1.5	Estimated - lower than copepod nauplii
Copepod nauplii	2	Estimated - lower than copepod (adult stage)
Crab	2.52	Decapod crustaceans - Taken from Cortes (1999)
Crustacean	2.52	Decapod crustaceans - Taken from Cortes (1999)
Diatoms	1	Assumed
Dinoflagellates	1	Assumed
Euphausid	2.2	Cortes (1999)
Gastropod	2.1	Mollusca taken from Cortes (1999)
Mollusc larvae	2.1	Mollusca taken from Cortes (1999)
Mysid	2.4	Based on the table from Jiming (1982) - Raymont (1963)
Phytoplankton other	1	Assumed
Shrimp	2.52	Decapod crustaceans - Taken from Cortes (1999)
Teleost	3.5	Pauly et al. (2000)
Teleost eggs	3.5	Pauly et al. (2000)
Teleost larvae	3.5	Pauly et al. (2000)
Tintinnid	2	Calculated from Karayanni et al. (2005), as they just eat primary producers and bacteria

References

Buffan-Dubau E, de Wit R, Castel J, (1996). Feeding selectivity of the harpacticoid copepod *Canuella perplexa* in benthic muddy environments demonstrated by HPLC analyses of chlorin and carotenoid pigments. Marine Ecology Progress Series, 137, pp.71-82

Cortés E (1999) Standardized diet compositions and trophic levels of sharks. – ICES Journal of Marine Science, 56: 707–717

Davis CC (1955) The marine and freshwater plankton, Michigan State University Press, East Lansing, Michigan

Jiming Y (1982). A tentative analysis of the trophic levels of North Sea fish. Mar. Ecol. Prog. Ser, 7, pp.247-252

Kaestner A (1967) Invertebrate zoology, Vol. 1, Interscience Publishers, New York

Karayanni H, Christaki U, Van Wambeke F, Denis M, Moutin T (2005) Influence of ciliated protozoa and heterotrophic nanoflagellates on the fate of primary production in the northeast Atlantic Ocean. Journal of Geophysical Research: Oceans, 110(C7)

Lebour MV (1922) The food of plankton organisms. J. mar. biol. Ass. U. K. 12: 644-677

Lebour MV (1924) The food of plankton organisms, II. J. mar. biol. Ass. U. K. 13: 70-92

Marshall SM, Orr AP (1972) The biology of a marine copepod, Springer-Verlag, Berli

Pauly D, Froese R, Sa-a P, Palomares ML, Christensen V, Rius J (2000) TrophLab manual. ICLARM, Los Baños, Laguna, Philippines

Raymont JG (1963) Plankton and productivity in the oceans, Pergamon Press, Oxford

Table A 3 - Size ranges of prey lengths used for Predator Prey Selection Ration (PPSR). Where a size range present the mid point of the size range is taken.

Prey Group	Size range	Reference
Amphipod	0.858 cm	DAPSTOM; Pinnegar (2014)
Appendicularia	5 mm (max. length)	Conway (2015) Page 230
Bivalve	0.05-0.2 mm	Peltic 2019; this study
Chaetognath	0.6 - 1.2 cm	DAPSTOM; Pinnegar (2014)
Cirripedes	380-870 µm	Walczyńska et al. (2019)

Cladocera	0.3-1.4 mm	Conway (2012b) Pages 13-16
Copepod - Calanoida	3 mm	Peltic 2019; this study
Copepod - Cyclopoida	0.5–1.5 mm	Peltic 2019; this study
Copepod - Harpacticoida	0.33 - 1.97 mm	Conway (2012b) Pages 120-131
Copepod eggs	0.05-0.08 mm	Conway (2012b) Page 40
Copepod nauplii	0.21-0.61 mm	Conway (2012b) Page 46
Crustacean	0.25-2 cm	DAPSTOM; Pinnegar (2014)
Diatoms	20-200 µm	Omori & Ikeda (1992)
Dinoflagellates	20 -350 µm	Sarjeant (1979)
Euphausid	1.43 cm	Peltic 2019; this study
Gastropod	0.16-0.8 mm	Peltic 2019; this study
Mollusc larvae	0.07 - 1 mm	Conway (2012a) Pages 118-119
Mysid	1.75cm	DAPSTOM; Pinnegar (2014)
Phytoplankton other	2- 20 microns	Finkel et al. (2010)
Shrimp	0.5-9cm	DAPSTOM; Pinnegar (2014)
Teleost	1.96cm	DAPSTOM; Pinnegar (2014)
Teleost eggs	0.91 - 1.7 mm	Conway (2015) Page 251
Teleost larvae	7.2 - 30 mm	Conway (2015) Pages 252-253
Tintinnid	0.02-0.2 mm	Conway. (2012a) Page 18

References

Conway DVP (2012a) Marine zooplankton of southern Britain. Part 1: Radiolaria, Heliozoa, Foraminifera, Ciliophora, Cnidaria, Ctenophora, Platyhelminthes, Nemertea, Rotifera and Mollusca. A.W.G. John (ed.). Occasional Publications. Marine Biological Association of the United Kingdom, No. 25, Plymouth, United Kingdom, 138 pp.

Conway DVP (2012b) Marine zooplankton of southern Britain. Part 2: Arachnida, Pycnogonida, Cladocera, Facetotecta, Cirripedia and Copepoda (ed. A.W.G. John).

Occasional Publications. Marine Biological Association of the United Kingdom, No 26 Plymouth, United Kingdom 163 pp.

Conway DVP (2015) Marine zooplankton of southern Britain. Part 3: Ostracoda, Stomatopoda, Nebaliacea, Mysida, Amphipoda, Isopoda, Cumacea, Euphausiacea, Decapoda, Annelida, Tardigrada, Nematoda, Phoronida, Bryozoa, Entoprocta, Brachiopoda, Echinodermata, Chaetognatha, Hemichordata and Chordata. A.W.G. John (ed.). Occasional Publications. Marine Biological Association of the United Kingdom, No. 27, Plymouth, United Kingdom, 271 pp.

Finkel ZV, Beardall J, Flynn KJ, Quigg, A, Rees TAV, Raven JA (2010) Phytoplankton in a changing world: cell size and elemental stoichiometry. Journal of plankton research, 32(1), pp.119-137.

Omori M, Ikeda T (1992) Methods in Marine Zooplankton Ecology. Malabar, USA: Krieger Publishing Company. ISBN 978-0-89464-653-9

Pinnegar JK (2014) DAPSTOM - An Integrated Database & Portal for Fish Stomach Records. Version 4.7. Centre for Environment, Fisheries & Aquaculture Science, Lowestoft, UK. February 2014, 39pp

Sarjeant WAS (1979) Dinoflagellates . In: Paleontology. Encyclopedia of Earth Science. Springer, Berlin, Heidelberg. https://doi.org/10.1007/3-540-31078-9_48

Walczyńska KS, Søreide, JE, Weydmann-Zwolicka A, Ronowicz M, Gabrielsen TM (2019) DNA barcoding of Cirripedia larvae reveals new knowledge on their biology in Arctic coastal ecosystems. Hydrobiologia, 837(1), pp.149-159

Table A 4 - Frequency of abundance (F%) and occurrence (O%) of six pelagic species in Celtic Sea ecoregion. TL = Total length of fish species, ±- standard deviation (SD). n = number of prey items within in each stomach. Seasons were defined by Spring (March – May); Summer (June – August); Autumn (September – October); December (December – February).

Species/Prey Group	Spring (MAM)				Summer (JJA)				Autumn (SON)				Winter (DJF)			
	TL ±SD	n	F%	O%	TL ±SD	n	F%	O%	TL ±SD	n	F%	O%	TL ±SD	n	F%	O%
Herring	21.81 ± 7.48				7.87 ± 0.32				19.68 ± 5.53				17.25 +/- 5.80			
Copepod - Calanoida		404.00	38.51	25.32		20.82	80.52	100.00		69.25	95.49	64.20		120.00	17.83	19.19
Copepod - Harpacticoida		-	-	-		3.22	12.46	100.00		-	-	-		-	-	
Crustacean		-	-	-		0.80	3.09	12.99		-	-	-		144.00	21.40	20.20
Euphausiid		76.00	7.24	69.62		-	-			-	-	-		258.00	38.34	48.99
Mysid		-	-	-		1.01	3.92	87.01		3.27	4.51	38.27		-	-	
Teleost eggs		569.00	54.24	8.86		-	-	-		-	-	-		151.00	22.44	19.19
Herring larvae	1.97 ± 0.12												0.98 ± 0.07			
Bivalve		1.00	16.17	1.18		-	-	-		-	-	-		12.36	7.02	43.55
Cirripedes		1.00	16.17	1.18		-	-	-		-	-	-		-	-	
Copepod - Calanoida		3.18	51.48	98.82		-	-	-		-	-	-		53.00	30.10	52.51
Copepod eggs		1.00	16.17	1.18		-	-	-		-	-	-		26.00	14.77	1.62
Mollusc larvae		-	-	-		-	-	-		-	-	-		39.00	22.15	6.57
Phytoplankton other		-	-	-		-	-	-		-	-	-		45.71	25.96	37.11
Anchovy	16.42 ± 2.11								14.68 ±3.04							
Amphipod		4.00	18.18	33.33		-	-	-		-	-	-		-	-	-
Copepod - Calanoida		4.00	18.18	33.33		-	-	-		141.00	56.85	73.53		-	-	-
Copepod - Cyclopoida		-	-	-		-	-	-		24.00	9.68	17.65		-	-	-
Crustacean		1.00	4.55	8.33		-	-	-		56.00	22.58	23.53		-	-	-
Diatoms		-	-	-		-	-	-		27.00	10.89	11.76		-	-	-
Euphausid		2.00	9.09	16.67		-	-	-		12.00	4.84	5.88		-	-	-
Shrimp		11.00	50.00	58.33		-	-	-		-	-	-		-	-	-

Sardine	21.93 ±2.21				23.7 ± 0.00				11.12 ± 3.77			-				
Amphipod		3.00	33.33	60.00		-	-	-		-	-	-		-	-	-
Bivalve		-	-	-		-	-	-		30.00	3.69	39.34		-	-	-
Copepod - Calanoida		3.00	33.33	60.00		13020.00	41.33	99.06		623.00	76.54	63.93		-	-	-
Crustacean		-	-	-		1191.00	3.78	36.79		-	-	-		-	-	-
Diatoms		-	-	-		15795.00	50.13	47.17		111.00	13.64	50.82		-	-	-
Dinoflagellates		-	-	-		-	-	-		50.00	6.14	45.90		-	-	-
Gastropod		1.00	11.11	20.00		-	-	-		-	-	-		-	-	-
Phytoplankton other		2.00	22.22	40.00		1500.00	4.76	2.83		-	-	-		-	-	-
Sardine larvae					2.39 +/- 0.00							-				
Copepod eggs	-	-	-	-		2.00	100.00	100.00		-	-	-		-	-	-
Mackerel	32.86 ± 6.17				31.80 ±3.64							-	33.3 ±2.69			
Appendicularia		853.83	11.42	9.24		-	-	-		-	-	-		18.33	28.57	85.71
Chaetognath		359.17	4.80	8.80		-	-	-		-	-	-		-	-	-
Copepod - Calanoida		3926.48	52.53	68.55		2220.83	85.05	76.11		-	-	-		4.50	7.01	85.71
Copepod nauplii		453.50	6.07	18.04		135.17	5.18	31.86		-	-	-		-	-	-
Phytoplankton other		1159.83	15.52	21.11		-	-	-		-	-	-		33.33	51.95	85.71
Teleost		-	-	-		-	-	-		-	-	-		8.00	12.47	14.29
Teleost eggs		361.52	4.84	20.82		170.00	6.51	20.35		-	-	-		-	-	-
Teleost larvae		360.74	4.83	8.43		85.17	3.26	7.96		-	-	-		-	-	-
Mackerel larvae					0.59 +/- 0.19							-				
Cladocera		-	-	-		2.00	12.63	7.41		-	-	-		-	-	-
Copepod - Calanoida		-	-	-		3.25	20.53	74.07		-	-	-		-	-	-
Copepod nauplii		-	-	-		3.17	20.00	3.70		-	-	-		-	-	-
Copepod eggs		-	-	-		6.00	37.89	33.33		-	-	-		-	-	-
Phytoplankton other		-	-	-		1.42	8.95	44.44		-	-	-		-	-	-
Sprat	10.26 ±2.01								7.02			-	10.08			
Copepod - Calanoida		424.00	71.86	77.78		-	-	-		538.00	16.12	49.37		13427.00	28.32	65.23
Copepod - Cyclopoida		-	-	-		-	-	-		2800.00	83.88	12.66		-	-	-

Copepod eggs		71.00	12.03	2.22		-	-	-		-	-	-		-	-	-
Diatoms		95.00	16.10	2.22		-	-	-		-	-	-		-	-	-
Teleost eggs		-	-	-		-	-	-		-	-	-		33983.00	71.68	93.80
Sprat larvae	0.58								0.85 ±2.18				0.48 ±1.40			
Bivalve		-	-	-		-	-	-		-	-	-		1.00	14.41	1.30
Copepod - Calanoida		1.20	12.50	8.57		-	-	-		1.14	25.81	72.73		-	-	-
Copepod - Harpacticoida		1.00	10.42	1.43		-	-	-		-	-	-		-	-	-
Copepod eggs		1.00	10.42	1.43		-	-	-		-	-	-		-	-	-
Diatoms		-	-	-		-	-	-		1.14	25.81	72.73		-	-	-
Phytoplankton other		6.40	66.66	90.00		-	-	-		1.14	25.81	72.73		5.94	85.59	93.51
Tintinnid		-	-	-		-	-	-		1.00	22.58	9.09		-	-	-
Horse mackerel	25.93 +/- 6.46								7.5 +/- 3.25			-				
Copepod - Calanoida		1028.00	79.38	30.77		-	-	-		343.00	70.87	76.19		-	-	-
Copepod - Cyclopoida		-	-	-		-	-	-		45.00	9.30	14.29		-	-	-
Crustacean		-	-	-		-	-	-		78.00	16.12	23.81		-	-	-
Euphausid		267.00	20.62	52.75		-	-	-		18.00	3.72	33.33		-	-	-
Horse mackerel larvae					1.28 +/- 0.27				2.87 +/- 0.71			-				
Cladocera		-	-	-		2.33	15.56	66.67		-	-	-		-	-	-
Copepod - Calanoida		-	-	-		5.67	37.78	100.00		7.00	58.33	85.71		-	-	-
Copepod - Cyclopoida		-	-	-		3.33	22.22	66.67		-	-	-		-	-	-
Crustacean		-	-	-		-	-			2.00	16.67	14.29		-	-	-
Diatoms		-	-	-		3.67	24.44	66.67		-	-	-		-	-	-
Euphausid		-	-	-		-	-	-		3.00	25.00	14.29		-	-	-

Table A 5 - Pairwise Pianka Index bootstrapped with 1000 iterations, 95% confidence interval, and calculated normalised spread across seasons.

Season	Species Pair	Pianka Index	Boot CI1	Boot CI2	Iterations	Spread	Normalised Spread
Spring	Anchovy-Herring	0.2	0	0.943	1000	0.943	471.500
Spring	Anchovy-Herring larvae	0.28	0	0.864	1000	0.864	308.571
Spring	Anchovy-Horse mackerel	0.348	0.123	0.985	1000	0.862	247.701
Spring	Anchovy-Mackerel	0.294	0	0.9	1000	0.9	306.122
Spring	Anchovy-Sardine	0.398	0	0.96	1000	0.96	241.206
Spring	Anchovy-Sprat	0.306	0	0.906	1000	0.906	296.078
Spring	Anchovy-Sprat larvae	0.057	0	0.635	1000	0.635	1114.035
Spring	Herring larvae-Horse mackerel	0.85	0	0.984	1000	0.984	115.765
Spring	Herring larvae-Mackerel	0.811	0	0.954	1000	0.954	117.633
Spring	Herring larvae-Sardine	0.549	0	0.908	1000	0.908	165.392
Spring	Herring larvae-Sprat	0.89	0	0.99	1000	0.99	111.236
Spring	Herring larvae-Sprat larvae	0.2	0	0.951	1000	0.951	475.500
Spring	Herring-Herring larvae	0.506	0	0.96	1000	0.96	189.723
Spring	Herring-Horse mackerel	0.584	0.094	1	1000	0.906	155.137
Spring	Herring-Mackerel	0.6	0	0.977	1000	0.977	162.833
Spring	Herring-Sardine	0.36	0	0.905	1000	0.905	251.389
Spring	Herring-Sprat	0.554	0	0.987	1000	0.987	178.159
Spring	Herring-Sprat larvae	0.104	0	0.768	1000	0.768	738.462
Spring	Horse mackerel-Mackerel	0.894	0	0.985	1000	0.985	110.179
Spring	Horse mackerel-Sardine	0.605	0	0.968	1000	0.968	160.000
Spring	Horse mackerel-Sprat	0.932	0	1	1000	1	107.296
Spring	Horse mackerel-Sprat larvae	0.174	0	0.905	1000	0.905	520.115
Spring	Mackerel-Sardine	0.691	0	0.966	1000	0.966	139.797
Spring	Mackerel-Sprat	0.889	0	0.98	1000	0.98	110.236
Spring	Mackerel-Sprat larvae	0.428	0	0.938	1000	0.938	219.159
Spring	Sardine-Sprat	0.602	0	0.963	1000	0.963	159.967
Spring	Sardine-Sprat larvae	0.513	0	0.974	1000	0.974	189.864
Spring	Sprat-Sprat larvae	0.198	0	0.953	1000	0.953	481.313
Summer	Herring-Horse mackerel larvae	0.709	0	0.978	1000	0.978	137.941
Summer	Herring-Mackerel	0.981	0	0.998	1000	0.998	101.733
Summer	Herring-Mackerel larvae	0.405	0	0.903	1000	0.903	222.963
Summer	Herring-Sardine	0.627	0	0.997	1000	0.997	159.011
Summer	Herring-Sardine larvae	0	0	0	1000	0	-
Summer	Horse mackerel larvae-Mackerel	0.715	0	0.991	1000	0.991	138.601
Summer	Horse mackerel larvae-Mackerel larvae	0.37	0	0.832	1000	0.832	224.865
Summer	Horse mackerel larvae-Sardine	0.813	0	0.992	1000	0.992	122.017
Summer	Horse mackerel larvae-Sardine larvae	0	0	0	1000	0	-

Summer	Mackerel larvae-Sardine	0.273	0	0.823	1000	0.823	301.465
Summer	Mackerel larvae-Sardine larvae	0.758	0.656	0.982	1000	0.326	43.008
Summer	Mackerel-Mackerel larvae	0.433	0	0.914	1000	0.914	211.085
Summer	Mackerel-Sardine	0.63	0	0.996	1000	0.996	158.095
Summer	Mackerel-Sardine larvae	0	0	0	1000	0	-
Summer	Sardine-Sardine larvae	0	0	0	1000	0	-
Autumn	Anchovy-Herring	0.903	0	0.994	1000	0.994	110.078
Autumn	Anchovy-Horse mackerel	0.979	0.664	1	1000	0.336	34.321
Autumn	Anchovy-Horse mackerel larvae	0.956	0	0.994	1000	0.994	103.975
Autumn	Anchovy-Sardine	0.917	0	0.999	1000	0.999	108.942
Autumn	Anchovy-Sprat	0.322	0.276	1	1000	0.724	224.845
Autumn	Anchovy-Sprat larvae	0.555	0	0.883	1000	0.883	159.099
Autumn	Herring-Horse mackerel	0.955	0	0.999	1000	0.999	104.607
Autumn	Herring-Horse mackerel larvae	0.861	0	1	1000	1	116.144
Autumn	Herring-Sardine	0.979	0	0.999	1000	0.999	102.043
Autumn	Herring-Sprat	0.188	0	1	1000	1	531.915
Autumn	Herring-Sprat larvae	0.515	0	0.866	1000	0.866	168.155
Autumn	Horse mackerel larvae-Sardine	0.845	0	0.995	1000	0.995	117.751
Autumn	Horse mackerel larvae-Sprat	0.163	0	0.995	1000	0.995	610.429
Autumn	Horse mackerel larvae-Sprat larvae	0.444	0	0.855	1000	0.855	192.568
Autumn	Horse mackerel-Horse mackerel larvae	0.954	0	1	1000	1	104.822
Autumn	Horse mackerel-Sardine	0.937	0	0.995	1000	0.995	106.190
Autumn	Horse mackerel-Sprat	0.304	0.283	1	1000	0.717	235.855
Autumn	Horse mackerel-Sprat larvae	0.493	0	0.904	1000	0.904	183.367
Autumn	Sardine-Sprat	0.185	0	0.999	1000	0.999	540.000
Autumn	Sardine-Sprat larvae	0.595	0	0.989	1000	0.989	166.218
Autumn	Sprat-Sprat larvae	0.097	0	0.793	1000	0.793	817.526
Winter	Herring larvae-Mackerel	0.529	0	0.886	1000	0.886	167.486
Winter	Herring larvae-Sprat	0.229	0	0.853	1000	0.853	372.489
Winter	Herring larvae-Sprat larvae	0.554	0.138	0.988	1000	0.85	153.430
Winter	Herring-Herring larvae	0.212	0	0.635	1000	0.635	299.528
Winter	Herring-Mackerel	0.039	0	0.329	1000	0.329	843.590
Winter	Herring-Sprat	0.523	0.276	1	1000	0.724	138.432
Winter	Herring-Sprat larvae	0	0	0	1000	0	
Winter	Mackerel-Sprat	0.042	0	0.476	1000	0.476	1133.333
Winter	Mackerel-Sprat larvae	0.84	0	0.991	1000	0.991	117.976
Winter	Sprat-Sprat larvae	0	0	0	1000	0	-

Appendix B

Table B 1 – Matching latitude and longitude of *in situ* measurements (FerryBox) and corresponding OLCI and MODIS- Aqua retrievals. Borders represent values with the same latitude and longitude.

Date Time	Latitude	Longitude	Log10 *in situ*	CHL_NN	CHL_OC4ME	MODIS
22/10/2019 15:55	49.6	-4.84	0.045	0.976	-0.488	-0.306
22/10/2019 15:56	49.6	-4.84	0.045	0.976	-0.488	-0.306
22/10/2019 15:57	49.6	-4.84	0.049	0.976	-0.488	-0.306
22/10/2019 15:58	49.6	-4.84	0.045	0.976	-0.488	-0.306
22/10/2019 15:59	49.6	-4.84	0.037	0.976	-0.488	-0.306
22/10/2019 16:00	49.6	-4.84	0.037	0.976	-0.488	-0.306
22/10/2019 16:01	49.6	-4.84	0.037	0.976	-0.488	-0.306
22/10/2019 16:02	49.6	-4.84	0.045	0.976	-0.488	-0.306
22/10/2019 16:03	49.6	-4.84	0.053	0.976	-0.488	-0.306
22/10/2019 16:04	49.6	-4.84	0.057	0.976	-0.488	-0.306
22/10/2019 16:05	49.6	-4.84	0.057	0.976	-0.488	-0.306
22/10/2019 16:06	49.6	-4.84	0.061	0.976	-0.488	-0.306
22/10/2019 16:07	49.6	-4.84	0.068	0.976	-0.488	-0.306
22/10/2019 16:08	49.6	-4.84	0.064	0.976	-0.488	-0.306
22/10/2019 16:09	49.6	-4.84	0.064	0.976	-0.488	-0.306
22/10/2019 16:10	49.6	-4.84	0.068	0.976	-0.488	-0.306
22/10/2019 16:11	49.6	-4.84	0.068	0.976	-0.488	-0.306
22/10/2019 16:12	49.6	-4.84	0.068	0.976	-0.488	-0.306
22/10/2019 16:13	49.6	-4.84	0.072	0.976	-0.488	-0.306
22/10/2019 16:14	49.6	-4.84	0.076	0.976	-0.488	-0.306
22/10/2019 16:15	49.6	-4.84	0.079	0.976	-0.488	-0.306
22/10/2019 16:16	49.6	-4.84	0.086	0.976	-0.488	-0.306
22/10/2019 16:17	49.6	-4.84	0.086	0.976	-0.488	-0.306
22/10/2019 16:18	49.6	-4.84	0.083	0.976	-0.488	-0.306
22/10/2019 16:19	49.6	-4.84	0.086	0.976	-0.488	-0.306
22/10/2019 16:21	49.6	-4.84	0.086	0.976	-0.488	-0.306
22/10/2019 16:22	49.6	-4.84	0.090	0.976	-0.488	-0.306
22/10/2019 16:24	49.6	-4.84	0.104	0.976	-0.488	-0.306
22/10/2019 16:25	49.6	-4.84	0.107	0.976	-0.488	-0.306
22/10/2019 16:27	49.6	-4.84	0.117	0.976	-0.488	-0.306
22/10/2019 16:28	49.6	-4.84	0.121	0.976	-0.488	-0.306
22/10/2019 18:14	49.6	-4.84	0.137	0.976	-0.488	-0.306
22/10/2019 18:15	49.6	-4.84	0.134	0.976	-0.488	-0.306
22/10/2019 18:16	49.6	-4.84	0.134	0.976	-0.488	-0.306
22/10/2019 18:17	49.6	-4.84	0.140	0.976	-0.488	-0.306
22/10/2019 18:18	49.6	-4.84	0.152	0.976	-0.488	-0.306
22/10/2019 18:19	49.6	-4.84	0.146	0.976	-0.488	-0.306
22/10/2019 18:20	49.6	-4.84	0.140	0.976	-0.488	-0.306
22/10/2019 18:21	49.6	-4.84	0.146	0.976	-0.488	-0.306
22/10/2019 18:22	49.6	-4.84	0.149	0.976	-0.488	-0.306

Date Time	Latitude	Longitude	Log10 *in situ*	CHL_NN	CHL_OC4ME	MODIS
22/10/2019 18:23	49.6	-4.84	0.143	0.976	-0.488	-0.306
22/10/2019 18:24	49.6	-4.84	0.134	0.976	-0.488	-0.306
22/10/2019 18:25	49.6	-4.84	0.127	0.976	-0.488	-0.306
22/10/2019 18:26	49.6	-4.84	0.134	0.976	-0.488	-0.306
22/10/2019 18:27	49.6	-4.84	0.143	0.976	-0.488	-0.306
22/10/2019 18:28	49.6	-4.84	0.146	0.976	-0.488	-0.306
22/10/2019 18:29	49.6	-4.84	0.152	0.976	-0.488	-0.306
22/10/2019 18:30	49.6	-4.84	0.152	0.976	-0.488	-0.306
22/10/2019 18:31	49.6	-4.84	0.152	0.976	-0.488	-0.306
22/10/2019 18:32	49.6	-4.84	0.146	0.976	-0.488	-0.306
22/10/2019 18:33	49.6	-4.84	0.146	0.976	-0.488	-0.306
22/10/2019 18:34	49.6	-4.84	0.152	0.976	-0.488	-0.306
22/10/2019 18:35	49.6	-4.84	0.155	0.976	-0.488	-0.306
22/10/2019 18:36	49.6	-4.84	0.155	0.976	-0.488	-0.306
22/10/2019 18:37	49.6	-4.84	0.152	0.976	-0.488	-0.306
22/10/2019 18:38	49.6	-4.84	0.155	0.976	-0.488	-0.306
22/10/2019 18:39	49.6	-4.84	0.152	0.976	-0.488	-0.306
22/10/2019 18:40	49.6	-4.84	0.149	0.976	-0.488	-0.306
22/10/2019 18:41	49.6	-4.84	0.149	0.976	-0.488	-0.306
22/10/2019 18:42	49.6	-4.84	0.146	0.976	-0.488	-0.306
22/10/2019 18:43	49.6	-4.84	0.143	0.976	-0.488	-0.306
22/10/2019 18:44	49.6	-4.84	0.140	0.976	-0.488	-0.306
22/10/2019 18:45	49.6	-4.84	0.134	0.976	-0.488	-0.306
22/10/2019 18:46	49.6	-4.84	0.137	0.976	-0.488	-0.306
22/10/2019 18:53	49.6	-4.84	0.146	0.976	-0.488	-0.306
22/10/2019 18:54	49.6	-4.84	0.143	0.976	-0.488	-0.306
22/10/2019 18:55	49.6	-4.84	0.140	0.976	-0.488	-0.306
22/10/2019 18:56	49.6	-4.84	0.137	0.976	-0.488	-0.306
22/10/2019 18:57	49.6	-4.84	0.134	0.976	-0.488	-0.306
22/10/2019 18:58	49.6	-4.84	0.137	0.976	-0.488	-0.306
22/10/2019 18:59	49.6	-4.84	0.130	0.976	-0.488	-0.306
22/10/2019 19:00	49.6	-4.84	0.127	0.976	-0.488	-0.306
22/10/2019 19:01	49.6	-4.84	0.114	0.976	-0.488	-0.306
22/10/2019 19:02	49.6	-4.84	0.111	0.976	-0.488	-0.306
21/10/2019 03:43	49.8	-5.13	0.143	0.709	-0.079	-0.511
21/10/2019 03:44	49.8	-5.13	0.143	0.709	-0.079	-0.511
21/10/2019 19:27	49.8	-5.13	0.029	0.709	-0.079	-0.511
21/10/2019 03:38	49.8	-5.11	0.149	0.898	-0.362	-0.453
21/10/2019 03:39	49.8	-5.11	0.149	0.898	-0.362	-0.453
21/10/2019 19:31	49.8	-5.11	0.029	0.898	-0.362	-0.453
21/10/2019 19:32	49.8	-5.11	0.025	0.898	-0.362	-0.453
21/10/2019 19:33	49.8	-5.11	0.025	0.898	-0.362	-0.453
21/10/2019 19:47	49.8	-5.11	0.041	0.898	-0.362	-0.453
21/10/2019 19:48	49.8	-5.11	0.037	0.898	-0.362	-0.453
21/10/2019 19:49	49.8	-5.11	0.037	0.898	-0.362	-0.453

Date Time	Latitude	Longitude	Log10 *in situ*	CHL_NN	CHL_OC4ME	MODIS
21/10/2019 20:20	49.8	-5.11	0.049	0.898	-0.362	-0.453
21/10/2019 03:35	49.8	-5.1	0.140	-0.488	-0.268	-0.453
21/10/2019 03:36	49.8	-5.1	0.146	-0.488	-0.268	-0.453
21/10/2019 03:37	49.8	-5.1	0.152	-0.488	-0.268	-0.453
21/10/2019 19:34	49.8	-5.1	0.029	-0.488	-0.268	-0.453
21/10/2019 19:35	49.8	-5.1	0.025	-0.488	-0.268	-0.453
21/10/2019 19:36	49.8	-5.1	0.029	-0.488	-0.268	-0.453
21/10/2019 19:37	49.8	-5.1	0.037	-0.488	-0.268	-0.453
21/10/2019 19:38	49.8	-5.1	0.041	-0.488	-0.268	-0.453
21/10/2019 19:39	49.8	-5.1	0.037	-0.488	-0.268	-0.453
21/10/2019 19:40	49.8	-5.1	0.041	-0.488	-0.268	-0.453
21/10/2019 19:41	49.8	-5.1	0.037	-0.488	-0.268	-0.453
21/10/2019 19:42	49.8	-5.1	0.037	-0.488	-0.268	-0.453
21/10/2019 19:43	49.8	-5.1	0.037	-0.488	-0.268	-0.453
21/10/2019 19:44	49.8	-5.1	0.037	-0.488	-0.268	-0.453
21/10/2019 19:45	49.8	-5.1	0.041	-0.488	-0.268	-0.453
21/10/2019 19:46	49.8	-5.1	0.041	-0.488	-0.268	-0.453
21/10/2019 19:50	49.8	-5.1	0.033	-0.488	-0.268	-0.453
21/10/2019 19:51	49.8	-5.1	0.029	-0.488	-0.268	-0.453
21/10/2019 19:52	49.8	-5.1	0.029	-0.488	-0.268	-0.453
21/10/2019 19:53	49.8	-5.1	0.033	-0.488	-0.268	-0.453
21/10/2019 19:54	49.8	-5.1	0.037	-0.488	-0.268	-0.453
21/10/2019 19:55	49.8	-5.1	0.037	-0.488	-0.268	-0.453
21/10/2019 19:56	49.8	-5.1	0.041	-0.488	-0.268	-0.453
21/10/2019 19:57	49.8	-5.1	0.037	-0.488	-0.268	-0.453
21/10/2019 19:58	49.8	-5.1	0.041	-0.488	-0.268	-0.453
21/10/2019 19:59	49.8	-5.1	0.037	-0.488	-0.268	-0.453
21/10/2019 20:00	49.8	-5.1	0.041	-0.488	-0.268	-0.453
21/10/2019 20:01	49.8	-5.1	0.037	-0.488	-0.268	-0.453
21/10/2019 20:02	49.8	-5.1	0.041	-0.488	-0.268	-0.453
21/10/2019 20:03	49.8	-5.1	0.037	-0.488	-0.268	-0.453
21/10/2019 20:04	49.8	-5.1	0.037	-0.488	-0.268	-0.453
21/10/2019 20:05	49.8	-5.1	0.041	-0.488	-0.268	-0.453
21/10/2019 20:06	49.8	-5.1	0.041	-0.488	-0.268	-0.453
21/10/2019 20:07	49.8	-5.1	0.041	-0.488	-0.268	-0.453
21/10/2019 20:08	49.8	-5.1	0.037	-0.488	-0.268	-0.453
21/10/2019 20:09	49.8	-5.1	0.041	-0.488	-0.268	-0.453
21/10/2019 20:10	49.8	-5.1	0.041	-0.488	-0.268	-0.453
21/10/2019 20:11	49.8	-5.1	0.049	-0.488	-0.268	-0.453
21/10/2019 20:12	49.8	-5.1	0.041	-0.488	-0.268	-0.453
21/10/2019 20:13	49.8	-5.1	0.045	-0.488	-0.268	-0.453
21/10/2019 20:14	49.8	-5.1	0.045	-0.488	-0.268	-0.453
21/10/2019 20:15	49.8	-5.1	0.045	-0.488	-0.268	-0.453
21/10/2019 20:16	49.8	-5.1	0.045	-0.488	-0.268	-0.453
21/10/2019 20:17	49.8	-5.1	0.045	-0.488	-0.268	-0.453
21/10/2019 20:18	49.8	-5.1	0.049	-0.488	-0.268	-0.453

Date Time	Latitude	Longitude	Log10 *in situ*	CHL_NN	CHL_OC4ME	MODIS
21/10/2019 20:19	49.8	-5.1	0.045	-0.488	-0.268	-0.453
21/10/2019 20:21	49.8	-5.1	0.049	-0.488	-0.268	-0.453
21/10/2019 20:22	49.8	-5.1	0.053	-0.488	-0.268	-0.453
21/10/2019 20:23	49.8	-5.1	0.061	-0.488	-0.268	-0.453
21/10/2019 20:24	49.8	-5.1	0.053	-0.488	-0.268	-0.453
21/10/2019 03:33	49.8	-5.09	0.127	-0.709	-0.110	-0.344
21/10/2019 03:34	49.8	-5.09	0.137	-0.709	-0.110	-0.344
21/10/2019 20:25	49.8	-5.09	0.049	-0.709	-0.110	-0.344
21/10/2019 20:26	49.8	-5.09	0.041	-0.709	-0.110	-0.344
21/10/2019 20:27	49.8	-5.09	0.041	-0.709	-0.110	-0.344
21/10/2019 20:28	49.8	-5.09	0.045	-0.709	-0.110	-0.344
21/10/2019 03:30	49.8	-5.08	0.146	-0.709	-0.173	-0.344
21/10/2019 03:31	49.8	-5.08	0.137	-0.709	-0.173	-0.344
21/10/2019 03:32	49.8	-5.08	0.130	-0.709	-0.173	-0.344
21/10/2019 20:29	49.8	-5.08	0.049	-0.709	-0.173	-0.344
21/10/2019 20:30	49.8	-5.08	0.057	-0.709	-0.173	-0.344
21/10/2019 20:31	49.8	-5.08	0.072	-0.709	-0.173	-0.344
15/10/2019 00:37	50.1	-3.17	-0.009	-0.472	0.189	0.130
15/10/2019 00:38	50.1	-3.17	-0.015	-0.472	0.189	0.130
15/10/2019 01:05	50.1	-3.17	-0.011	-0.472	0.189	0.130
15/10/2019 01:06	50.1	-3.17	-0.009	-0.472	0.189	0.130
15/10/2019 01:07	50.1	-3.17	-0.009	-0.472	0.189	0.130
15/10/2019 01:08	50.1	-3.17	-0.009	-0.472	0.189	0.130
15/10/2019 01:09	50.1	-3.17	-0.018	-0.472	0.189	0.130
15/10/2019 01:10	50.1	-3.17	-0.017	-0.472	0.189	0.130
15/10/2019 01:11	50.1	-3.17	-0.014	-0.472	0.189	0.130
15/10/2019 01:12	50.1	-3.17	-0.019	-0.472	0.189	0.130
15/10/2019 01:13	50.1	-3.17	-0.016	-0.472	0.189	0.130
15/10/2019 01:14	50.1	-3.17	-0.012	-0.472	0.189	0.130
15/10/2019 01:15	50.1	-3.17	-0.012	-0.472	0.189	0.130
15/10/2019 01:16	50.1	-3.17	-0.013	-0.472	0.189	0.130
15/10/2019 01:17	50.1	-3.17	-0.008	-0.472	0.189	0.130
15/10/2019 01:18	50.1	-3.17	-0.011	-0.472	0.189	0.130
15/10/2019 01:19	50.1	-3.17	-0.014	-0.472	0.189	0.130
15/10/2019 01:20	50.1	-3.17	-0.012	-0.472	0.189	0.130
15/10/2019 17:59	50.1	-3.17	-0.022	-0.472	0.189	0.130
15/10/2019 18:00	50.1	-3.17	-0.016	-0.472	0.189	0.130
15/10/2019 00:39	50.1	-3.16	-0.015	-0.252	0.110	0.130
15/10/2019 00:40	50.1	-3.16	-0.013	-0.252	0.110	0.130
15/10/2019 00:41	50.1	-3.16	-0.014	-0.252	0.110	0.130
15/10/2019 00:42	50.1	-3.16	-0.016	-0.252	0.110	0.130
15/10/2019 00:43	50.1	-3.16	-0.015	-0.252	0.110	0.130
15/10/2019 00:44	50.1	-3.16	-0.020	-0.252	0.110	0.130
15/10/2019 00:45	50.1	-3.16	-0.020	-0.252	0.110	0.130
15/10/2019 00:46	50.1	-3.16	-0.018	-0.252	0.110	0.130

Date Time	Latitude	Longitude	Log10 *in situ*	CHL_NN	CHL_OC4ME	MODIS
15/10/2019 00:47	50.1	-3.16	-0.019	-0.252	0.110	0.130
15/10/2019 00:48	50.1	-3.16	-0.018	-0.252	0.110	0.130
15/10/2019 00:49	50.1	-3.16	-0.018	-0.252	0.110	0.130
15/10/2019 00:50	50.1	-3.16	-0.016	-0.252	0.110	0.130
15/10/2019 00:51	50.1	-3.16	-0.016	-0.252	0.110	0.130
15/10/2019 00:52	50.1	-3.16	-0.016	-0.252	0.110	0.130
15/10/2019 00:53	50.1	-3.16	-0.013	-0.252	0.110	0.130
15/10/2019 00:54	50.1	-3.16	-0.014	-0.252	0.110	0.130
15/10/2019 00:55	50.1	-3.16	-0.011	-0.252	0.110	0.130
15/10/2019 00:56	50.1	-3.16	-0.012	-0.252	0.110	0.130
15/10/2019 00:57	50.1	-3.16	-0.012	-0.252	0.110	0.130
15/10/2019 00:58	50.1	-3.16	-0.012	-0.252	0.110	0.130
15/10/2019 00:59	50.1	-3.16	-0.010	-0.252	0.110	0.130
15/10/2019 01:00	50.1	-3.16	-0.007	-0.252	0.110	0.130
15/10/2019 01:01	50.1	-3.16	-0.017	-0.252	0.110	0.130
15/10/2019 01:02	50.1	-3.16	-0.015	-0.252	0.110	0.130
15/10/2019 01:03	50.1	-3.16	-0.012	-0.252	0.110	0.130
15/10/2019 01:04	50.1	-3.16	-0.015	-0.252	0.110	0.130
15/10/2019 18:01	50.1	-3.16	-0.013	-0.252	0.110	0.130
15/10/2019 18:02	50.1	-3.16	-0.013	-0.252	0.110	0.130
15/10/2019 15:25	50.3	-3.29	-0.049	-0.157	0.236	0.048
15/10/2019 15:26	50.3	-3.29	-0.049	-0.157	0.236	0.048
15/10/2019 15:27	50.3	-3.29	-0.047	-0.157	0.236	0.048
15/10/2019 15:28	50.3	-3.29	-0.049	-0.157	0.236	0.048
15/10/2019 15:29	50.3	-3.29	-0.050	-0.157	0.236	0.048
15/10/2019 15:30	50.3	-3.29	-0.050	-0.157	0.236	0.048
15/10/2019 15:31	50.3	-3.29	-0.050	-0.157	0.236	0.048
15/10/2019 15:32	50.3	-3.29	-0.052	-0.157	0.236	0.048
15/10/2019 15:33	50.3	-3.29	-0.052	-0.157	0.236	0.048
15/10/2019 16:07	50.3	-3.29	-0.027	-0.157	0.236	0.048
15/10/2019 16:08	50.3	-3.29	-0.027	-0.157	0.236	0.048
15/10/2019 16:09	50.3	-3.29	-0.027	-0.157	0.236	0.048
15/10/2019 16:10	50.3	-3.29	-0.027	-0.157	0.236	0.048
15/10/2019 16:11	50.3	-3.29	-0.025	-0.157	0.236	0.048
15/10/2019 16:12	50.3	-3.29	-0.022	-0.157	0.236	0.048
15/10/2019 16:13	50.3	-3.29	-0.020	-0.157	0.236	0.048
15/10/2019 16:14	50.3	-3.29	-0.020	-0.157	0.236	0.048
15/10/2019 16:15	50.3	-3.29	-0.020	-0.157	0.236	0.048
15/10/2019 16:16	50.3	-3.29	-0.021	-0.157	0.236	0.048
15/10/2019 16:17	50.3	-3.29	-0.018	-0.157	0.236	0.048
15/10/2019 16:18	50.3	-3.29	-0.023	-0.157	0.236	0.048
15/10/2019 16:19	50.3	-3.29	-0.027	-0.157	0.236	0.048
15/10/2019 16:20	50.3	-3.29	-0.027	-0.157	0.236	0.048
15/10/2019 16:21	50.3	-3.29	-0.018	-0.157	0.236	0.048
15/10/2019 16:22	50.3	-3.29	-0.018	-0.157	0.236	0.048
15/10/2019 16:23	50.3	-3.29	-0.014	-0.157	0.236	0.048

Date Time	Latitude	Longitude	Log10 *in situ*	CHL_NN	CHL_OC4ME	MODIS
15/10/2019 16:24	50.3	-3.29	-0.013	-0.157	0.236	0.048
15/10/2019 16:25	50.3	-3.29	-0.013	-0.157	0.236	0.048
15/10/2019 16:26	50.3	-3.29	-0.006	-0.157	0.236	0.048
15/10/2019 16:27	50.3	-3.29	0.000	-0.157	0.236	0.048
15/10/2019 16:28	50.3	-3.29	-0.001	-0.157	0.236	0.048
15/10/2019 16:28	50.3	-3.29	-0.001	-0.157	0.236	0.048
15/10/2019 16:29	50.3	-3.29	-0.001	-0.157	0.236	0.048
15/10/2019 16:29	50.3	-3.29	-0.001	-0.157	0.236	0.048
15/10/2019 16:30	50.3	-3.29	0.004	-0.157	0.236	0.048
15/10/2019 16:31	50.3	-3.29	0.009	-0.157	0.236	0.048
15/10/2019 16:32	50.3	-3.29	0.009	-0.157	0.236	0.048
15/10/2019 16:33	50.3	-3.29	0.009	-0.157	0.236	0.048
15/10/2019 16:34	50.3	-3.29	0.009	-0.157	0.236	0.048
15/10/2019 16:35	50.3	-3.29	0.013	-0.157	0.236	0.048
15/10/2019 16:36	50.3	-3.29	0.013	-0.157	0.236	0.048
15/10/2019 16:37	50.3	-3.29	0.021	-0.157	0.236	0.048
15/10/2019 16:38	50.3	-3.29	0.021	-0.157	0.236	0.048
15/10/2019 16:39	50.3	-3.29	0.021	-0.157	0.236	0.048
15/10/2019 16:40	50.3	-3.29	0.017	-0.157	0.236	0.048
15/10/2019 16:41	50.3	-3.29	0.021	-0.157	0.236	0.048
15/10/2019 19:28	50.3	-3.29	0.017	-0.157	0.236	0.048
15/10/2019 19:29	50.3	-3.29	0.017	-0.157	0.236	0.048
15/10/2019 19:30	50.3	-3.29	0.013	-0.157	0.236	0.048
15/10/2019 19:31	50.3	-3.29	0.013	-0.157	0.236	0.048
15/10/2019 19:40	50.3	-3.29	0.013	-0.157	0.236	0.048
15/10/2019 19:41	50.3	-3.29	0.013	-0.157	0.236	0.048
15/10/2019 19:42	50.3	-3.29	0.013	-0.157	0.236	0.048
15/10/2019 19:43	50.3	-3.29	0.017	-0.157	0.236	0.048
15/10/2019 19:44	50.3	-3.29	0.013	-0.157	0.236	0.048
15/10/2019 19:45	50.3	-3.29	0.013	-0.157	0.236	0.048
15/10/2019 19:46	50.3	-3.29	0.013	-0.157	0.236	0.048
15/10/2019 19:47	50.3	-3.29	0.009	-0.157	0.236	0.048
15/10/2019 19:48	50.3	-3.29	0.009	-0.157	0.236	0.048
15/10/2019 19:49	50.3	-3.29	0.013	-0.157	0.236	0.048
15/10/2019 19:50	50.3	-3.29	0.017	-0.157	0.236	0.048

Appendix C

Ecopath Model

Table C 1 - Ecopath groups adapted from Hernvann et al. (2020)

Common name	**Latin name**	**Ecopath group**	**Comments**
Northern gannet Common murre Razorbills Atlantic puffin	*Sula bassana* *Uria aalge* *Alca torda* *Fratercula arctica*	Plunge and pursuit divers seabirds	
Herring gull Yellow-legged gull Lesser black-backed gull great black-backed gull Kittiwakes	*Larus argentatus* *Larus michachellis* *Larus fuscus* *Larus maritimus* *Rissa tridactyla*	Surface feeders seabirds	They mainly differ from plunge and pursuit divers by their higher consumption of discards
Minke whale Humpback whale Sei whale Fin whale Blue whale	*Balaenoptera acutorostrata* *Megaptera novaengliae* *Balaenoptera borealis* *Balaenoptera physalus* *Balaenoptera musculus*	Baleen whales	
Harbour porpoise Common dolphin Striped dolphin Bottlenose dolphin Risso's dolphin White-beaked dolphin Atlantic White-sided dolphin False Killer Whale Long-finned Pilot Whale Short-finned Pilot Whale Killer Whale (Orca) Halichoerus grypus Phoca vitulina Gervais beaked whale True's beaked whale pygmy sperm whale dwarf sperm whale	*Phocoena phocoena* *Delphinus delphis* *Stenella coeruleoalba* *Tursiops truncates* *Grampus griseus* *Lagenorhynchus albirostris* *Lagenorhynchus acutus* *Pseudorca crassidens* *Globicephala melas* *Globicephala macrorhynchus* *Orcinus orca* *Grey seal* *Harbour seal* *Mesoplodon europaeus* *Mesoplodon mirus* *Kogia breviceps* *Kogia simus*	Toothed whales and Seals	
Thresher Bluntnose sixgill shark Shortfin mako Porbeagle Blue shark Tope shark	*Alopias vulpinus* *Hexanchus griseus* *Isurus oxyrinchus* *Lamna nasus* *Prionace glauca* *Galeorhinus galeus*	Pelagic sharks	
Shagreen ray Blue skate White skate Angelshark Longnose spurdog Marbled electric ray Picked dogfish	*Leucoraja fullonica* *Raja batis* *Raja alba* *Squatina squatina* *Squalus blainville* *Torpedo marmorata* *Squalus acanthias*	Piscivorous demersal elasmobranchs	Demersal sharks and rays that feed largely on fish, especially pelagic species

Starry smooth-hound	*Mustelus asterias*	Benthivorous demersal elasmobrancs	Demersal sharks and rays that mainly feed on benthic invertebrates and, to a lesser extent, on small benthic fish
Cuckoo ray	*Leucoraja naevus*		
Smooth-hound	*Mustelus mustelus*		
Blonde ray	*Raja brachyura*		
Spotted ray	*Raja montagui*		
Thornback ray	*Raja clavata*		
Blackmouth catshark	*Galeus melastomus*		
Common stingray	*Dasyatis pastinaca*		
Common eagle ray	*Myliobatis aquila*		
Sandy ray	*Raja circularis*		
Longnosed skate	*Raja oxyrinchus*		
Undulate ray	*Raja undulata*		
Small-spotted catshark	*Scyliorhinus canicula*		
Nursehound	*Scyliorhinus stellaris*		
Small-eyed ray	*Raja microocellata*		
Blackbellied angler	*Lophius budegassa*	Anglerfish	
Angler(=Monk)	*Lophius piscatorius*		
European seabass	*Dicentrarchus labrax*	Sea bass	
European hake	*Merluccius merluccius*	Hake	
Atlantic cod	*Gadus morhua*	Cod	
Haddock	*Melanogrammus aeglefinus*	Haddock	
Whiting	*Merlangius merlangus*	Whiting	
Megrim	*Lepidorhombus whiffiagonis*	Megrim	
Norway pout	*Trisopterus esmarkii*	Pouts	
Pouting(=Bib)	*Trisopterus luscus*		
Poor cod	*Trisopterus minutus*		
European plaice	*Pleuronectes platessa*	Plaice	
Common sole	*Solea solea*	Sole	
European conger	*Conger conger*	Piscivorous demersal fish	Demersal fish mainly that feed on fish, both benthic and pelagic. Usually of large size (max. length > 60cm).
Pollack	*Pollachius pollachius*		
Turbot	*Psetta maxima*		
Brill	*Scophthalmus rhombus*		
Ling	*Molva molva*		
John dory	*Zeus faber*		
Common lingue	*Molva macrophthalma*		
Common dentex	*Dentex dentex*		
Meagre	*Argyrosomus regius*		
Saithe(=Pollock)	*Pollachius virens*		
Atlantic halibut	*Hippoglossus hippoglossus*		
Silver scabbardfish	*Lepidopus caudatus*		
Blackbelly rosefish	*Helicolenus dactylopterus*		
Wreckfish	*Polyprion americanus*		
European eel	*Anguilla anguilla*		
Atlantic salmon	*Salmo salar*		
Sea trout	*Salmo trutta*		
Black Sea brill	*Psetta maeotica*		
Atlantic thornyhead	*Trachyscorpia cristulata*		
Barracudas nei	*Sphyraena spp*		
Spotted seabass	*Dicentrarchus punctatus*		
Four-spot megrim	*Lepidorhombus boscii*		

Greater forkbeard	*Phycis blennoides*	Epibenthivorous demersal fish	Demersal fish that mainly feed on benthic invertebrates, especially crustacean decapods, as well as on some small demersal fish. Usually of medium size (max. length between 30 and 60 cm)
Fourbeard rockling	*Enchelyopus cimbrius*		
Red gurnard	*Chelidonichthys cuculus*		
Surmullet	*Mullus surmuletus*		
Blackspot seabream	*Pagellus bogaraveo*		
Argentine	*Argentina sphyraena*		
Three-bearded rocling	*Gaidropsarus vulgaris*		
Tub gurnard	*Chelidonichthys lucerna*		
Grey gurnard	*Eutrigla gurnardus*		
Red scorpionfish	*Scorpaena scrofa*		
Black scorpionfish	*Scorpaena porcus*		
Comber	*Serranus cabrilla*		
Greater weever	*Trachinus draco*		
Atlantic wolffish	*Anarhichas lupus*		
Gilthead seabream	*Sparus aurata*		
Streaked gurnard	*Chelidonichthys lastoviza*		
Thicklip grey mullet	*Chelon labrosus*		
Ballan wrasse	*Labrus bergylta*		
Axillary seabream	*Pagellus acarne*		
Common pandora	*Pagellus erythrinus*		
Black seabream	*Spondyliosoma cantharus*		
Golden grey mullet	*Liza aurata*		
Thinlip grey mullet	*Liza ramada*		
Flathead grey mullet	*Mugil cephalus*		
Piper gurnard	*Eutrigla lyra*		
Lumpfish(=Lumpsucker)	*Cyclopterus lumpus*		
Grey triggerfish	*Balistes capriscus*		
Longfin gurnard	*Chelidonichthys obscurus*		
Lesser weever	*Echiichthys vipera*		
Lesser weever	*Labrus mixtus*		
Amer. Plaice	*Hippoglossoides platessoides*		
Cuckoo wrasse	*Pagrus pagrus*		
Common dab	*Limanda limanda*	Endobenthivorous demersal fish	Benthic fish mainly that feed on benthic invertebrates, especially polychaetes, gastropods and bivalves (large part of the endobenthos). Mainly flatfish of medium or large size.
Witch flounder	*Glyptocephalus cynoglossus*		
Lemon sole	*Microstomus kitt*		
Thickback sole	*Microchirus variegatus*		
Sand sole	*Solea lascaris*		
European flounder	*Platichthys flesus*		
Dragonet	*Callionymus lyra*	Small benthivorous demersal fish	Demersal fish that feed on benthic invertebrates and large proportions of plankton and/or micronekton. Usually of small size (max. length < 30 cm). They represent important fish prey for other demersal fish.
Spotted ragonet	*Callionymus maculatus*		
Fivebeard rockling	*Ciliata mustela*		
Sand goby	*Pomatoschistus minutus*		
Butterfly blenny	*Blennius ocellaris*		
Imperial scaldfish	*Arnoglossus imperialis*		
Scale-rayed wrasse	*Acantholabrus palloni*		
Mediterranean scaldfish	*Arnoglossus laterna*		
Solenette	*Buglossidium luteum*		
Fries's goby	*Lesueurigobius friesii*		
Greater pipefish	*Syngnathus acus*		
Black goby	*Gobius niger*		
Norwegian topknot	*Phrynorhombus norvegicus*		
Lozano's goby	*Pomatoschistus lozanoi*		

Red bandfish	*Cepola macrophthalma*	Suprabenthivorous demersal fish	Demersal fish feeding on benthic invertebrates and large proportions of plankton and/or micronekton. Usually of small size (max length < 30 cm). They play an important role in the transfer of organic material from the pelagic to the demersal compartment.
Silvery pout	*Gadiculus argenteus*		
Silvery lightfish	*Maurolicus muelleri*		
Bogue	*Boops boops*		
Greater argentine	*Argentina silus*		
Greater sand-eel	*Hyperoplus immaculatus*		
Great sandeel	*Hyperoplus lanceolatus*		
Small sandeel	*Ammodytes tobianus*		
Transparent goby	*Aphia minuta*		
Smooth sandeel	*Gymnammodytes semisquamatus*		
Longspine snipefish	*Macrorhamphosus scolopax*		
Blue whiting	*Micromesistius poutassou*	Blue whiting	
Boarfish	*Capros aper*	Boarfish	
Atlantic mackerel	*Scomber scombrus*	Mackerel	
Atlantic horse mackerel	*Trachurus trachurus*	Horse mackerel	
Atlantic herring	*Clupea harengus*	Herring	
European sprat	*Sprattus sprattus*	Sprat	
European pilchard	*Sardina pilchardus*	Sardine	
Garfish	*Belone belone*	Large Pelagic fish	
Atlantic bonito	*Sarda sarda*		
Golden redfish	*Sebastes marinus*		
Albacore	*Thunnus alalunga*		
Atlantic bluefin tuna	*Thunnus thynnus*		
Swordfish	*Xiphias gladius*		
Atlantic pomfret	*Brama brama*		
Little tunny	*Euthynnus alletteratus*		
Skipjack tuna	*Katsuwonus pelamis*		
European anchovy	*Engraulis encrasicolus*	Anchovy	Previously medium pelagic fish group
Broadtail shortfin squid	*Illex coindetii*	Squids	Pelagic and bentho-pelagic squids.
Northern shortfin squid	*Illex illecebrosus*		
European squid	*Loligo vulgaris*		
European flying squid	*Todarodes sagittatus*		
European common squid	*Alloteuthis subulata*		
Veined squid	*Loligo forbesi*		
lesser flying squid	*Todaropsis eblanae*		
Common cuttlefish	*Sepia officinalis*	Benthic cephalopods	
Pink cuttlefish	*Sepia orbignyana*		
Elegant cuttlefish	*Sepia elegans*		
Bobtail squid	*Sepiola sp*		
Horned octopus	*Eledone cirrhosa*		
Common octopus	*Octopus vulgaris*		
Stout bobtail	*Rossia macrosoma*		
Norway lobster	*Nephrops norvegicus*	Norway lobster	
Edible crab	*Cancer pagurus*		

European lobster Spinous spider crab Velvet swimcrab Common spiny lobster	*Homarus gammarus* *Maja squinado/brachydactyla* *Necora puber* *Palinurus elephas*	Commercial large crustaceans	
Shrimps			Benthic Shrimps-like invertebrates
Commercial bivalves			Bivalve suspension feeders that are commercially exploited (e.g. Pectinids)
Suprabenthos			Suspension feeders (e.g.mysids) that live in the water layer close to the seabed and with sufficient swimming ability to move within this layer
Suspension and surface deposit feeders			Susupension feeder filtering suspended particles from the seabed plus deposivores feeding on particles at the sediment-water interface (e.g., polychaetes, reg. urchins, amphiurids, isopods, cumaceans)
Subsurface deposit feeders			Deposivorous organisms that feed on particles within the sediments, by ingesting and filtering sediment or by directly selecting particles (mainly polychaetes, few amphipods and irregular urchins)
Carnivores and necrophages			Benthic invertebrates that are either predators or scavengers (small crabs, squat lobsters, welks, ophiurids, worms, amphipods...)
Benthic meiofauna			Invertebrates living in the sediment (nematods)
Macrozooplankton			Zooplankton of size ≥ 1cm (omnivorous and carnivorous; they mainly include euphausiids, large carnivorous plankton, gelatinous, tunicates, thecostomates, chaetognathes, and larvae)
Mesozooplankton - Large			Zooplankton of size ≥ 2mm and < 1cm. (larger copepods, with limited planktivorous behaviour)
Mesozooplankton - Small			Zooplankton of size ≥ 0.5mm and < 2mm (essentially herbivorous copepods)
Microzooplankton			Zooplankton of size < 0.5mm (ciliates and heterotrophic flagellates)
Phytoplankton - Large			Phytoplankton of size ≥ 5 μm. Mainly diatoms and dinoflagellates
Phytoplankton - Small			Phytoplankton of size < 5 μm. Nano- and picoplankton

Table C 2 - Diet matrix input for Celtic Sea Ecopath model

	Prey \ predator	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**
1	Seabirds - Divers																									
2	Seabirds - Surface feeders																									
3	Baleen whales																									
4	Toothed cetaceans / Seals																									
5	Pelagic sharks				0.023	0.001																				
6	Carnivorous demer. elasmobranchs				0.003	0.009																				
7	Benthivorous demer. elasmobranchs				0.005		0.001																			
8	Sea bass								0.022																	
9	Anglerfish large				0.048	0.012				0.001		0.006		0.002		0.001			0.006			0.001				
10	Anglerfish small									0.000		0.000	0.001	0.001		0.000			0.000			0.001				
11	Hake large				0.007	0.002				0.005		0.004							0.000			0.025				
12	Hake small								0.000	0.001	0.002	0.020	0.002	0.002	0.002	0.001			0.001			0.001				
13	Cod large				0.002	0.008	0.001			0.008						0.002						0.004				
14	Cod small					0.007	0.000			0.003	0.002					0.001			0.002			0.002	0.001			
15	Whiting				0.000	0.003	0.000	0.004	0.001	0.026	0.005	0.001	0.002	0.007	0.002	0.003			0.000			0.022	0.002			
16	Haddock					0.010	0.008	0.007		0.005	0.002			0.014	0.004	0.016			0.007			0.003	0.002			
17	Pouts				0.138	0.207	0.153	0.127	0.114	0.266	0.260	0.099	0.022	0.147	0.057	0.241	0.002	0.016	0.115			0.155	0.025			
18	Megrim									0.029	0.007	0.004		0.012	0.003				0.008							
19	Sole								0.012	0.003				0.009	0.005											
20	Plaice				0.001		0.001		0.006	0.001				0.010	0.002				0.001			0.000				
21	Piscivorous demer. fish				0.027	0.006			0.002	0.041				0.001								0.016				
22	Epibenthivorous demer. fish	0.067			0.037	0.057	0.004	0.005	0.005	0.066	0.011	0.007	0.014	0.006	0.042	0.004		0.016	0.045			0.110				

23	Endobenthivorous demer. fish			0.108		0.120	0.013		0.009	0.047	0.026			0.001	0.006				0.021			0.002	0.002			
24	Suprabenthivorous demer. fish			0.031	0.095			0.000	0.006	0.008	0.019	0.010	0.023	0.004	0.010	0.015	0.001		0.052			0.046			0.027	
25	Small benthivorous demer. fish						0.024	0.016	0.006	0.016	0.263	0.001	0.018	0.029	0.014	0.006	0.000	0.009	0.075		0.000	0.053	0.136	0.013		0.030
26	Mackerel	0.062	0.032	0.020	0.022	0.003	0.031	0.012	0.100	0.022	0.003	0.034		0.007	0.005	0.008			0.006			0.011			0.001	
27	Horse mackerel	0.549	0.400		0.037	0.020	0.368		0.211	0.138		0.357	0.336	0.016		0.137			0.071			0.096				
28	Boarfish				0.000		0.005	0.001				0.001				0.002			0.005			0.001				
29	Sprat		0.004		0.018	0.027	0.067	0.005	0.075			0.021	0.001	0.005	0.002	0.092	0.003		0.021			0.017				
30	Blue whiting				0.029		0.013	0.066	0.001	0.032	0.064	0.225	0.012	0.013	0.002	0.045			0.036			0.110				
31	Pilchard	0.128	0.145		0.041	0.002	0.004		0.013			0.024	0.005			0.018			0.002			0.015				
32	Herring	0.140	0.079	0.079	0.091	0.071	0.065	0.011		0.040	0.089	0.038		0.011	0.010	0.036	0.002					0.013	0.004			
33	Pelagic fish - Large				0.015	0.040	0.002					0.001														
34	Anchovy	0.014	0.015	0.001		0.015			0.013			0.006	0.008	0.016		0.014										
35	Squids			0.039	0.235	0.303	0.007	0.015	0.000	0.018	0.004	0.000	0.003	0.068	0.005	0.002			0.005			0.010	0.000			
36	Benthic cephalopods			0.016	0.082		0.024	0.003	0.007	0.035	0.000	0.000	0.008	0.001	0.002	0.030	0.002		0.009	0.055		0.035	0.006			
37	Commercial crustaceans						0.001	0.047	0.001					0.005	0.006						0.006	0.030				
38	Nephrops						0.016	0.012		0.013				0.036	0.026	0.004		0.001	0.004			0.009	0.001		0.001	
39	Commercial bivalves													0.001	0.003					0.005						
40	Shrimps					0.063	0.006	0.094	0.110	0.018	0.024	0.060	0.018	0.178	0.236	0.086	0.007	0.097	0.193	0.012	0.001	0.045	0.100	0.030	0.048	0.022
41	Carnivorous/Necrophagous benth. inv.						0.007	0.381	0.138	0.007	0.012	0.010	0.003	0.351	0.486	0.010	0.419	0.109	0.179	0.168	0.180	0.017	0.169	0.172	0.004	0.114
42	Suspension/Surface detritus feeder benth. inv.						0.006	0.027	0.114	0.011	0.021	0.043	0.023	0.029	0.015	0.035	0.427	0.030	0.015	0.684	0.513		0.070	0.479	0.011	0.321
43	Subsurface deposit feeder benth. inv.							0.005			0.005	0.003	0.000	0.014	0.003	0.019	0.078	0.001	0.002	0.064	0.278		0.001	0.092		0.120
44	Suprabenthos							0.010	0.035			0.024	0.229	0.001	0.001	0.016	0.012	0.243	0.107	0.008	0.017	0.012	0.362	0.060	0.012	0.094
45	Benthic meiofauna																			0.001						0.013
46	Macrozooplankton		0.025				0.173						0.273	0.004	0.001	0.041	0.033	0.365	0.010	0.002	0.004		0.011	0.003	0.403	0.273
47	Mesozooplankton - Large		0.098	0.389				0.062					0.000	0.000	0.019	0.015	0.010	0.079				0.065	0.062	0.087	0.055	0.005

48	Mesozooplankton - Small		0.033	0.318				0.083					0.000	0.000	0.032	0.099	0.004	0.027				0.070	0.045	0.063	0.439	0.010
49	Microzooplankton																									
50	Bacteria																									
51	Phytoplankton - Large																						0.001			
52	Phytoplankton - Small																									
53	Discards	0.040	0.170																							
54	Detritus							0.008										0.007								
	Import				0.043	0.015				0.142	0.178															

	Prey \ predator	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
1	Seabirds - Divers																									
2	Seabirds - Surface feeders																									
3	Baleen whales																									
4	Toothed cetaceans / Seals																									
5	Pelagic sharks								0.009																	
6	Carnivorous demer. elasmobranchs																									
7	Benthivorous demer. elasmobranchs	0.029																								
8	Sea bass																									
9	Anglerfish large																									
10	Anglerfish small										0.000															
11	Hake large																									
12	Hake small										0.001	0.001														
13	Cod large																									
14	Cod small										0.000															
15	Whiting																									
16	Haddock							0.020																		
17	Pouts	0.031	0.044					0.021	0.002		0.126															

18	Megrim																
19	Sole																
20	Plaice																
21	Piscivorous demer. fish										0.005						
22	Epibenthivorous demer. fish		0.046						0.002		0.055	0.001					
23	Endobenthivorous demer. fish								0.015								
24	Suprabenthivorous demer. fish	0.029	0.044			0.047		0.027	0.015		0.265	0.006					
25	Small benthivorous demer. fish		0.045			0.005		0.020			0.013	0.062	0.038	0.001			
26	Mackerel	0.030							0.004		0.008						
27	Horse mackerel	0.033							0.119								
28	Boarfish								0.016								
29	Sprat	0.038	0.046					0.041	0.009		0.021						
30	Blue whiting	0.033	0.004			0.026					0.025						
31	Pilchard								0.011								
32	Herring							0.071	0.012		0.016						
33	Pelagic fish - Large								0.016								
34	Anchovy																
35	Squids	0.034	0.045			0.008			0.065		0.051	0.001					
36	Benthic cephalopods	0.035	0.040			0.009		0.021	0.015	0.048	0.003	0.015					
37	Commercial crustaceans											0.104	0.023				
38	Nephrops					0.003					0.004	0.015					
39	Commercial bivalves												0.030				0.003
40	Shrimps	0.026	0.046	0.003	0.028	0.010		0.016	0.012	0.060	0.054	0.077	0.188	0.022		0.016	
41	Carnivorous/Necrophagous benth. inv.	0.040	0.046	0.037	0.043	0.016	0.061	0.021	0.041	0.063	0.003	0.638	0.298	0.275		0.183	0.060
42	Suspension/Surface detritus feeder benth. inv.	0.042	0.046	0.032	0.076	0.018	0.168	0.036	0.004	0.074		0.001	0.127	0.220		0.227	0.337
43	Subsurface deposit feeder benth. inv.			0.004		0.002				0.041			0.174	0.242		0.115	0.192

44	Suprabenthos	0.036	0.046	0.051		0.041				0.059		0.076		0.044		0.040						0.104				
45	Benthic meiofauna						0.071			0.086				0.033		0.040			0.319	0.034						
46	Macrozooplankton	0.090	0.047	0.049	0.014	0.727	0.103	0.240	0.118	0.023	0.038		0.066	0.055		0.031										
47	Mesozooplankton - Large	0.059	0.211	0.606	0.177	0.066	0.102	0.185		0.193	0.246					0.011						0.110				
48	Mesozooplankton - Small	0.412	0.234	0.218	0.660	0.022	0.447	0.280		0.350	0.067	0.001				0.019				0.038		0.245	0.111			
49	Microzooplankton															0.121				0.113		0.125	0.167	0.051	0.048	
50	Bacteria																	0.053	0.130	0.150	0.091				0.095	
51	Phytoplankton - Large	0.002	0.009		0.003		0.003			0.003				0.050	0.150	0.011	0.012	0.531	0.001	0.206		0.125	0.417	0.290	0.143	
52	Phytoplankton - Small														0.300			0.106	0.000	0.206		0.125	0.231	0.581	0.381	0.050
53	Discards												0.002	0.002												
54	Detritus						0.047						0.054	0.055	0.550	0.186	0.396	0.309	0.549	0.253	0.909	0.166	0.074	0.077	0.333	0.950
	Import								0.516																	

Table C 3 - Landing and discards data used in the Celtic Sea Ecopath model.

Group name	Landings	Discards
Seabirds - Divers	0	0
Seabirds - Surface feeders	0	0
Baleen whales	0	0
Toothed cetaceans / Seals	0	0
Pelagic sharks	8.20E-05	0
Carnivorous demer. elasmobranchs	0.000605401	0.000748524
Benthivorous demer. elasmobranchs	0.02490495	0.005088647
Sea bass	0.006589839	1.16E-06
Anglerfish		
Anglerfish large	0.09399714	0.01409957
Anglerfish small	0	0
Hake		
Hake large	0.1150131	0.01580429
Hake small	0	0.007904518
Cod		
Cod large	0.02703563	0.004055345
Cod small	0.0001	1.50E-05
Whiting	0.03786847	0.008559649
Haddock	0.04408928	0.002223412
Pouts	0.007539383	0.002454433
Megrim	0.008124045	0.000438419
Sole	0.005498093	0.000310251
Plaice	0.002878779	0.002691078
Piscivorous demer. fish	0.03406675	0.000647852
Epibenthivorous demer. fish	0.02089451	0.006492905
Endobenthivorous demer. fish	0.0132659	0.001546983
Suprabenthivorous demer. fish	0	0.000178213
Small benthivorous demer. fish	3.83E-06	0.01200964
Mackerel	0.05614861	0.000329932
Horse mackerel	0.01533125	6.34E-05
Boarfish	1.00E-08	0
Sprat	0.003571554	0
Blue whiting	0.001145128	0
Pilchard	0.03754269	8.55E-05
Herring	0.06054229	5.93E-05
Pelagic fish - Large	0.01702151	6.34E-05
Anchovy	0.00045001	0
Squids	0.006516982	3.86E-05
Benthic cephalopods	0.01890354	0.001276399
Commercial crustaceans	0.01672701	1.80E-05
Nephrops	0.01520238	0.000969947

Commercial bivalves	0.1184508	0.01982821
Shrimps	0.000176399	0.002581829
Carnivorous/Necrophagous benth. inv.	0.08823019	0
Suspension/Surface detritus feeder benth. inv.	1.34E-06	6.03E-06
Subsurface deposit feeder benth. inv.	0	0
Suprabenthos	0	0
Benthic meiofauna	0	0
Macrozooplankton	0	0
Mesozooplankton - Large	0	0
Mesozooplankton - Small	0	0
Microzooplankton	0	0
Bacteria	0	0
Phytoplankton - Large	0	0
Phytoplankton - Small	0	0
Discards	0	0
Detritus	0	0

Table C 4 - PREBAL diagnostics and how the criteria have been met.

Criteria	Celtic Sea model results	Comment
Biomass should span 5-7 orders of magnitude	Spans 6 orders of magnitude	_
Biomass slope (log scale) around 5-10% decline with increasing TL	9.3%	_
Are any functional group biomasses notably above/below the line?	Met	Below B: - The two seabird functional groups: B values; as stated in Hernvann et al., (2020) lower biomass compared with neighbouring areas have been well described; potential anthropogenic impacts - Discards but results only regulated by fishing; - Benthic invertebrate groups: B estimated by the model and support predation of multiple compartments including themselves
Compared across taxa, the ratio between predator and prey biomass should be <1 and ~1-2 decimal places, depending on TL	Met	_
PB should decline with increasing TL (excluding homeotherms)	Met	Low values for whales; high values for cephalopods

QB should decline with increasing TL (excluding homeotherms)	Met	Q/B especially high for seabirds
No taxa should have PB greater than phytoplankton	Met	_
PQ should fall below 1 for all functional groups	Met	true for all groups except for homeotherms with low values
PR should fall below 1 for all functional groups	Met	_
EE should fall below 1 for all functional groups	Met	_
Total consumption and production should decrease with increasing TL	Met	_

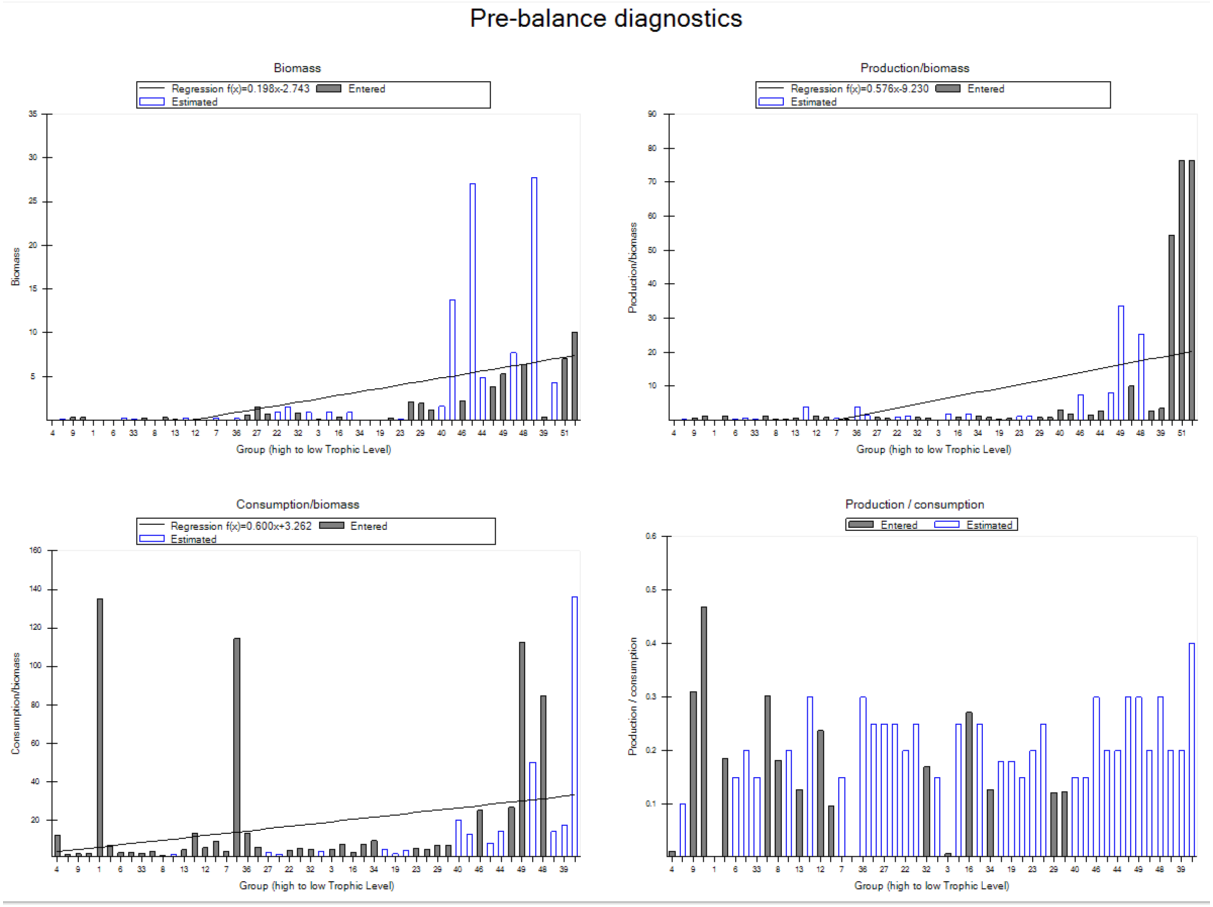


Figure C 1 - PREBAL diagnostic figures for updated 2013 Ecopath model

Ecosim Model

Table C 5 - Ecosim input parameters taken from Hernvann et al. (2020)

	Group name	Max rel. P/B	Max rel. feeding time	Feeding time adjust rate	% of oth. mortality sens. to chg. in feeding time	Predator effect on feeding time	Density-dep. catchability	QBmax / QBo	Switching power parameter
1	Seabirds - Divers	2	1.25	0.5	1	0	1	3	2
2	Seabirds - Surface feeders	2	1.25	0.5	1	0	1	3	2
3	Baleen whales	2	1.25	0.1	1	0	1	3	2
4	Toothed cetaceans / Seals	2	1.25	0.1	1	0	1	3	2
5	Pelagic sharks	2	1.25	0.1	1	0	1	10	2
6	Carnivorous dem. elasmobranchs	2	1.25	0.1	1	1	1	3	1
7	Benthivorous dem. elasmobranchs	2	1.25	0.1	1	1	1	3	1
8	Sea bass	2	1.25	0.1	1	1	1	3	2
	Anglerfish								
9	Anglerfish adult	2	1.25	0.1	1	1	1	3	1
10	Anglerfish juvenile	2	1.25	0.2	1	0.75	1	3	1
	Hake								
11	Hake adult	2	1.25	0.1	1	1	1	3	2
12	Hake juvenile	2	1.25	0.2	1	0.75	1	3	1
	Cod								
13	Cod adult	2	1.25	0.1	1	1	1	3	2
14	Cod juvenile	2	1.25	0.2	1	1	1	3	2
15	Whiting	2	1.25	0.1	1	1	1	3	2
16	Haddock	2	1.25	0.1	1	1	1	3	1
17	Pouts	2	1.25	0.1	1	1	1	3	2
18	Megrim	2	1.25	0.1	1	1	1	3	1

19	Sole	2	1.25	0.5	1	1	1	10	0.5
20	Plaice	2	1.25	0.5	1	1	1	10	0.5
21	Piscivorous demersal fish	2	1.25	0.1	1	1	1	3	2
22	Epibenthivorous demersal fish	2	1.25	0.1	1	1	1	3	2
23	Endobenthivorous demersal fish	2	1.25	0.5	1	1	1	10	0.5
24	Suprabenthivorous demersal fish	2	1.25	0.1	1	0.75	1	3	0
25	Small benthivorous demersal fish	2	1.25	0.5	1	0.75	1	3	0.5
26	Mackerel	2	1.25	0.5	1	0.5	1	3	0
27	Horse mackerel	2	1.25	0.5	1	0.5	1	3	0
28	Boarfish	2	1.25	0.5	1	0.5	1	3	0
29	Sprat	2	1.25	0.5	1	0.5	1	3	0
30	Blue whiting	2	1.25	0.5	1	0.5	1	3	0
31	Pilchard	2	1.25	0.5	1	0.5	1	3	0
32	Herring	2	1.25	0.5	1	0.5	1	3	0
33	Pelagic - Large	2	1.25	0.1	1	1	1	10	1
34	Pelagic - Medium	2	1.25	0.5	1	0.5	1	3	0
35	Squids	2	1.25	0.1	1	1	1	3	1
36	Benthic cephalopods	2	1.25	0.1	1	1	1	3	1
37	Commercial crustaceans	2	1.25	0.1	1	0.75	1	3	1
38	Nephrops	2	1.25	0.1	1	0.75	1	3	1
39	Commercial bivalves	2	1	0.05	0	0	1	3	0
40	Shrimps	2	1.25	0.1	1	0.5	1	3	1
41	Carnivores/Necrophages	2	1.25	0.1	1	0.5	1	3	1
42	Suspension/Surface detritus Feeders	2	1.25	0.1	1	0.5	1	3	0

43	Subsurface deposit feeders	2	1.25	0.1	1	0.5	1	3	0
44	Suprabenthos	2	1.5	1	1	0.5	1	3	0
45	Benthic meiofauna	2	1.5	1	0	0	1	3	0
46	Macrozooplankton	2	1.5	1	1	0	1	3	1
47	Mesozooplankton - Large	2	1.5	1	1	0	1	3	0
48	Mesozooplankton - Small	2	1.5	1	1	0	1	3	0
49	Microzooplankton	2	1.5	1	1	0	1	3	0
50	Bacteria	2	1.5	0.05	1	0	1	3	0
51	Phytoplankton - Large	2	1	0.5	1	0	1	1000	0
52	Phytoplankton - Small	2	1	0.5	1	0	1	1000	0

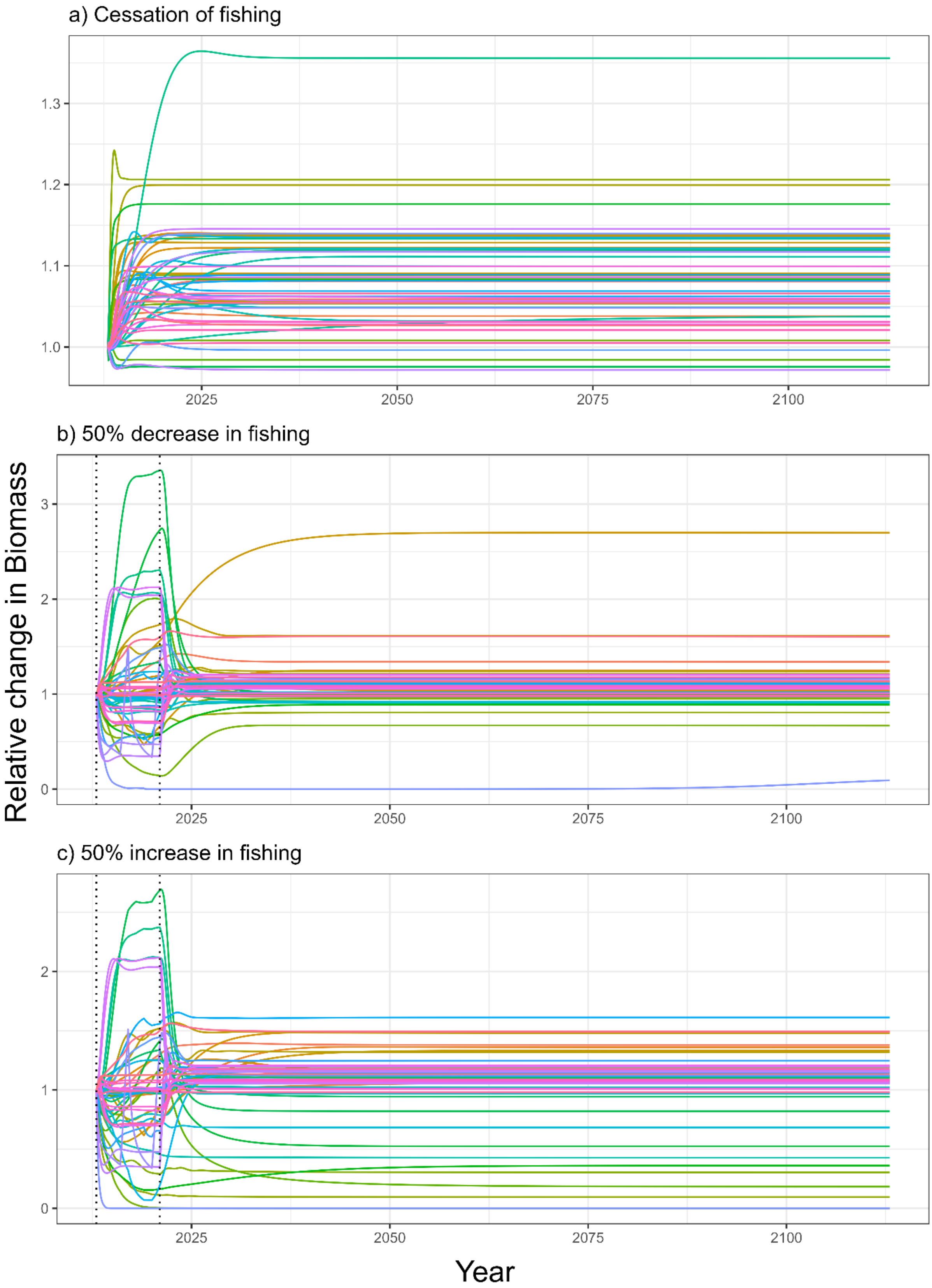


Figure C 2 - Stability testing of EwE model over 100 years. a) Complete cessation of fishing, b) 50% decrease of fishing and c) 50% increase of fishing. Dotted representation duration of change in fishing.